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FINAL REPORT

Endangered Butterflies as a Model System for Managing Source-Sink Dynamics on Department of Defense Lands

SERDP Project RC-2119

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14. ABSTRACT

Through a combination of field studies and state-of-the-art quantitative models, we used three species of endangered butterflies as a model system to rigorously investigate the source-sink dynamics of species being managed on military lands. Butterflies have numerous advantages as models for source-sink dynamics, including rapid generation times and relatively limited dispersal, but they are subject to the same processes that determine source-sink dynamics of longer-lived, more vagile taxa.

15. SUBJECT TERMS

Appalachian brown, Baltimore checkerspot, correlated random walk, Fender's blue, fire, floods, habitat restoration, hardwood removal, herbicide, host plant, life cycle, models, population dynamics, source sink dynamics, spatially explicit individual based model (SEIBM), St. Francis satyr, Taylor's checkerspot

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List of Acronyms

ABB	Appalachian Brown Butterfly
AFB	Air Force Base
AIC	Akaike Information Criterion
ANOVA	Analysis of Variance
BACI	Before After Control Impact
BCa	Bias-Corrected and Accelerated
CI	Confidence Interval
CJS	Cormack-Jolly-Seber Model
CV	Coefficient of Variation
dAIC	Difference in Akaike Information Criterion
GIS	Geographic Information System
GLM	Generalized Linear Model
GLMM	Generalized Linear Mixed Models
GPS	Global Positioning System
GR	Growth Rate
INCA	INsect Count Analyzer
JAGS	Just Another Gibbs Sampler
KSS	Kierstead, Slobodkin and Skellam
LM	Linear Model
LMM	Linear Mixed Model
LTRE	Life Table Response Experiments
MLE	Maximum Likelihood Estimate
MSARNG	Mississippi Army National Guard
NAD	North American Datum
NAS	Naval Air Station
ODD	Overview, Design concepts, Details
PMJM	Preble's Meadow Jumping Mouse
POPAN	Population Analysis
PVC	Polyvinyl chloride
PY	Pollard-Yates
SD	Standard Deviation
SE	Standard Error
SEIBM	Spatially Explicit Individual-Based Model
SELES	Spatially-Explicit Landscape Event Simulator
SERDP	Strategic Environmental Research and Development Program
SFS	Saint Francis Satyr
TERS	Threatened, Endangered, or Rare Species
USACE	United States Army Corps of Engineers
USAF	United States Air Force
USFWS	United States Fish and Wildlife Service
UTM	Universal Trans Mercator

Keywords : Appalachian brown, Baltimore checkerspot, correlated random walk, Fender's blue, fire, floods, habitat restoration, hardwood removal, herbicide, host plant, life cycle, models, population dynamics, source sink dynamics, spatially explicit individual based model (SEIBM), St. Francis satyr, Taylor's checkerspot.

Abstract

1.1 Background and Objective

Background: Department of Defense (DoD) lands provide the best available habitat for numerous threatened, endangered and at-risk species (TER-S), and many of these species are currently managed on military lands by controlled disturbances (e.g. fires) or by de novo restoration of habitat. However, these management strategies run the risk of converting sources (where births exceed deaths) into sinks (where deaths exceed births) or of creating ecological traps - low-quality but attractive restored habitat that bleeds animals from nearby sources, threatening metapopulation viability. In addition, disturbance during and successional changes in habitat quality following management or restoration may lead local habitat patches to cycle from sink to source status and back.

Objective: Through a combination of field studies and state-of-the-art quantitative models, we used three species of endangered butterflies as a model system to rigorously investigate the source-sink dynamics of species being managed on military lands. Butterflies have numerous advantages as models for source-sink dynamics, including rapid generation times and relatively limited dispersal, but they are subject to the same processes that determine source-sink dynamics of longer-lived, more vagile taxa.

1.2 Technical Approach: For two of our focal species, we used previous restorations and ongoing management to study temporal source-sink dynamics. For the third, initiated new restoration, allowing us to examine management effects in a controlled experiment. We measured demography and movement at all phases of the disturbance cycle following management or restoration. We used these data to parameterize detailed spatially explicit individual-based simulation models (SEIBMs) linked to real landscapes with dynamic changes in habitat quality due to management. We also validated our general approach by comparing patterns in our focal species to general, cross-taxa, patterns. To further generalize our results, we extended our approach to other TER-S insect populations to inform additional management questions.

1.3 Results: For our focal species work, we found that, in most cases, habitat restoration was creating “source” habitat. In all cases, restoration had both positive and negative effects on individual vital rates, and it was necessary to integrate these effects across the life cycle to calculate the net effects of restoration. Our cross-species analysis broadly validated use of correlated random walk models with edge behavior as a basis for prediction spatial population dynamics, and revealed an important empirical pattern, specifically that animals tend to have faster movement in lower-quality habitat. This pattern means that matrix and sink habitat may increase connectivity in mixed-used landscapes, even when it does not enhance population viability.

1.4 Benefits: Using these field-measured vital rates, we developed system specific simulation models to evaluate different management scenarios. These were presented to local managers at a capstone workshop. Our work also revealed some previously unknown aspects of species biology, including the importance of species interactions (mutualism, competition, and predation) in determining the source-sink status of restoration. In some cases, this understanding immediately redirected management efforts. In others (usually, cases in which our detailed mechanistic studies differed from managers *a priori* opinions), we hope that this will cause managers to think more carefully about assumptions and perhaps prioritize research to evaluate their expectations, if not immediately changing management. More generally, our case studies demonstrate (1) the importance of measuring vital rates throughout a species life cycle, in the field, in order to assess the impacts of land management, (2) a range of simple to detail-rich modeling approaches for making these assessments, and examples of when such approaches are most useful, and (3) assessment of the main impacts of widely-used restoration tools, including herbicides, fire, artificial dams, and hardwood removal.

2 Objective

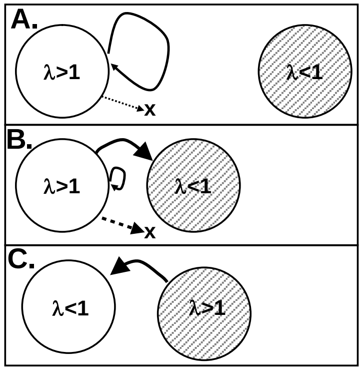
2.1 Background

2.1.1 Consequences of Source Sink Dynamics

Although abundance and habitat choice are often assumed to be reliable indicators of habitat quality, ecologists have known for decades that immigration can allow populations to persist in unsuitable sites (where deaths outnumber births) and that habitat preference does not necessarily match habitat quality (van Horne 1983, Holt 1985, Pulliam 1988). Adding low-quality (i.e., sink) habitat to a landscape, as may occur during restoration, may increase or decrease metapopulation viability (reviewed by Dias 1996, Schlaepfer et al. 2002, Battin 2004, Gilroy and Sutherland 2007). At one extreme, if animals move to low-quality habitat only when source habitat is fully occupied, adding sink habitat to a landscape increases overall metapopulation size and, consequently, viability (Pulliam 1988). At the other extreme, if animals perceive sink habitat to be high quality, adding sinks to a landscape creates ecological traps that may lead to extinction of both the source and sink populations (Donovan and Thompson 2001). Although there is evidence of this most worrisome result - negative impacts of low-quality habitat on populations in high quality habitat - for birds in fragmented landscapes (e.g., Weldon and Haddad 2005), as well as from highly contrived experimental situations (e.g., Gundersen et al. 2001), we know little about whether habitat management and restoration have the potential to create ecological traps for any species. Furthermore, habitat quality is unlikely to be static in time; patches that act as sinks in some circumstances may serve as sources in others (cf. Boughton 1999, Crone et al. 2001). Therefore, improperly classifying sinks as permanent traps and removing them from the portfolio of management options may reduce the success of conservation efforts. The conceptual model that underpins our project is that the source-sink status of habitat patches is dynamic in space and time, and that managers can use knowledge of dynamic sources and sinks to guide habitat restoration and management (Fig. 2.1.1-1).

Our work focused on butterflies, which have proven to be key model species for understanding spatial ecology, including metapopulations (Hanski 1999, Boggs *et al.* 2003), source-sink dynamics (Boughton 1999, 2000), and climate-induced range shifts (Parmesan *et al.* 1999). Butterflies are an ideal model system for studying source-sink dynamics because their short life-spans and relatively limited dispersal make it feasible to monitor their population dynamics and movement over multiple generations within the timeframe of a single study. Nonetheless, the basic processes of local population growth and dispersal behavior that underlie butterfly source-sink dynamics are the same ones that govern the dynamics of other species for which DoD has management responsibility (including amphibians, birds, and large carnivores). These processes are far more amenable to study in butterflies, so we will develop butterflies as a model system, then demonstrate the applicability of our approach to vertebrates (see Transition plan, below). Moreover, as multiple butterfly species are currently targets of management and habitat restoration efforts on military lands (Table 2.1.2-1), the question of whether such efforts are creating sources or sinks is directly important to DoD, above and beyond the value of butterflies as models for other TER-S species.

We investigated the source-sink status of restored and remnant habitat for three endangered butterfly species found on military lands (Table 2.1.2-1): Fender's blue butterfly (FBB, *Icaricia icarioides fenderi*) in Oregon; the St. Francis' satyr (SFS, *Neonympha mitchellii francisci*) at Ft. Bragg, NC, and the Taylor's checkerspot butterfly (TCB, *Euphydryas editha taylori*) at Ft. Lewis, WA. We proposed to study these 3 species jointly for several reasons. First, all are species of conservation concern: FBB is found only in remnant prairies in western Oregon, SFS is known only from Ft. Bragg, and TCB is an endemic species of rapidly disappearing prairies in the Pacific Northwest, with some of its largest populations at Ft. Lewis. Second, all 3 species are the targets of management and/or restoration efforts that run the risk of converting sources to sinks or creating traps, at least initially. Third, all 3 species have similar ecologies: all are historically dependent on habitats created by disturbance (fire in the case of FBB and TCB, and transient wetlands created by the construction and abandonment of beaver dams in the case of SFS) and/or on host plants that are themselves disturbance-dependent. Given this similarity, what we learn about one species may “add value” to studies of the others. Fourth, members of our team have done extensive work on the first 2 species, but as two separate research groups; working together will facilitate the application of field and modeling methods that have been developed for one species to the others. Finally, the third species, on which neither group has worked in the past, offers the opportunity to assess how well our models can be extended to other endangered butterflies.



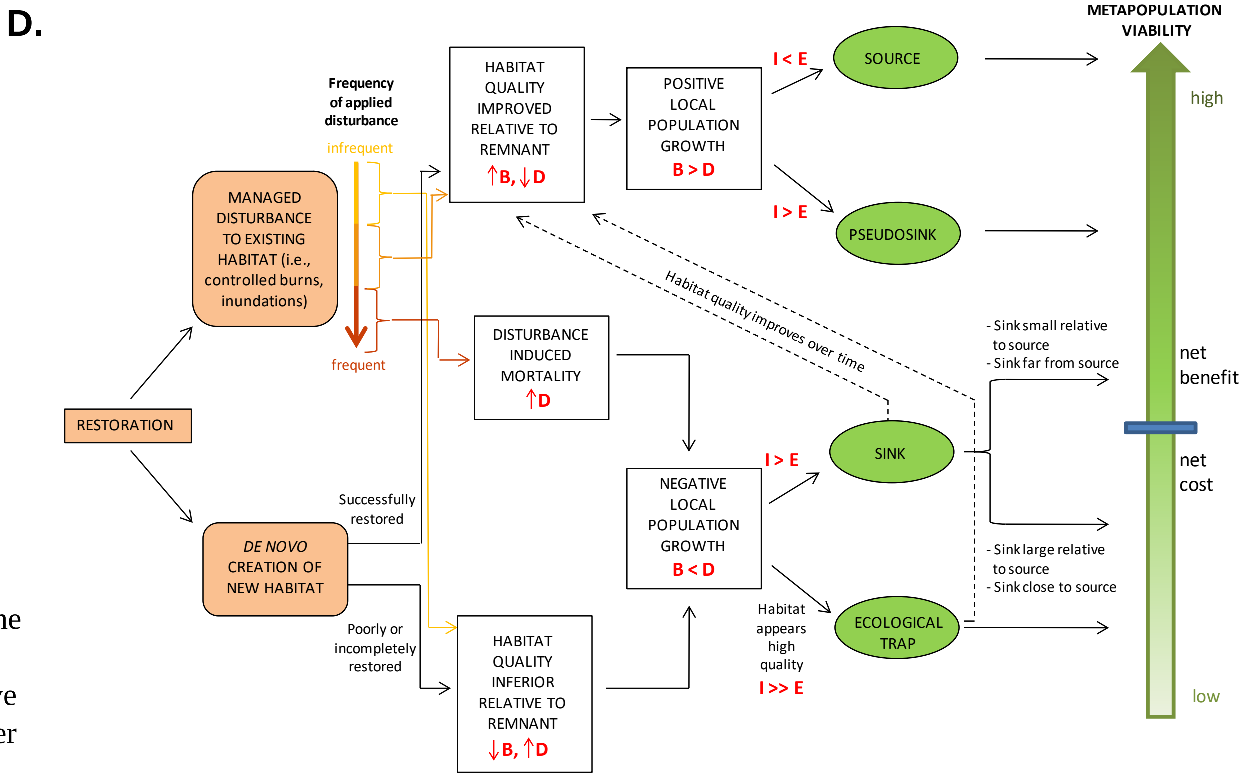


Figure 2.1.1-1. The importance of spatial and temporal variation for source-sink-trap dynamics. (***A-C***)***:*** Caricature of temporal variation in source-sink dynamics. In (A,B), a remnant patch (left) is a source (population growth rate □>1), but the poorly (or recently) restored patch (shaded) is a sink. Animals that leave the remnant patch (arrows) can either return to it, move to the nearby restored patch, or die in the matrix (dashed arrow ending in X). If the restored patch is near the remnant, as in (B), it may bleed the population in the remnant, possibly to extinction, by drawing animals to the trap, or by causing more to enter the matrix where mortality may be higher than in the remnant. This undesirable trap effect of poorly restored habitat could be weaker when the restored patch is farther from (A), not accessible from, or less attractive than the remnant source. (C). At a different time, the restored patch may have matured into a source, while the remnant may be a temporary sink (e.g., soon after management); in this case, the restored patch may enhance metapopulation persistence by contributing migrants to the remnant. (***D***)***:*** Interactive effects of management, demography, and dispersal on metapopulation viability. Orange boxes indicate management actions and green boxes indicate potential outcomes. B and D are birth and death rates. I is the immigration rate of animals into a patch, and E is the emigration rate of individuals out of the patch. Text in red indicates data that resource managers would need to collect to unambiguously predict source/sink status. In addition to measuring these parameters for three focal species, a key goal of our research is to ask how well simple models and data can capture source-sink dynamics, as opposed to creating complex models including all these parameters for all TER-S species managed by DoD.

2.1.2 Relevance to DoD

Department of Defense (DoD) lands provide the best available habitat for numerous threatened, endangered and at-risk (TER-S) species. Many of these species do best on DoD lands because they require disturbance-dependent habitats such as those created by fires and localized floods, and DoD resource managers can manage these disturbances with techniques that are difficult or impossible to employ on private lands. Ideally, such management creates population **sources** that increase metapopulation viability. However, habitat management often has both beneficial and detrimental effects on populations of TER-S species. For example, where fires are necessary in grasslands to control woody plants and improve habitat quality for wildlife, those fires often kill animals, particularly less mobile juveniles. In this case, too-frequent management runs the risk of creating **sinks** rather than sources.

In addition to managing existing habitat, DoD promotes TER-S species through habitat restoration. Restoration offers DoD managers the opportunity to enhance metapopulation viability of TER-S species by increasing the number of populations, as well as to mitigate for impacts of military activities on existing populations. However, restoration typically involves disturbance with heavy machinery over several

Table 2.1.2-1. Representative butterfly species managed on military lands (focal species in the present study are in bold)

Species	**Status**	**Location**
Carson wandering skipper	Endangered	Sierra Army Depot (CA)
Fender's blue - FBB	**Endangered**	**Camp Adair & USACE Fern Ridge (OR)**
Karner blue	Endangered	Fort McCoy (WI)
Quino checkerspot	Endangered	Camp Pendleton (CA)
St. Francis satyr - SFS	**Endangered**	**Ft. Bragg (NC)**
Smith's blue	Endangered	Ft. Ord (CA)
Oregon silverspot	Threatened	Camp Rilea (OR)
Mardon skipper	Candidate	Fort Lewis (WA)
Taylor's checkerspot - TCB	**Endangered**	**Fort Lewis (WA)**
Puget blue	State-listed	Fort Lewis (WA)

years, often followed by long periods of establishment and succession. Furthermore, although such restoration surely improves highly degraded lands, we are not always able to create lands that are functionally equivalent to high-quality remnant habitat (Bernhardt et al. 2005). Therefore, restoration has the potential to create ecological sinks that actually decrease viability of endangered species, rather than enhancing viability.

Both habitat management and restoration may create, at least for some time period, conditions that exceed the natural range of variation in habitat quality. Therefore, restoration and management have the potential to create habitat that animals *perceive* as high-quality, but that in fact acts as a population sink (Battin 2004, Gilroy and Sutherland 2007). These ecological **traps** that draw animals away from sources would likely decrease viability of TER-S species, rather than promoting recovery (Donovan and Thompson 2001). However, in spite of the possibility for well-intentioned actions to harm TER-S species, and in spite of longstanding calls to use restoration as an “acid test” of ecological understanding, the ecological community is largely failing to collect the data needed to assess the source-sink consequences of habitat management and restoration.

2.2 Study Species

2.2.1 Fender’s Blue Butterfly

The federally endangered Fender's blue butterfly (*Plebejus icarioides fenderi*) is restricted to remnant native prairies in western Oregon, USA. Habitat is defined by the presence of its larval hosts, Kincaid’s lupine (*Lupinus oreganus*, federally threatened) and spur lupine (*L. arbustus*). Fender’s blue are nectar generalists; females select nectar from native wildflower species while male foraging behavior is less selective (Thomas & Schultz 2016). Females oviposit in May, and larvae hatch a few weeks later. Larvae enter diapause as lupines begin to senesce. Post-diapause larvae begin feeding the following spring in March and pupate in April. Fender's blue movement can be described as a correlated random walk with preference at patch boundaries (Schultz 1998, Schultz and Crone 2001), and slower diffusion in breeding habitat than in matrix (e.g. Schultz 1998, 0.5 m^2/s vs 8.6 m^2/s). Lifetime displacement is on the scale of a hundred meters to few kilometers.

2.2.2 St. Francis' Satyr/Appalachian Brown Butterfly

The St. Francis satyr (*Neonympha mitchellii francisci*) is a small, brown butterfly that is a subspecies of *Neonympha mitchellii*. The St. Francis' satyr is bivoltine, with adults emerging in late May through early June, and in late July through early August. Extensive searching has determined that St. Francis' satyrs occur only on Fort Bragg military base, located in central North Carolina (Kuefler et al. 2008). Ft. Bragg is in the Sandhills region, and supports mostly longleaf pine forest with bottomland hardwood forests along stream floodplains. These streams dissect much of the terrain, but drainages are often interrupted by dirt roads used as fire breaks spaced every ≈200 m. Historically, fire played a large role in suppressing woody undergrowth along stream corridors and maintaining open herbaceous meadows. However, fire suppression is now common throughout the region. Current management plans at Fort Bragg include burning the pine understory approximately every three years, and largely exclude fire from riparian zones.

This stream network is also often modified by beavers, which dam portions of a creek to create flooded ponds that usually kill most standing hardwoods. Once these dams are abandoned and flood waters subside, the habitat is ideal for supporting wetland plants such as sedges in the *Carex* family. This includes *C. mitchelliana*, which is thought to be the main host plant for St. Francis' satyr larvae based its successful use in captive rearing and its ubiquity in sites where St.

Francis' satyrs are found. Other potential host plants that could support St. Francis' satyr larvae include *C. lurida* and *C. atlantica*, which larvae will eat in captivity, and *C. turgenscens*, which is widespread throughout the wetlands in artillery ranges.

Due to the rarity of St. Francis' satyrs, a similar species, the Appalachian Brown *(Satyrodes appalachia)* is often used in research as a surrogate species. The Appalachian Brown is a bivoltine butterfly that is dependent on the same wetland habitats as St. Francis' satyrs and is locally abundant. The host plants of *S. appalachia* are thought to be primarily sedge (e.g., *Carex*) species (Kuefler et al. 2008). Previous research has shown the Appalachian Brown to be an appropriate surrogate to use in place of the St. Francis' satyr (Hudgens et al. 2012) for which ethical concerns preclude most experimental manipulation.

2.2.3 Taylor's/ Baltimore Checkerspot

Text borrowed from Brown & Crone 2016a, 2016b

The Baltimore checkerspot butterfly is the state insect of Maryland (U.S.A.), where populations are in decline (Frye et al. 2013). It is also ecologically and morphologically similar to several at-risk checkerspot subspecies, including the federally listed Taylor's checkerspot (*Euphydryas editha taylori*; Bennett et al. 2013, Severns and Breed 2014a), Bay checkerspot (*E. editha bayensis*; Wahlberg et al. 2004), and Quino checkerspot (*E. editha quino*; Mattoni et al. 1997). The Baltimore checkerspot is a univoltine butterfly species occurring in colonies of tens to thousands of adults in the eastern United States (Scott 1986, Scholtens 1991). Females mate once and lay clutches of tens to hundreds of eggs on the underside of leaves of one of two host plant species: the native white turtlehead (*Chelone glabra* L., Plantaginacae) used throughout the range, and the introduced English plantain (*Plantago lanceolata* L., Plantaginaceae) used in parts of the range (Bowers et al. 1992). Gregarious early instar larvae coinhabit silken nests and drop to the ground in late autumn to overwinter (Bowers et al. 1992). In spring, postdiapause larvae emerge to feed on nearby host plants and species with similar chemical compounds, pupate, and emerge as adults in late spring to early summer (Stamp 1982).

3 Materials and Methods

3.1 Fender's Blue Butterfly

3.1.1 Statistical Analysis direct planting

We used monitoring data from Willow Corner to evaluate whether the 2003 restoration project caused that population to decline. We hypothesized that planting a strip of native plants around existing lupine patches created a population sink, because butterflies spent time foraging in this "nectar buffer", which lacked larval host plants for oviposition. These behavioral observations were accompanied by a noticeable decline in butterfly abundance. However, that decline could have been due to other factors, such as poor weather conditions site-wide, and cumulative impacts of research on individuals and habitat. To evaluate this hypothesis, we compared population dynamics at Willow Corner, the restoration site, to two other sites at Willow Creek, which experienced similar weather conditions but did not have the same kind of restoration treatment.

We fit three competing models of density independent population growth. First, we evaluated simple population growth with no systematic changes in growth rate:

$$N_t = \lambda^t N_0 \qquad \text{eq(1)}$$

Second, if populations crashed in year x, but population growth rate was constant before and after the crash, then, for t > x, populations should grow (or decline) as follows:

$$N_t = \lambda^{t-x}\ N_x P_s\ = \lambda^{t-x}\ P_s\ [\lambda^x N_0] \qquad \text{eq(2)}$$

where P_s is the proportion of butterflies that survive the crash, and all other parameters are as defined above. Finally, if the cause of the population crash also affected subsequent population growth rates, population dynamics after the crash would be described by:

$$N_t = (\lambda\Delta_\lambda)^{t-x}\ N_x P_s\ = (\lambda\Delta_\lambda)^{t-x}\ P_s\ [\lambda^x N_0] \qquad \text{eq(3)}$$

where Δ_λ indicates the proportional change in population growth rate, i.e., growth rate after the crash divided by growth rate before the crash. Using these relationships, we estimated parameters for each model by linearizing the models and estimating parameters using linear regressions.

Table 3.1.1-1. AICc model comparison of three population models.

		ΔAICc[1] at site…		
Model	np[2]	Main	North	Bailey
eq. 1	4	10.1	**0.0**	0.5
eq. 2	5	2.9	0.5	**0.0**
eq. 3	6	**0.0**	2.7	2.3

[1] Difference from the best model, based on Akaike's "An Information Criterion", corrected for small sample size. Values of 0 indicate the best model, and values < 2 indicate models that are effectively tied with the best model.

[2] number of parameters in each model

Dynamics at Willow Corner differed from the other sites, but not in the way we had expected. Willow Corner was the only site that experienced an unambiguous crash in 2005 (Table 2 and Figure 3). The monitoring data provide no evidence of a population crash at one of the two other sites, Willow Creek North (Table 3.1.1-1, Figure 3.1.1-1), and mixed evidence for a crash at the third site, Bailey Hill (Figure 3.1.1-1). Willow Corner was also the only site at which population growth rates differed before and after the crash; however, after the crash, population growth rates were higher than before, not lower (at Willow Corner: $\ln[\Delta_\lambda] = 0.24 \pm 0.10$, $t = 2.54$, $P = 0.025$; at Willow Creek North: $\ln[\Delta_\lambda] = 0.21 \pm 0.18$, $t = 1.18$, $P = 0.256$; at Bailey Hill: $\ln[\Delta_\lambda] = 0.24 \pm 0.21$, $t = 1.13$, $P = 0.278$; Figure 3.1.1-1). These results suggest that the population crash in 2005 at Willow Corner was at least partly due to the short-term negative effects of restoration and the nectar buffer. However, because population growth rates were higher after the crash, this effect seems to be very short-lived, and effectively moderated by lupine planting in later years that prevented ecological trap effects of restoration. In addition, there were management burns at Willow Corner in 2005 and 2007. Burning would be a plausible alternative hypothesis for a crash in 2005. These fires may be improving habitat quality and may be partly responsible for faster population growth after the crash. A final caveat is that patterns are not that different across the three sites. The main contribution to differences in statistical significance is the size of the error bars, not the values of the coefficients. In addition, these analyses rule out a hypothesis that had been of concern to managers, specifically, the idea that research is negatively affecting the Willow Creek population, since recent population growth rates have been significantly higher than past growth rates.

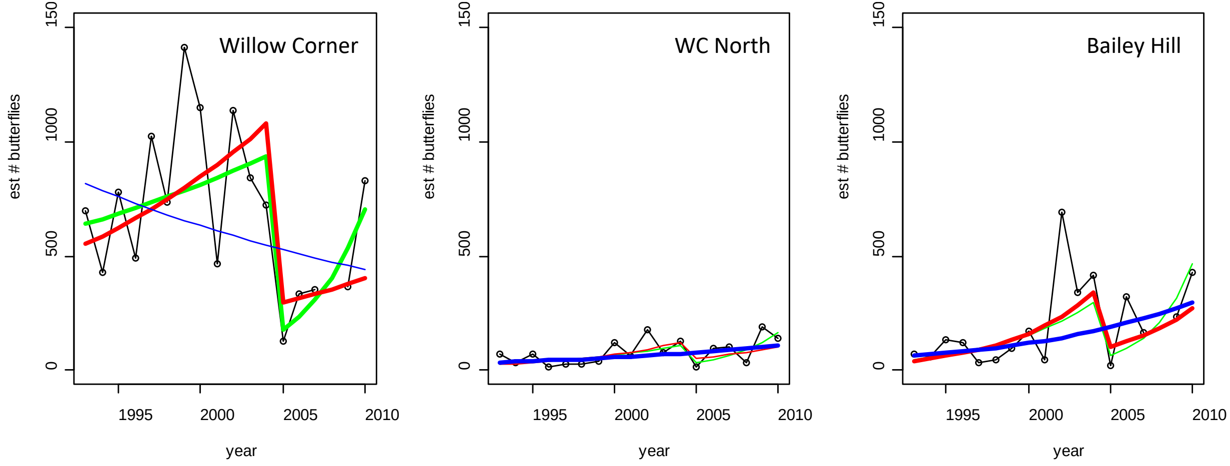


Figure 3.1.1-1. Population dynamics of Fender's blue butterfly at three sites at the Willow Creek preserve. Blue line = simple exponential growth (eq 1 a&b); red line = exponential growth with a population crash in 2005 (eq 2a&b); green line = exponential growth with a crash in 2005 and different growth rates before and after the crash (eq 3a&b). The thickest lines indicate the best-supported models for each population.

Based on this analysis, we explored effects of direct planting, using previously-published population parameters (Schultz 1998, Schultz & Crone 2001, McIntire et al. 2007), as opposed to including additional potential effects of ecological traps created by the patterning of Fender's blue hostplants in relation to surrounding habitat.

3.1.2 Implementation of SEIBMs direct planting

3.1.2.1: Model Description

To explore the effects of different planting strategies on Fender's blue population dynamics, we developed theoretical landscapes that only contain lupine and prairie habitat. Our model simulates how a butterfly's population dynamics respond to four different spatial scenarios of planting lupine habitat, compares how the responses change with landscape scale, and further compares how responses change with varying edge behavior and environmental stochasticity. We used an existing spatially-explicit agent-based model built for Fender's blue butterfly (FendNet; McIntire et al. 2007), using the Spatially-Explicit Landscape Event Simulator (SELES; Fall and Fall 2001) to build and run model simulations. Simulation output was analyzed using R (R Core Team 2013).

In our model, we track individual butterflies and residence time in lupine. We include habitat-specific movement modeled as a bias-correlated random walk (Schultz and Crone 2001). Male behavior differs from female behavior, and because colonization depends only on females, our model is female-only as in other simulation models with this species (McIntire et al. 2007, Severns et al. 2013). We incorporate environmental stochasticity estimated from annual fluctuations in observed population growth rate to account for stochastic population changes between years (McIntire et al. 2007; Schultz and Hammond 2003). The dimension of time is tracked as steps (ticks), where one day is equivalent to 140 steps, based on time budget analysis (Schultz and Crone 2001). Thus, an average flight season of 42 days becomes 5880 steps, and an average adult lifespan of 15 days becomes 2100 steps. Because most butterflies live an average of 15 days with a few living much longer, lifespan is drawn from a truncated negative exponential distribution of 2100 steps at the beginning of each flight period (McIntire et al. 2007;

Crone and Schultz 2003). A successful oviposition event is a constant per-step probability of laying an egg that survives to adult, if a butterfly is in lupine habitat. During model simulation, butterflies emerge at once and move until either the end of their lifespan, or the end of the flight season. Butterfly population dynamics and residence time (in steps) in lupine are emergent properties of habitat-specific behavior.

3.1.2.2: Management Scenarios and Analysis

We developed four spatial scenarios of planting lupine habitat within a given landscape, and designed three landscapes of different scales for each planting scenario (Table 3.1.2.1). Each planting scenario contained a constant total area of six hectares of lupine, with the degree of fragmentation (e.g., number of lupine patches) differing among scenarios. In the first scenario, all six hectares of lupine are planted into a single patch. For the second scenario, four lupine patches are planted, each with an area of 1.5 hectares. Nine lupine patches are planted in the third scenario, each with an area of 0.67 hectares. In the fourth scenario, 25 lupine patches are planted, with each patch having an area of 0.24 hectares. The three landscapes for each scenario are 25 hectares, 100 hectares, and 250 hectares, with lupine patches evenly spread across the landscape. Thus, in total, we designed a suite of twelve management scenarios (Figure 3.1.2.1).

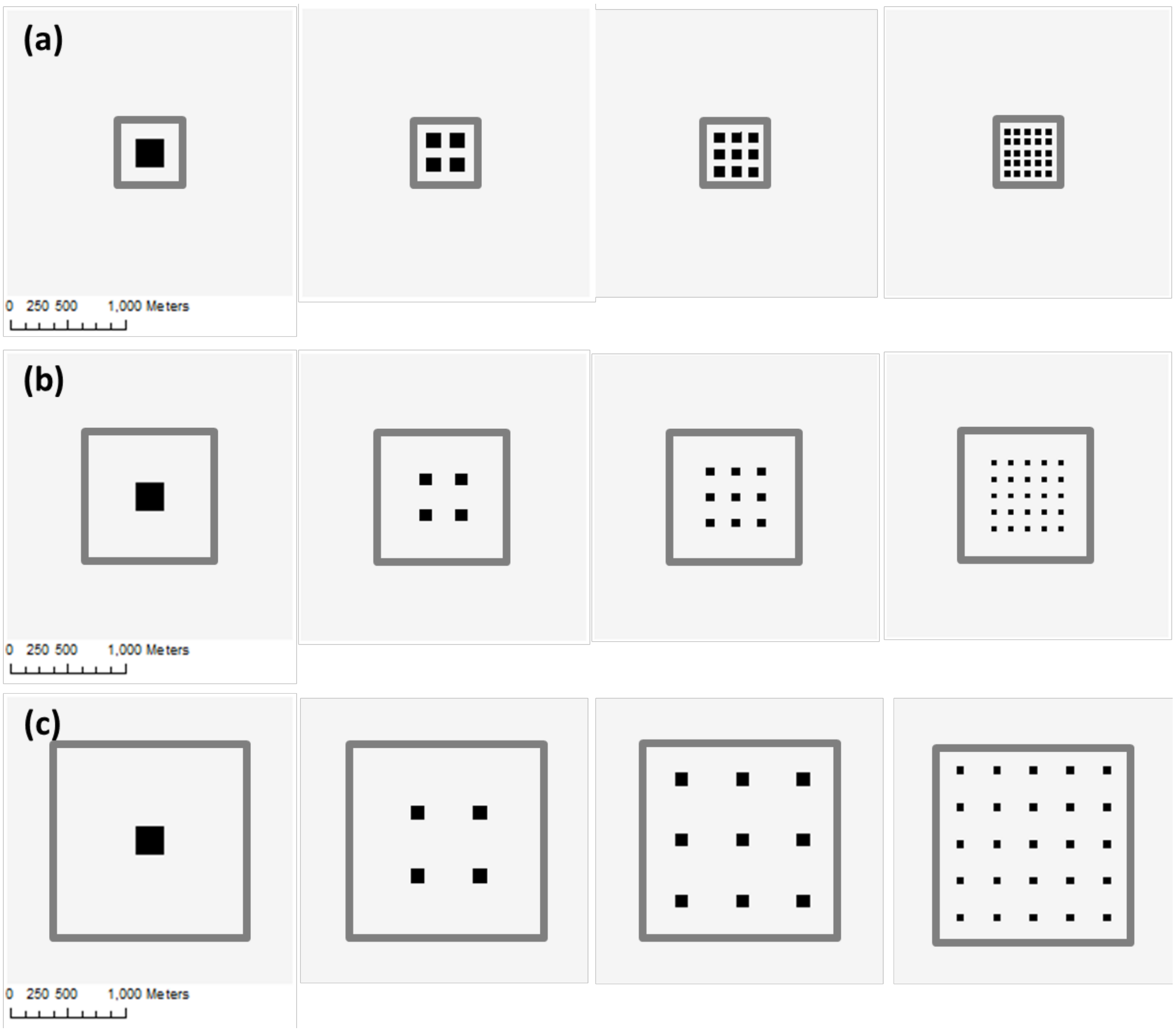
Each management scenario was repeated twice with differing parameters. In the first case, environmental stochasticity independently varies for each lupine patch each year. In the second case, we changed environmental stochasticity to be the same across all lupine patches, only varying each year. For the third case, environmental stochasticity varies independently for each patch each year, but we excluded edge behavior at lupine/prairie boundaries. Simulations were run for 50 years with an initial population of 500 butterflies spread evenly across lupine patches at the beginning of each simulation. We ran 500 replicates of each management scenario and parameter set.

We analyzed population dynamics over time for each management scenario by calculating the mean and standard deviation of population size each year over all replicates. To assess how residence time changes under each scenario, we used a zero-intercept regression to calculate the mean number of days in lupine per butterfly over all years and all replicates. Finally, we used a nonlinear least squares approach in R to estimate the intrinsic rate of increase and 95% confidence intervals for each scenario using a density-dependent population growth model.

Table 3.1.2.1. Details of lupine planting scenarios.

Scenario	Site Area (ha)	Patches within Site	Individual Patch Area (ha)	Distance Between Patches (m)	Environmental Stochasticity
1	25	1	6	0	Uncorrelated
2	25	4	1.5	85	Uncorrelated
3	25	9	0.67	63.5	Uncorrelated
4	25	25	0.24	42.5	Uncorrelated
5	100	1	6	0	Uncorrelated
6	100	4	1.5	252	Uncorrelated
7	100	9	0.67	188.5	Uncorrelated
8	100	25	0.24	125.8	Uncorrelated
9	250	1	6	0	Uncorrelated
10	250	4	1.5	445	Uncorrelated
11	250	9	0.67	333.5	Uncorrelated
12	250	25	0.24	222.5	Uncorrelated
13	25	1	6	0	Correlated
14	25	4	1.5	85	Correlated
15	25	9	0.67	63.5	Correlated
16	25	25	0.24	42.5	Correlated
17	100	1	6	0	Correlated
18	100	4	1.5	252	Correlated
19	100	9	0.67	188.5	Correlated
20	100	25	0.24	125.8	Correlated
21	250	1	6	0	Correlated
22	250	4	1.5	445	Correlated
23	250	9	0.67	333.5	Correlated
24	250	25	0.24	222.5	Correlated

Figure 3.1.2.1. Maps of lupine planting scenarios. (a) shows the 25 ha site. (b) shows the 100 ha site. (c) shows the 250 ha site. Black = lupine, light gray = prairie (matrix), dark gray outline = outline of site.



3.1.3 Model validation and simplification direct planting

3.1.3.1: Model Validation

Our model is calibrated by Fender's blue biology using parameters estimated in the field and an existing model framework (Schultz and Crone 2001; McIntire et al. 2007). Because of the hypothetical nature of the model landscape, we do not have observed field data to compare to simulation output. However, we were able to use our control scenario, a single six-hectare lupine patch, to verify simulation output. Specifically, we used residence time predictions of previous spatial models used to estimate minimum patch size for the species (Crone and Schultz 2003). Output from simulation matched residence time predictions for a six-hectare patch. Thus, our model captures the necessary biology to test the effects of different planting scenarios on butterfly population dynamics.

3.1.4 Field Data monitoring movement and demography fire management

Our study was conducted at Baskett Slough National Wildlife Refuge in Oregon, USA ($44^0$57'N, $123^0$15'W). We located experimental plots in the upland area known as Baskett Butte where hostplant lupine is comprised of a hybrid population of Kincaid's and spur lupine (Figure 1, Severns, Meyers & Tran 2012). Baskett Butte encompasses one of few remaining remnants of Willamette Valley prairie with a Fender's blue population (USFWS 2010). For the years of our experiment, 2011-2014, Baskett Butte was estimated to support 700-1900 Fender's blue butterflies (Fitzpatrick 2014).

We initiated the experiment in Spring 2011. Pretreatment data were collected in June 2011, prescribed burns were lit in October 2011, and post-treatment data were collected in Spring 2012, 2013 and 2014. The experiment followed a blocked design with burning assigned randomly to half of each of four replicate fingers of prairie vegetation located on the west-facing slope of Baskett Butte. Areal extent of burns varied from 0.07 to 0.42 ha based on area within each prairie finger. Strips of oak woodland separated these blocks. Each replicate contained 20 1m x 1m plots with at least 30% cover of hostplant lupine (total of 2 x 20 x 4 = 160 m^2 plots). One objective of this experiment was to quantify the effects of a cool-season (fall) burn, for comparison with past analyses based on a hot-season (summer) burn (Schultz & Crone 1998).

Demographic response

Each season, we monitored demographic response by counting eggs in each lupine plot in June and damaged lupine leaves (an index of post-diapause larvae; Warchola *et al*. 2015) in each lupine plot in April. Fender's blue larvae leave characteristic foraging signs in which they completely consume emerging lupine leaves before the leaflets expand, leaving short stems with small remnants of the leaflets. Since larvae are cryptic and difficult to detect, we used characteristic feeding damage as a measure of larval presence. Larval foraging is an index of Fender's blue larva abundance, with an average of 22 damaged leaves per larva (Warchola *et al.* 2015).

Behavioral response to disturbance

We assessed behavioral response to fire by quantifying adult movement paths in relation to fire treatments. We released 20 females at random points along each of four burn boundaries in May-June 2012 and mapped their flight paths (following methods in Schultz 1998). Briefly, we searched our research area at Baskett Slough, netted butterflies, cooled them and moved them to the release location, generally moving them less than 50m from the point of capture. Upon release, we followed butterflies and flagged each location at which the butterfly landed or every 20 seconds while in flight for up to 15 flags. We noted time at each flagged point. We used a

Magellan Promark III GPS to locate the position of each flag to the nearest 10 cm. In addition to flagging each flight path, we created a map of the burn boundary and lupine boundaries with 1 m accuracy. We calculated length and time of each move step, and turning angle relative to flying in a straight line as well as habitat burn status and lupine presence at each flag. We used these flight paths to quantify edge behavior (similar to edge releases in Schultz 1998). Specifically, we created circles in ArcGIS at 1, 2 and 5 m radius from each release point along the boundary. We recorded whether the butterfly crossed each circle perimeter into the burned or unburned side.

Analysis of Experimental Data

Demography

We analyzed effects of fire on butterfly demography and movement behavior using generalized linear mixed models (GLMMs; lme4 package in R, Bates, Maechler & Walker 2015). This analysis breaks the life cycle into two stages: eggs and post-diapause larvae (estimated from leaf damage, see "Experiment" above). Vital rates are therefore the number of eggs produced per post-diapause larva, and survival of eggs through diapause to the post-diapause larval stage. We did not explicitly measure vital rates of the adult life stage because the scale of adult movement does not correspond to the scale of experimental treatments; these vital rates are implicitly included by estimating fecundity as the number of eggs in June per post-diapause larva in April.

We analyzed the number of eggs in June per larva in April (i.e., per capita reproduction) using Poisson family, log-link GLMMs. Because larvae grow into adults that fly at a larger scale than the plots, the analysis included larvae from all plots, and egg counts from plots in each treatment. We included counts at all three time periods (April larvae, June eggs in burned plots, and June larvae in unburned plots) as fixed effects, and manipulated the design matrix of the GLMM to obtain the ratio of eggs in burned and unburned plots to larvae across both treatment plots. All models also included random effects of block and an observation-level random effect to account for overdispersion (Elston et al. 2001). Sample sizes in each year differed slightly: 320 plots (summed across life stages) in 2012, 298 plots in 2013, and 316 in 2014. Differences were driven by the fact that lupines in individual plots may not re-emerge from roots in all years, or lupine may be temporarily absent in some plots due to herbivory from voles. In addition to testing differences among treatments, we used a GLMM to estimate average eggs per larva in control plots across all years, for use in models for years when we did not collect larval data, e.g., 2011, the year before the burn. This model included a random effect of year, and an interaction of stage × year to account for among-year variation in the ratio of eggs per larva.

Following Warchola *et al.* (2015), we estimated overwinter survival from the ratio of damaged leaves in April to eggs in the previous June. We estimated this ratio using Poisson family, log-link GLMMs, with damaged leaves in April as the dependent variable, and ln-transformed eggs in June as an offset. Models also included burn treatment as a fixed effect, and effects of burn × block and plot within block as random effects. To scale damaged leaves to the actual number of larvae, we used the estimated ratio of larvae per damaged leaf in each year reported by Warchola *et al.* (2015, their Table S2).

Dispersal behavior

We used Gaussian (normal) family GLMMs with random effects of Path ID (“Butterfly”) and block (“Finger”) to test whether flight path parameters differed among burned and unburned areas, lupine and non-lupine patches, and their interactions. Move length, turning angle and move time were dependent variables. Models also included burn treatment and habitat (lupine/non-lupine) as fixed effects, and random effects of individual butterfly, block and plot within block as random effects. We tested these effects using marginal (Type II) hypothesis tests (Anova function in the car package in R, Fox & Weisberg 2011). Move lengths and move times were log-transformed prior to analysis, and cosines of turning angles were, first, scaled to be from 0 (180° reversals) to 1 (straight lines), then logit-transformed to approximate normality. We analyzed the proportion of butterflies that moved to the burned side (relative to 50:50 null hypothesis), and tested whether this proportion differed between lupine and non-lupine release points. Analyses were conducted using binomial family, logit link GLMMs, with burn finger as a random effect (lupine (finger) effects did not improve models, dAIC > 3 for all distances (where dAIC is the difference in Akaike Information Criterion).

3.1.5 Statistical analysis fire management

Matrix model with succession:

We used our experimental data to construct a model of butterfly population dynamics with fire and post-fire succession, with demographic differences between habitat stages in the year of the burn, 1 year post-fire, 2 years post-fire and 3+ years post-fire. We chose this time scale based on our demographic data. We did not include directed movement toward higher-quality post-disturbance habitat because we did not observe this behavior. We chose a deterministic model rather than a stochastic one because we only conducted experimental burning in one year and cannot estimate year-to-year variability in demographic rates. This model can be written in a general sense in terms of three processes.

Fire and habitat succession are described by the following transition matrix:

$$B_{mx} = \begin{bmatrix} b_0 & b_1 & b_2 & b_3 \\ (1-b_0) & 0 & 0 & 0 \\ 0 & (1-b_1) & 0 & 0 \\ 0 & 0 & (1-b_2) & (1-b_3) \end{bmatrix}$$

Where b_i is the probability of fire i years after a burn, starting with 0 in the year of the burn, and fire effects last for two years. For most management scenarios, we expect that $b_i = 0$ for all i except b_3 (Scenario 1, below). We also consider cases where $b_0 = b_1 = b_2 = b_3$, i.e., burning without respect to recent fire history (Scenario 2, below).

The next matrix describes survival of butterflies, as a function of time since fire:

$$S_{mx} = \begin{bmatrix} s_0 & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 \\ 0 & 0 & s_2 & 0 \\ 0 & 0 & 0 & s_3 \end{bmatrix}$$

where s_i is the survival through diapause of butterflies i years after fire.

The third matrix describes reproduction, and includes transitions from each habitat to each habitat type, based on movement of adults. In this matrix f_i refers to the total fecundity of individuals who spend time in habitat i. In the absence of local dispersal (an assumption that will be explored below) and assuming no attraction toward higher-quality habitat, fecundity is divided among successional stages in proportion to their abundance on the landscape, p_i. In a steady-state system, p_i is defined by the leading eigenvector of B_{mx}, normalized to one:

$$F_{mx} = \begin{bmatrix} f_0p_0 & f_0p_0 & f_0p_0 & f_0p_0 \\ f_1p_1 & f_1p_1 & f_1p_1 & f_1p_1 \\ f_2p_2 & f_2p_2 & f_2p_2 & f_2p_2 \\ f_3p_3 & f_3p_3 & f_3p_3 & f_3p_3 \end{bmatrix}$$

Note that an individual’s reproduction depends only on the habitat composition of the landscape, not on the habitat type where it eclosed. We adjust this model to allow for local dispersal by allocating a proportion of eggs to a butterfly's natal habitat type, and the rest to random habitat quality, e.g.,

$$\widetilde{F_{mx}} = \begin{bmatrix} (1-\delta)f_0 + \frac{\delta}{4}f_0p_0 & \frac{\delta}{4}f_0p_0 & \frac{\delta}{4}f_0p_0 & \frac{\delta}{4}f_0p_0 \\ \frac{\delta}{4}f_1p_1 & (1-\delta)f_1 + \frac{\delta}{4}f_1p_1 & \frac{\delta}{4}f_1p_1 & \frac{\delta}{4}f_1p_1 \\ \frac{\delta}{4}f_2p_2 & \frac{\delta}{4}f_2p_2 & (1-\delta)f_2 + \frac{\delta}{4}f_2p_2 & \frac{\delta}{4}f_2p_2 \\ \frac{\delta}{4}f_3p_3 & \frac{\delta}{4}f_3p_3 & \frac{\delta}{4}f_3p_3 & (1-\delta)f_3 + \frac{\delta}{4}f_3p_3 \end{bmatrix}$$

Where δ is the amount of local dispersal (Horvitz & Schemske 1986; Crone 2016).

Putting these processes together, one obtains the relationship:

$$N_{t+1} = F_{mx}S_{mx}B_{mx} \times N_t$$

where N_t is a vector of the number of butterflies at time t, across the four habitat stages. Alternatively, one can write:

$$T_{mx} = F_{mx}S_{mx}B_{mx}$$

and

$$N_{t+1} = T_{mx} \times N_t$$

This simplification means we can use the tools of matrix population models to analyze dynamics in successional environments (e.g. Lehtila *et al.* 2006; Pascarella, Aide & Zimmerman 2007).

Scenario analyses

Using the successional matrix model, we compared effects of fires that are targeted at late-successional habitat (typical of managed burns; hereafter Scenario 1) and fires that affect all successional stages equally (typical of wildfires, or cases where managers cannot exactly control the locations of burns; hereafter Scenario 2). Scenario 1 is to burn only habitat 3 or more years since fire, using $b_i = 0$ for $i < 3$. Scenario 2 is to burn the same proportion of all habitat types (as defined by time since burning) in each burn. We compare population growth rate (λ, the long-term per capita growth rate across all habitat types) across the potential range of habitat burned (0 to 100% each year) for each strategy. We evaluated the effects of different values of b_i (the proportion of habitat burned) and δ (local dispersal) for each scenario. All of the above analyses are prospective (*sensu* Caswell 2000) in the sense that they compare the effects of possible future management when each system is at equilibrium. We also conducted retrospective (*sensu* Caswell 2000) analysis of how variation in vital rates affected population viability (life table response experiments, LTRE, Caswell 1989), modified to our successional model). In the LTRE, we compare population growth rate with no effects of fire to population growth rates with each demographic response added individually to the model. For example, in assessing the importance of fire effects on larval survivorship in the year after the fire, we compared population growth rate in the model with parameters set at baseline levels without fire to population growth rate in the model with demographic effect of fire only on larval survivorship in the year after fire. We evaluated the LTRE using Scenario 1 (late-successional burning only) with b_3 set to the optimal portion of stage 3 successional habitat burned and with Scenario 2 (fire across all habitat, regardless of time since fire).

3.1.6 Implementation of SEIBMS fire management

3.1.6.1: Study Area

Some of the fastest-growing Fender's blue populations inhabit four sites surrounding Fern Ridge Reservoir in Eugene, OR, with metapopulation size reaching approximately 5,810 individuals in 2015 (Fitzpatrick 2015; Table 3.1.6-1). Managers with the U.S. Army Corps of Engineers implement mowing and herbicide application to control invasive grasses and woody species and are restoring Fender's blue host plant and nectar species within the sites. Controlled burns are sometimes applied in the sites, and managers seek to structure burn plans to maximize metapopulation growth rate (W. Messinger, pers. comm.). Thus, our model landscape includes the four primary Fender's blue populations in the Fern Ridge Reservoir metapopulation (Figure 3.1.6-1). We use a 2-meter pixel resolution of the Fern Ridge landscape, mapped using a spatial reference of NAD 1983 UTM Zone 10N. The landscape is composed of lupine patches, prairie, open woods, and reservoir. Kincaid's lupine patches total 1.6 ha in area, ranging from the largest site containing 0.85 ha to the smallest site containing 0.12 ha (Table 3.1.6-1).

The prairie matrix is characterized by a mosaic of native and invasive prairie grasses and encroaching woody vegetation. The structure of the forested areas is open, similar to other sites in the species' range. Because butterflies behave similarly at the edge of reservoir and at the edge of wooded areas (Smokey 2016, unpubl. data), for the purposes of our model, we classify the Fern Ridge Reservoir as open woods. In total, the three habitat types in our landscape are lupine habitat, prairie matrix, and open woods matrix.

3.1.6.2: Model Description

We follow the ODD (overview, design concepts, details) protocol (Grimm et al. 2006, 2010) to describe our model and include exhaustive in section 3.1.6.4. Our model simulates how a butterfly metapopulation's growth rate responds to three different spatial configurations of fire disturbance in the landscape, and compares how responses change with intensity of disturbance. The model distinguishes egg contributions between natal and immigrant butterflies at each site to test the role of immigrants on population recovery post-fire under each management scenario. We used NetLogo (Wilensky 1999) to build and run model simulations and R (R Core Team 2013) to analyze simulation output.

Male behavior differs from female behavior, and because colonization depends only on females, our model is female-only as in other simulation models with this species (McIntire et al. 2007, Severns et al. 2013). Controlled burns in the Fender's blue range occur during autumn, which is also the timing of historic Native American fires (Hamman et al. 2011). We track individual butterflies and eggs, fire disturbance on the landscape, residence time for each habitat type, and connectivity patterns between sites in our model. We distinguish individuals as either immigrant or natal butterflies, where immigrants are individuals that did not eclose in a given site, but rather dispersed to it. It follows that natal butterflies are individuals that eclosed in a given site. Our model includes habitat-specific movement, with boundary crossing behavior at open woods and reservoir (water) edge (Schultz and Crone 2001; Schultz et al. 2012). Fire disturbance has a dynamic effect on habitat quality, and impacts growth rate depending on time since fire. We model this dynamic by incorporating the effects of burning on larval survival and fecundity into a disturbance multiplier that depends on time since fire. Using vital rate estimates from experimental burns (Schultz and Crone 1998; Warchola et al., in press), we calculate population growth rate in treatment *i* in years since fire *b* as the product of larval survival multiplied by fecundity:

$$\lambda_{i,b} = s_{i,b} \times f_{i,b} \tag{1}$$

where $\lambda_{i,b}$ is population growth rate, $s_{i,b}$ is larval survival, and $f_{i,b}$ is fecundity. Specifically, *b* ranges from 0 to 3, where 0 is the burn year, 1 is one year since fire, 2 is two years since fire, and 3 is three or more years since fire. The disturbance multiplier in year since fire *b* is then calculated as the ratio of population growth rate in burn treatments to unburn treatments:

$$D_b = \frac{\lambda_{B,b}}{\lambda_{U,b}} \tag{2}$$

where D_b is the disturbance multiplier, $\lambda_{B,b}$ is the population growth rate in burned areas, and $\lambda_{U,b}$ is the population growth rate in unburned areas.

We incorporate environmental stochasticity estimated from annual fluctuations in observed population growth rate to account for stochastic population changes between years (McIntire et al. 2007; Schultz and Hammond 2003). The dimension of time is tracked as steps (ticks), where one day is equivalent to 140 steps, based on time budget analysis (Schultz and Crone 2001). Thus, an average flight season of 42 days becomes 5880 steps, and an average adult lifespan of 15 days becomes 2100 steps. Because most butterflies live an average of 15 days with a few living much longer, lifespan is drawn from a truncated negative exponential distribution of 2100 steps at the beginning of each flight period (McIntire et al. 2007; Crone and Schultz 2003). A successful oviposition event is a constant per-step probability of laying an egg that survives to adult, if a butterfly is in lupine habitat. During model simulation, butterflies emerge at once and move until either the end of their lifespan, or the end of the flight season. Residence time (in steps) in lupine of natal and immigrant butterflies are emergent properties of habitat-specific behavior. Thus, population size in year t+1 becomes:

$$N_{t+1} = \left(p \times R_{N,t} + p \times R_{I,t}\right) \times E_t \times D_b \tag{3}$$

where p is per-step probability of successful oviposition, $R_{N,t}$ is the residence time of natal butterflies, $R_{I,t}$ is the residence time of immigrant butterflies, and E_t is environmental stochasticity.

3.1.6.3: Management Scenarios and Analysis

We developed three spatial scenarios of partitioning lupine habitat for fire disturbance across the landscape, and chose four years as a constant fire return interval following management suggestions of previous studies (Pickens and Root 2009; Schultz and Crone 1998; Warchola et al., *in press*). The first scenario burns all lupine habitat at a site ("whole" scenario) once every four years. Here, one site is burned every year. The second scenario partitions sites into halves ("half" scenario), such that half of the lupine habitat is burned within a site once every other year. In this case, two sites are burned every year. The third scenario partitions sites into quarters ("quarter" scenario), such that a quarter of the lupine habitat is burned within a site each year with each quarter being burned every four years. Under this scenario, each site is burned each year. Burning always occurs in the first year of simulation, and simulations run for 20 years to iterate through five fire return intervals in the landscape. Our model was not sensitive to initial burning conditions, and model output was similar between the first ten and last ten years of simulation (unpubl. analysis).

Each scenario was modeled twice, once for early-season burns and once for late-season burns. Early-season burns in August scorch more of the landscape, and hereafter will be referred to as "hot" burns. Late-season burns in October are cooler and disturb less of the landscape, and hereafter will be referred to as "cool" burns. Cool burns are less expensive for managers, and may be more appealing in conservation plans (M. McKinley, pers. comm.). Thus, we developed cool burns and hot burns for each of our scenarios. Demographic parameters for fire intensity come from experimental hot and cool burns (Schultz and Crone 1998; Warchola et al., *in press*) in a major Fender's blue population at Baskett Slough National Wildlife Refuge in Dallas, OR. In total, we have six fire management scenarios for our model, plus a *status quo* scenario without fire disturbance. For each of the seven scenarios, we ran 500 replicates. We then repeated all seven scenarios using a life-table response experiment approach by removing egg contributions of immigrant butterflies, such that the only contributions to population size in year t+1 are from natal butterflies.

We analyzed population growth rate response to fire at the metapopulation and site level for each scenario. Because Fender's blue is univoltine, we calculated annual geometric growth rate λ as the ratio of population size in year t+1 to year t. Values were transformed to a log-scale and we estimated mean yearly geometric growth rate over all years and all simulations for each scenario. We used standard errors to estimate 95% confidence intervals for these means, and back-transformed parameter estimates.

To assess the relative contribution of immigrant eggs in the year after fire, we estimated the proportion ρ of eggs laid by immigrants to all eggs:

$$\rho_j = \frac{R_{I,j}}{R_{N,j}+R_{I,j}} \tag{4}$$

where ρ_j is the proportion of immigrant eggs the year after fire in site j, $R_{\mathrm{I},j}$ is the residence time of immigrants, and $R_{\mathrm{N},j}$ is the residence time of natal butterflies. In this case, natal butterflies are individuals that survived fire the previous year. To estimate the proportion for the metapopulation, we added all steps made by immigrant butterflies in sites one year post-fire, divided by all steps made in those sites one year post-fire, over each fire return interval:

$$\rho_m = \frac{R_{I,f}+R_{I,f+1}+R_{I,f+2}+R_{I,f+3}}{(R_{N,f}+R_{I,f})+(R_{N,f+1}+R_{I,f+1})+(R_{N,f+2}+R_{I,f+2})+(R_{N,f+3}+R_{I,f+3})} \tag{5}$$

where ρ_{m} is the proportion of immigrant eggs the year after fire over the fire return interval, $R_{\mathrm{I},f}$ is the residence time of immigrants in sites one year post-fire in year f, and $R_{\mathrm{N},f}$ is the residence time of natal butterflies in sites one year post-fire in year f. Specifically, f is the first year of the fire return interval, and ranges from 1 to 4. Thus, we accounted for the landscape-scale process over a full disturbance period.

Because the number of eggs is directly proportional to number of moves in habitat, we translate proportion of steps to proportion of eggs. We assumed a normal distribution for calculating mean proportions given sufficient replication, and estimated mean proportions for each site and for the metapopulation over the first three fire return intervals of each scenario. Given the skew of proportions toward zero, we used bootstrapping to estimate 95% bias-corrected and accelerated (BCa) confidence intervals using the package simpleboot in R (R Core Team 2013).

To estimate extirpation risk for each of the four populations for each scenario, we constructed binomial extirpation probabilities and confidence intervals. Given a sample size of 500 replicates for each scenario, we assumed a successful trial to be at least one extirpation during a 20-year simulation. Thus, we could estimate the probability of an extinction event in 20 years for each of the four populations and each scenario. In addition, we totaled the number of times each population was extirpated in each scenario over all 20-year simulations to calculate extirpation frequency.

3.1.6.4: Detailed Model Protocol

Purpose: Fire disturbance is a powerful tool to maintain early-successional landscapes for many species. Controlled burns help to maximize the quality of habitat throughout a landscape. Subdividing a landscape into multiple burn units allows for recolonization after fire, buffering potential negative mortality impacts across a population. Managers with the U.S. Army Corps of Engineers are implementing burn plans across four major populations of the endangered Fender’s blue butterfly. Our model explores how a metapopulation’s growth rate response to fire disturbance changes between three different spatial configurations of burn units in the landscape. We compare how these responses change between two intensities of fire disturbance using empirical field data. Finally, we quantify the role of contributions of eggs from immigrant butterflies on site population recovery post-fire.

State variables and scales: The model comprises four hierarchical levels: individual butterflies, habitat, management sites, and management subsites. Individuals are given state variables for identity, lifespan, and identity of the site where the butterfly eclosed. The landscape is composed of four major sites with independent populations, and it is broken into three major habitat types. Each site is given state variables for identity, spatial orientation, fire management, burn year, number of years since a fire event, and environmental stochasticity. Depending on the fire management variable, sites may remain whole, or be divided into two or four subsites. If a site is divided into subsites, each subsite is given state variables for identity, burn year, number of years since a fire event, and environmental stochasticity. The three major habitat types are lupine, prairie, and open woods. Each habitat is given state variables for step length, turning angle, and residence time of individuals in the habitat. Lupine is given an additional state variable for per-step probability of oviposition.

Fire disturbance introduces a dynamic effect of habitat quality, which is implemented in the model as growth rate multipliers. Depending on a site’s or subsite’s number of years since a fire event, the population next year is affected by a growth rate multiplier. Four growth rate multipliers are used: burn year, 1 year post-fire, 2 years post-fire, and 3+ years post-fire. Multipliers are estimated from butterfly vital rates using empirical field data from an experimental burn (Schultz and Crone 1998; Warchola et al., in press). Detailed explanations of these vital rates and calculations for growth rate multipliers can be found in Warchola et al. (in press).

The model depicts the Fern Ridge landscape in Eugene, OR. Four major Fender's blue butterfly populations are present in the landscape, and each population is considered one management unit. The left, top, right, and bottom extents of the model world are 477329, 4884321, 481218, and 4880955, respectively, in units of meters and spatial reference of NAD 1983 UTM Zone 10N. The world grid is 1944 by 1682 boxes mapped at a 2-meter pixel resolution, with each pixel representing one of three habitat types. Previous agent-based models with the Fender's blue butterfly have used both 1-meter and 2-meter pixel resolutions, which correspond to the resolution of both host plant mapping in the landscape and the scale of butterfly movement when tracked in the field. Length of time in the model is tracked as steps (ticks), where 140 steps is equivalent to one day. A flight season is defined as 5880 steps, or ~39 days. This temporal resolution is retained from previous agent-based models with the butterfly (McIntire et al. 2007).

Process overview and scheduling: Each simulation year is broken into 5880 time steps (ticks) that represent an average flight season of ~39 days. A site's fire management, burn year, and initial population size is chosen at the beginning of each simulation, and each site or subsite updates its years since fire disturbance at the end of each flight period. At the beginning of each flight season, all butterflies emerge at once. During each time step, butterflies move, oviposit if on lupine patch, or die if at the end of their lifespan. Habitats update residence times and butterflies update the identity of their last site of residence. At the end of the flight season, any remaining butterflies still alive are killed. Environmental stochasticity is drawn for each site at the end of each flight period and, if applicable to the scenario, applied to subsites. The model counts all eggs laid at each site or subsite, adjusts the count depending on the site or subsite's environmental stochasticity for that year, and then adjusts the count depending on the site or subsite’s time since fire disturbance. The adjusted counts become the next year’s population. Thus, population dynamics in the model use annual adult-to-adult transitions. The model iterates in this fashion for a total of 20 simulation years.

Design concepts: The basic principles of the model are that individuals move through the landscape with habitat-specific parameters, have some per-step probability of laying an egg that produces an adult next year if on lupine habitat, and die at the end of their lifespan. Management scenarios divide sites in the landscape into respective burn units with corresponding timings of fire disturbance. The effects of fire on larval mortality and fecundity are incorporated into growth rate multipliers based on time since fire, such that the model applies the necessary demographic effects of fire depending on the timing and location of a population in the landscape.

Population dynamics, movement, and metapopulation processes emerge as a result of the adaptive modeling process. Specific emergent dynamics include growth rate and spatial distribution of the total population in each simulation year.

Individuals are not given adaptive traits and do not make decisions that either directly or indirectly improve their fitness, nor do individuals estimate consequences of their decisions. Thus, the model does not attempt to quantify the fitness consequences of individual behaviors or assume that those behaviors affect individual fitness.

Individuals are able to sense the type of habitat they are on, and if they draw a move that crosses a boundary. Thus, individual butterflies move and oviposit according to the habitat in the landscape. Individuals sense the identity of the site or subsite they are on, thus quantifying where butterflies disperse in the landscape.

There is no interaction between individuals and individuals do not form social groups. The model is female-only and does not implement any interaction among individuals. Demographic and movement parameters are represented as probabilities or drawn from empirical probability distributions. Movement processes are drawn from exponential and wrapped normal empirical probability distributions for step lengths and turning angles, respectively (McIntire et al. 2007; Schultz and Crone 2001). Crossing into open woods habitat is a probabilistic event (Schultz et al. 2012). Movement in lupine edge is modeled as a bias-correlated random walk (Schultz and Crone 2001). When a butterfly is on a lupine patch, oviposition is probabilistic. Negative exponential and log-normal empirical probability distributions are used when drawing lifespan and environmental stochasticity, respectively (McIntire et al. 2007). For probabilistic events, the model compares input probabilities with output from a randomly generated number between 0-1. If the random number is less than the input probability, the event occurs.

At the end of each simulation year, the model records counts of eggs laid by site and subsite. The counts are adjusted for environmental stochasticity, followed by a growth rate multiplier for years since fire disturbance. This allows us to observe adult-to-adult transitions and extinction/colonization events in each year across the various locations of the landscape. From this, we can calculate mean geometric growth rate and tally extinction events. Through a simulation year, the model updates the number of moves made by butterflies in habitat by site.

These moves are counted both for immigrant butterflies (butterflies that did not eclose, but rather flew to the site) and natal butterflies (butterflies that did eclose in the site), and sums reported at the end of each simulation year. This allows us to calculate mean proportion of eggs laid by immigrant butterflies in all years of simulation. In addition, the model updates the number of moves made by immigrant butterflies to a site during each step of a simulation year, allowing us to observe dispersal events through the landscape.

Initialization: During model initialization, the landscape is loaded, the fire regime is set, and butterflies are added to the landscape. Habitat types in the landscape are constant for each scenario. Depending on the scenario, the fire regime will differ, and partition sites into subsites appropriately. Individual butterflies are added to each site at given starting populations, randomly moving to lupine patches within the site and drawing unique lifespans from a truncated negative exponential distribution with a mean of 2100 time steps. The identity of the site where a butterfly lives updates at the beginning of the simulation and for each time step, such that movement between sites can be quantified during simulation.

Input: Major inputs for the model include the Fern Ridge landscape, starting population sizes from 2009 survey data, and movement parameters and demographic vital rates. The model depicts the Fern Ridge landscape in Eugene, OR with left, top, right, and bottom extents of the model world 477329, 4884321, 481218, and 4880955, respectively, in units of meters and spatial reference of NAD 1983 UTM Zone 10N. Starting population sizes are 242 for Shore Lane, 188 for Spires Lane, 210 for Eaton Lane, and 580 for Green Oaks; these numbers are constant at the beginning of each simulation regardless of fire scenario and come directly from population surveys (Fitzpatrick 2015). Parameter estimation for movement rules is found in McIntire et al. (2007), Schultz and Crone (2001), and Schultz et al. (2012). See Table 3.1.6-2 for a complete list of input variables.

Submodels: The model reads in the raster landscape and assigns color-coding and patch-only variables: a patch’s site number, subsite number, habitat type, direction (in degrees) to the closest lupine patch, residence time, natal residence time, immigrant residence time, and connectivity tracking variable. The site number identifies a lupine patch as belonging to one of four major sites. The subsite number identifies a lupine patch as belonging to one of four quadrants of a major site. The habitat type identifies a pixel as prairie matrix, open woods matrix, lupine edge, or lupine. Direction identifies a patch's direction to the closest lupine pixel, a value used in movement rules. Residence time tracks the total number of butterfly steps spent in a patch. Natal residence time tracks the total number of butterfly steps spent in a patch where the patch's site and the butterfly's site of eclosure are the same. Immigrant residence time tracks the total number of butterfly steps spent in a patch where the patch's site and the butterfly's site of eclosure are different. The connectivity tracking variable is a unique number given to individuals, updated at every tick such that the model tallies when a butterfly has moved to a different site (e.g., a dispersal event). Finally, each patch within a site or subsite is given a time since fire variable.

At the beginning of each simulation, butterflies are given turtle-only variables: lifespan, natal site, and recent site. Lifespan is based off of a truncated negative exponential probability distribution with a mean of 2100 steps, and butterflies die when at the end of their lifespan or when the simulation year is over at 5880 steps. Butterflies are given identities for the site in which they eclosed, and during each step, the variable identifying their most recent site is updated for use in tracking dispersal events.

Depending on the fire scenario, the fire regime will partition sites into subsites. In the case of a whole fire scenario, sites are not partitioned and subsite-level tracking is not used. In the case of a half fire scenario, sites are partitioned into halves using numerical identifiers in the raster map such that approximately 50% of each site's lupine habitat is in each subsite. In the case of the quarter fire scenario, sites are partitioned into quarters using numerical identifiers in the raster map such that approximately 25% of each site's lupine habitat is in each subsite. The timing for each initial burn in the landscape is dependent on the fire scenario. The time since fire disturbance is set at the beginning of simulation (depending on fire scenario) and updated at the end of each year of simulation. If the time since fire variable equals zero, a patch is burned in that year.

Movement processes are drawn from exponential and wrapped normal empirical probability distributions for step lengths and turning angles, respectively (McIntire et al. 2007; Schultz and Crone 2001). Crossing into open woods habitat is a probabilistic event (Schultz et al. 2012). Movement in lupine edge is modeled as a bias-correlated random walk (Schultz and Crone 2001). When a butterfly is on a lupine patch, oviposition is probabilistic. During each dispersal step, butterflies update their variable for most recent site and update the residence time for the habitat patch they are on. If the butterfly moves to a different site in a given step, it updates a global list for tracking dispersal events between sites. See Figure 3.1.6-2 for a visual.

The model tracks population-level changes between each flight season of 5880 steps. At the end of the flight season, the model draws environmental stochasticity for each site based on a log-normal distribution with a mean of 0 and variance of 0.6 (McIntire et al. 2007). Counts of eggs occur by site or subsite depending on the fire regime, and the value for environmental stochasticity is multiplied to the count. Depending on the fire regime and time since fire, a disturbance growth rate multiplier is applied to the counts which become the starting population for the next year of simulation. During this submodel, the model resets global lists used in tracking, updates time since fire for each site/subsite, and records output. See Figure 3.1.6-3 for a visual.

Table 3.1.6-1. Kincaid's lupine areas and Fender's blue population sizes at Fern Ridge.

Site	**Kincaid's lupine (ha)**	**Population in 2015**	**Relative Site Size (based on area)**
Shore Lane	0.12	263	Small
Spires Lane	0.38	473	Medium
Eaton Lane	0.25	692	Small
Green Oaks	0.85	4382	Large

Table 3.1.6-2. Summary of parameter values.

Overview of processes, parameters, and default values of parameters of the Fender's blue butterfly fire model	
Parameter	Value
Number of sites	4
Number of simulation years	20
Demography	
Lifespan	2100
Per-step oviposition probability	0.0021157
Late-Season Disturbance	
Burn year growth rate multiplier	0.454172
1 year post-fire growth rate multiplier	2.358433
2 years post-fire growth rate multiplier	1.157507
3+ years post-fire growth rate multiplier	1
Early-Season Disturbance	
Burn year growth rate multiplier	0.2186
1 year post-fire growth rate multiplier	4.1105
2+ years post-fire growth rate multiplier	1
Movement – Lupine	
Turning angle (degrees)	49
Step length (meters)	2.1
Movement – Lupine edge	
Turning angle (degrees)	47
Step length (meters)	6.2
Bias	0.38
Movement – Prairie	
Turning angle (degrees)	23
Step length (meters)	8.8
Movement – Open woods and reservoir	
Turning angle (degrees)	27
Step length (meters)	6.1
Boundary crossing probability	0.05
Environmental Stochasticity	
Mean	0
Variance	0.6

Figure 3.1.6-1. Map of the Fern Ridge metapopulation. 1 = Shore Lane, 2 = Spires Lane, 3 = Eaton Lane, 4 = Green Oaks, white = prairie matrix, black = lupine host plant, dark gray = open woods, light gray = Fern Ridge Reservoir (water)

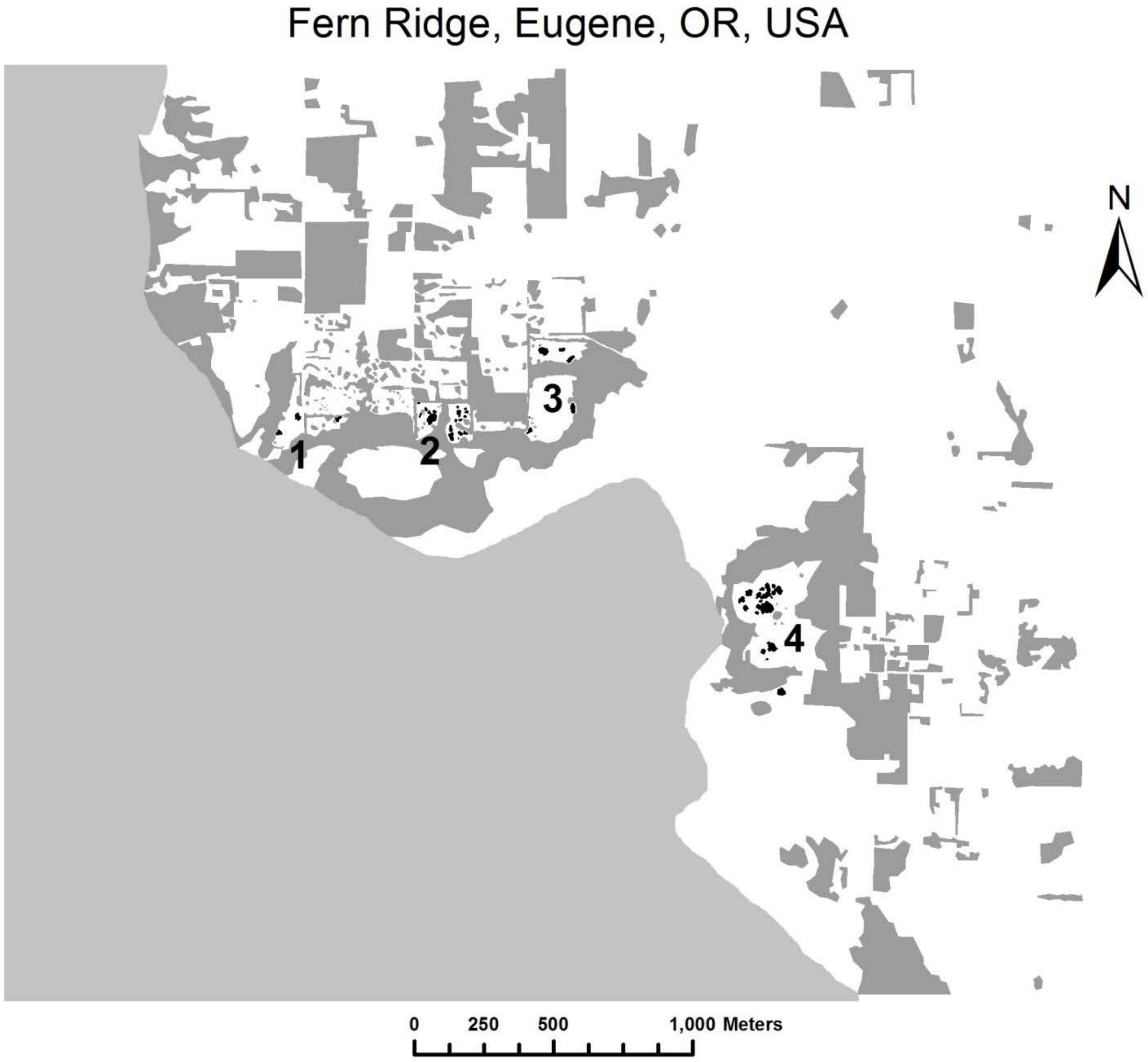


Figure 3.1.6-2. Logical flowchart of the adult flight period as a model process.

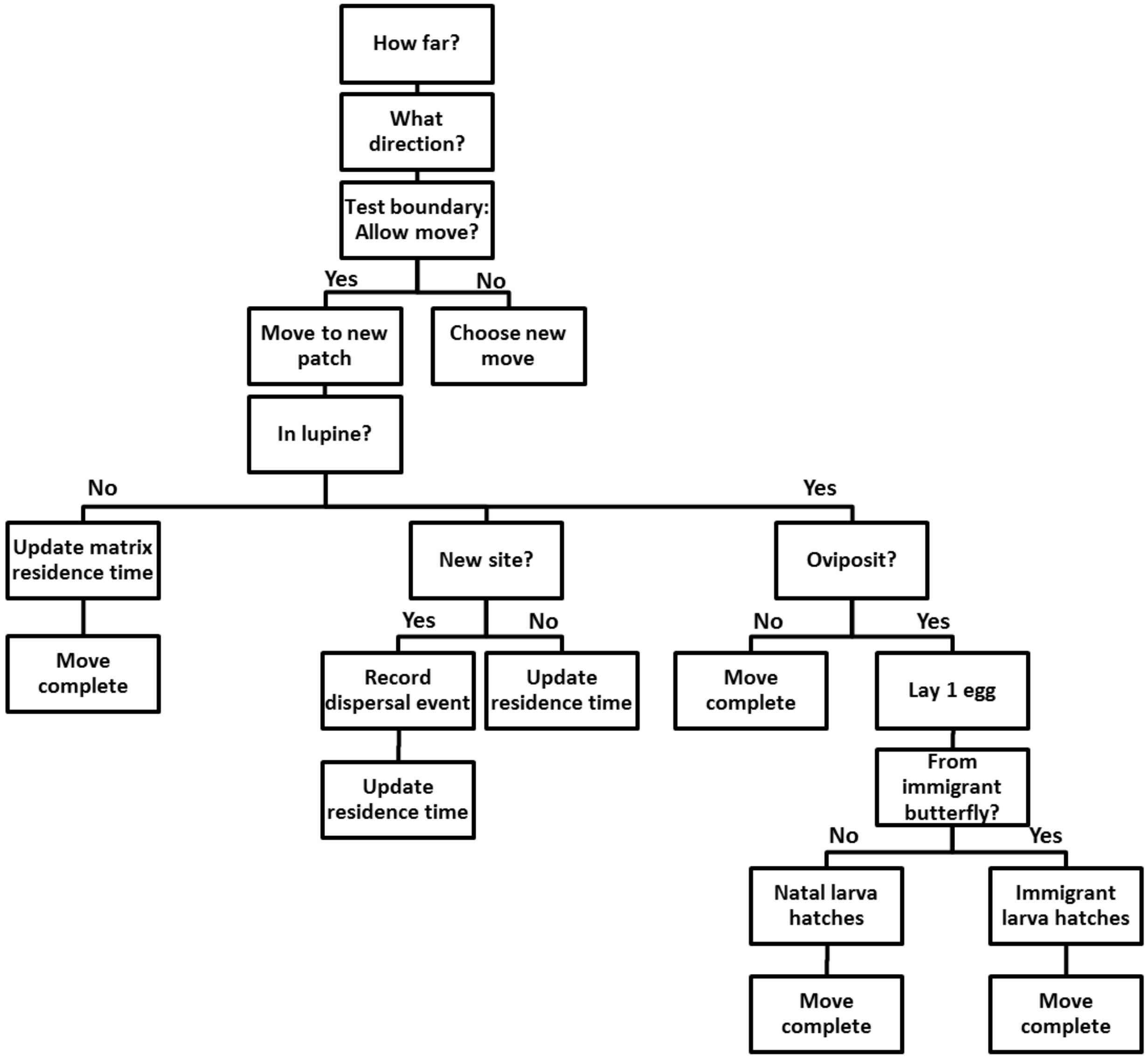
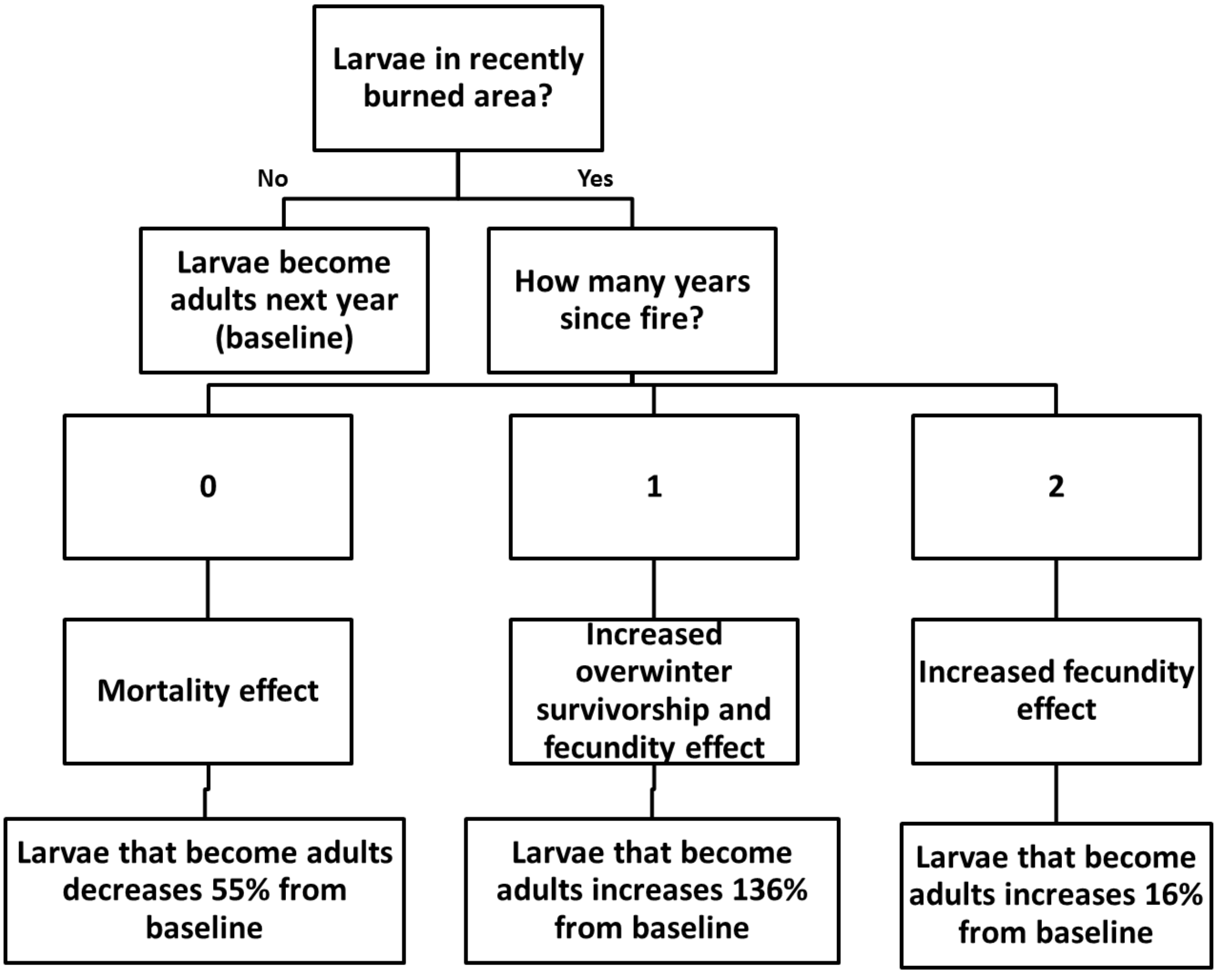


Figure 3.1.6-3. Logical flowchart of adult-to-adult transitions between flight periods (cool fire).



3.1.7 Model validation and simplification fire management

3.1.7.1: Model Calibration

Previous simulation models with the butterfly accurately captured *status quo* population and movement dynamics across the majority of the range, but underestimate population growth at Fern Ridge (McIntire et al. 2007; Severns et al. 2013). To account for this difference, we modeled the per-step probability of successful oviposition p as the ratio of population growth rate to residence time in lupine (*sensu* Crone and Schultz 2003):

$$p = \frac{\lambda_{obs}}{R} \tag{1}$$

where R is residence time, in steps, and λ_{obs} is observed population growth rate. We estimated λ_{obs} using a nonlinear least squares approach with the SSlogis function in R and observed Fender's blue populations from 1993 – 2015. Then, we estimated R as the average residence time per butterfly using our simulation model, and validated the simulation estimate matched observed residence times from a mark-recapture study in the landscape. Thus, we solved for the per-step probability of successful oviposition at Fern Ridge, and simulation output of yearly metapopulation growth rates under *status quo* management was consistent with observed metapopulation dynamics in the landscape.

3.1.7.2: Model Validation Process

Summary: We fit logistic and exponential population growth models using a nonlinear least squares approach in R to observed Fender's blue butterfly counts from 1993 – 2015 at four sites in the Fern Ridge landscape in Eugene, Oregon (Table 3.1.7-1). We found a signal of carrying capacity at three sites and described intrinsic rate of increase (r) and population growth rate (λ) for all sites. To account for potential biases in model fit given the change of sampling methods in 2010, we fit additional models with an adjustment parameter (β) and found two sites could potentially be influenced by the change in methods (Table 3.1.7-2). Using spatially-explicit individual-based simulation with environmental stochasticity and open woods in the Fern Ridge landscape, we quantified average residence time (steps) per butterfly in each site. When a butterfly is assumed to spend its entire life (2100 steps) in habitat with a per-tick probability of an adult next year equivalent to 1/933 (0.0010718), expected population growth rate is 2.25. Using this mathematical approach with exponential population growth rates at Fern Ridge sites coupled with site-specific mean residence times per butterfly from simulation, we calculated an adjusted per-tick probability of an adult next year (Table 3.1.7-3). With this adjusted probability (0.0021157) and new estimate of carrying capacity at 10,000 butterflies per hectare, we simulated 100 20-year replicates and quantified site-specific geometric growth rates and found simulation predictions were slightly less than observed population growth rates, but with some variance (Table 3.1.7-4).

Methods: We used a nonlinear approach using the nls() and SSlogis() functions in R to estimate carrying capacity and intrinsic rate of increase parameters for the Fender's Blue butterfly. Using Greg Fitzpatrick's report, "2015 Status of the Fender's Blue Butterfly in the Willamette Valley, Oregon" containing population sampling estimates at Fern Ridge, data were separated into four sites (Shore Lane, Spires Lane, Eaton Lane, and Green Oaks), and the total sum of these sites, all by year. Data were assigned an arbitrary number 0 from 1993-2009 and 1 from 2010-2015 to account for possible differences when sampling methods changed in 2010 for use in estimating an adjustment parameter, described below.

We reported parameter estimates of carrying capacity and intrinsic rate of increase along with 95% confidence intervals for growth rate for the logistic model, and reported parameter estimates of intrinsic rate of increase and 95% confidence intervals for growth rate for the exponential model. We used anova methods to test whether the logistic model fit observed data significantly better than the exponential model. We plotted model fit versus observed data for each site and for all of Fern Ridge from 1993-2015, and then projected model fit an additional 25 years into the future. Given the slight difficulty in fitting the logistic model to the observed data for Eaton Lane, we created a log-likelihood profile varying K from 5,000 to 100,000 in increments of 1,000 and discovered a negligible increase in model fit with increasing carrying capacity. So, we assumed an arbitrary K of 10,000 for the site in order for the nonlinear least squares function to converge in R and provide an estimate of intrinsic rate of increase for the site. To explore potential influence of the change of sampling methods in 2010, we adapted both the logistic and exponential models to estimate an adjustment parameter β using the term $(1 + \beta*yD)$, where yD is the arbitrary number 0 for years 1993 to 2009, and 1 for years 2010 to 2015. If the change in methods significantly changes the data, we expect model estimates of β will be significantly different from 0. In other words, if the change in methods at Green Oaks results in observed population estimates being 1.5 times higher, the β parameter will approximately equal to 0.5 and significantly different from 0. We used anova methods to test whether the models with the adjustment term fit the observed data significantly better than the models without the adjustment term.

Using spatially-explicit individual-based simulation, we ran 100 20-year replicates without fire, with environmental stochasticity, with open woods at a 0.05 per-step boundary crossing probability, and carrying capacity of 3930 butterflies per hectare in the Fern Ridge landscape, and quantified average residence time (steps) per butterfly in each site. Starting numbers of butterflies for simulation were at carrying capacity to give a high sample size for residence time. From the intrinsic rate of increase parameters from the logistic and exponential growth models without the adjustment term, we calculated population growth rate for each site. We used the relationship between population growth rate and residence time to establish adjusted per-step probabilities of an adult next year (λ = per-step probability adult next year * steps in lupine). Specifically, we divided population growth rate by residence time in steps to give the values for per-step probability of an adult next year. As an example, if we assume a butterfly spends its entire life in lupine (2100 steps) with a per-step probability of an adult next year of 1/933, the corresponding population growth rate is 2.25.

We assumed that Fern Ridge has been experiencing an intrinsic rate of increase most similar to an exponential population model, meaning that the most plausible population growth rates and adjusted per-step probabilities of an adult next year would be from estimates and calculations with the exponential growth model. We assumed that the estimated carrying capacity of ~15,000 butterflies for all of Fern Ridge would serve as a reasonable ceiling for use in simulation, so taking this number with the ~1.5 hectares of lupine habitat present in the landscape yields a new estimate of carrying capacity of ~10,000 butterflies per hectare for simulation. Using the adjusted per-step probability of 0.0021157 from the exponential model and estimated carrying capacity of ~10,000 butterflies per hectare from the logistic model along with environmental stochasticity and 0.05 per-step probability of crossing into open woods, we repeated 100 20-year simulations without fire to evaluate new model predictions of population growth rate. Further, to test whether these parameter estimates result in growing populations, we started simulations with 100 butterflies in each site.

3.1.7.3: Model Validation with Mark-Recapture

We conducted a mark-recapture study with the Fender's blue butterfly in the Fern Ridge landscape to quantify observed residence times at each site. To assess residence time, we marked 30 female butterflies in each of five primary USACOE sites in the Fern Ridge area of Eugene, OR. Butterflies were marked on both hindwings with a three-dot system. To assess connectivity, we marked 60 female butterflies in the largest population. We marked an additional 15 females at a small site and used resighting methods to assess residence time and connectivity. Sites were searched at least every other day for marked butterflies, weather permitting, and regions between sites of the landscape were searched multiple times through the flight season to document movement events. GPS locations of marked butterflies were documented upon initial marking and each recapture event.

Of the 150 butterflies marked in primary sites, we recaptured 88 females at least one time, with a total of 155 recapture events through the flight season. The longest documented residence time was 21 days (Table 3.1.7-5). None of the 60 females from the largest population were recaptured. We documented a total of 9 movements to a different site among the five primary sites (Table 3.1.7-6). We documented 3 unmarked butterflies in regions between sites, suggesting some movement through the broader landscape.

We used the package RMark with program R (R Core Team 2013) to model apparent survival and estimate residence time for Fern Ridge. Assuming constant apparent survival and recapture probability, observed residence time for female butterflies in the landscape was 4.95 (95% CI: 4.02 – 6.11) days (Table 3.1.7-7). This key validation result falls within the range of predicted residence time from simulation (see Table 3.1.7-3).

Table 3.1.7.1. Summary of logistic and exponential growth models.

Site	**Logistic model**			**Exponential model**			**anova**
	K estimate	*r* estimate	*λ* 95% conf	*r* estimate	*λ* estimate	*λ* 95% conf.	p-value
Shore Lane	198.7985	2.770	0.182 – 2.15	0.11363	1.12	1.06 – 1.19	0.1204
Spires Lane	1834.809	0.1804	1.11 – 1.71	0.15492	1.17	1.13 – 1.21	0.6651
Eaton Lane	10000**	0.3409	1.27 – 1.82	0.32794	1.39	1.21 – 1.60	NA
Green Oaks	4003.5543	0.7660	1.67 – 4.50	0.27558	1.32	1.24 – 1.40	0.007913
Total Fern Ridge	14970	0.3074	1.25 – 1.67	0.2467	1.28	1.24 – 1.32	0.3367

Table 3.1.7-2. Summary of logistic and exponential growth models with adjustment term.

Site	**Logistic model**				**Exponential model**			
	β param.	β st. err.	β p-value	anova p-value	β param.	β st. err.	β p-value	anova p-value
Shore Lane	0.2442	0.3057	0.434	0.3748	-0.55127	0.20118	0.01262	0.08242
Spires Lane	0.2315	0.3359	0.4990	0.448	0.24975	0.32812	0.45544	0.3937
Eaton Lane	-0.8065	0.1375	9.74e-06	0.003074	-0.85899	0.07534	3.34e-10	0.0006983
Green Oaks	-0.4171	0.4711	0.38709	0.6093	1.50280	1.36098	0.283	0.04675
Total Fern Ridge	0.1079	0.3393	0.75395	0.7457	0.2241	0.2856	0.4418	0.3809

Table 3.1.7-3. Summary of residence times and adjusted per-step probabilities of an adult next year for both growth models.

Site	Residence Time (steps/butterfly)	Logistic Model		Exponential Model	
		Growth Rate λ, exp(r)	*Per-step probability adult next year (GR/res. time)*	*Growth Rate λ, exp(r)*	*Per-step probability adult next year (GR/res. time)*
Shore Lane	605	15.96	0.02638	1.12	0.0018512
Spires Lane	562	1.20	0.0021352	1.17	0.0020819
Eaton Lane	652	1.41	0.0021626	1.39	0.0021319
Green Oaks	604	2.15	0.0035596	1.32	0.0021854
Total Fern Ridge	605	1.36	0.0022479	1.28	0.0021157

Table 3.1.7-4. Summary of simulation model predictions with new estimated parameters.

Site	**Exponential Model Growth Rate Estimate**		**Simulation Model Growth Rate Estimate**	
	λ Estimate	λ 95% conf.	λ Geometric Mean	λ 95% conf.
Shore Lane	1.12	1.06 – 1.19	0.53	0.50-0.56
Spires Lane	1.17	1.13 – 1.21	1.03	1.01-1.04
Eaton Lane	1.39	1.21 – 1.60	0.90	0.87-0.92
Green Oaks	1.32	1.24 – 1.40	1.14	1.12-1.16
Total Fern Ridge	1.28	1.24 – 1.32	1.15	1.14-1.17

Table 3.1.7-5. Summary of mark-recapture study.

Site	# Marked	# Unique Recaps	# Total Recaps	Longest Residence Time
West Shore	30	11	17	11 days
West Spires	30	21	41	11 days
East Spires	30	23	31	12 days
North Eaton	30	16	24	20 days
South Eaton	30	17	42	21 days

Table 3.1.7-6. Summary of observed connectivity.

Connectivity	To West Shore	To West Spires	To East Spires	To North Eaton	To South Eaton
From West Shore	■	0	0	0	0
From West Spires	0	■	6	0	0
From East Spires	0	2	■	0	0
From North Eaton	0	0	0	■	1
From South Eaton	0	0	0	0	■

Table 3.1.7-7. Summary of mark-recapture analysis.

Parameter	Estimate	Lower 95% CI	Upper 95% CI
Apparent survival	0.8170091	0.7798673	0.8490969
Recapture probability	0.2479	0.2062823	0.2947956
Residence time (days) (“lifespan”, 1/-lnS)	4.95	4.02	6.11

3.2 Saint Francis' Satyr/ Appalachian Brown

3.2.1 Field Data Hardwood removal/inundation

To create restoration sites, in the spring of 2011 we established four restoration areas, each containing four 30m x 30m experimental plots. In each area, plots were randomly assigned to one of four treatments in a factorial design: 1) manual removal of most trees; 2) installation of temporary dams; 3) both tree removal and installation of dams; and 4) no manipulation. Tree removal was intended to increase light availability within wetlands to encourage herbaceous plant growth. We intentionally left ≈10% of the trees in order to mimic the canopy structure found in beaver-created wetlands in our area. We maintained tree removal treatments by cutting back the re-sprout of trees and shrubs in 2012 and 2013 to suppress hardwood canopy regeneration. Damming was intended to increase soil moisture and the amount of standing water, a key requirement for sedges. In dammed plots, we installed 0.5 m high and 1 m wide water-filled temporary coffer dams (Aquadam Inc., Scotia, CA, USA) across the length of the downstream edge of the plot, which inundated ≈10 m of the downstream portion of the plot. Within each plot we established 27 uniformly distributed 1.5 × 1.5 m vegetation subplots that were surveyed for percent cover of all sedge species and the major vegetation types (e.g. grasses, forbs, and shrubs) prior to restoration in Spring 2011, as well as in Fall 2011, Spring 2012, and Spring 2013.

3.2.2 Monitor movement and demography

Movement

We observed both Appalachian Browns and St. Francis' satyrs at all treatment plots in all four experimental blocks. Two observers controlled digital compasses (KVH Datascopes) mounted on PVC poles inside the plots. Butterflies were either released from the center of the 30m x 30m plot or observed in natural flight. The pair of observers recorded synchronous bearings of the target butterfly every 5 seconds while it was moving. Observations stopped when butterflies stopped moving for more than 30 minutes or left the plot (Kuefler et al. 2010).

Using trigonometry and the observer bearings, the length of each 5-second move and turn angle between consecutive moves were calculated for all butterflies with 3 or more recorded moves. From the move lengths and turn angles, we calculated the mean squared displacement per move (hereafter R_n^2/n), which measures the spread of a population over space (Turchin 1998). A larger R_n^2/n indicates that the butterflies are moving more quickly (longer move lengths) and more directly (smaller turn angles). We compared the distributions of move lengths, turn angles, and R_n^2/n from different species and treatment sites using the Kolmogorov-Smirnoff test. Confidence intervals were measured by creating bootstrapped datasets (10000 repetitions) and taking the middle 95% of results.

Demography

To estimate the direct and indirect effects of restoration treatments on Appalachian brown demography, we estimated egg survival and larval to adult survival independently. To estimate egg survival, we placed greenhouse raised, potted *C. mitchelliana* plants with a known number of eggs into our established experimental restoration plots and counted the number of eggs that remained after 48 hours. We first caged wild-caught Appalachian brown females on potted sedge plants in a greenhouse at Ft. Bragg, and counted the number of eggs laid. Each restoration plot received one pair of potted sedges, one randomly assigned to a predator exclusion treatment and a second that was accessible to all predators. Plants in the predator exclusion treatment were enclosed in a cage constructed from a 20L fine mesh fabric paint strainer and bent wire. A 15-cm band of Tanglefoot® insect barrier was applied to pots to exclude crawling predators. Paired plants were placed in the center of each restoration plot on dry ground within five meters of each other. All plants were removed from the field after 48 hours and we counted the number of eggs remaining.

To estimate survival over the larval and pupal stages, we deployed a known number of larvae into experimental arenas created in each plot and counted the number of butterflies that emerged. We constructed larval arenas by removing the ends of a standard 55 gallon polyethylene food grade drum and cutting the remainder into thirds, resulting in an approximately 57 cm diameter x 35 cm tall ring. At six randomly chosen locations in each plot, rings were buried approximately 10 cm into the ground surrounding naturally occurring, mature *C. mitchelliana*. In one block with low sedge abundance, field cages were placed around greenhouse raised and transplanted *C. mitchelliana* plants. We randomly assigned each arena to a predator-free or predator-accessible treatment. Predator-free arenas were enclosed with tulle netting that was secured to the outside of the rings using nylon straps and tied at the top of a vertical support structure to hold the fabric off the plants. All potential predators were manually removed from predator-free arenas prior to addition of larvae. Arenas accessible to predators remained open during larval development, but once pupae were observed, arenas were enclosed with tulle netting to facilitate capture of emerging adults. Five larvae varying in age from first to third instars (most commonly second instars) were placed into each arena in a block on the same day. Larvae were left to develop in the field. After the observation of pupae, arenas were checked daily for newly emerged adults until no butterflies were found for five consecutive days.

3.2.3 Statistical analysis hardwood removal/inundation

To assess changes in the plant community resulting from restoration treatments, we performed a Before After Control Impact (BACI) linear mixed effects analysis using the lmer function in the lme4 package (Bates et al. 2013) and the ANOVA function in the car package (Fox and Weisberg 2011) in the statistical platform R 3.0.2 (R Development Core Team 2013). Our model contained fixed effects of tree removal, damming, and year, all interaction terms, and a random effect of plot. We used a Type II Wald chi-square test to evaluate the effect of restoration on: (1) percent cover of *Carex mitchelliana* (the most likely host plant species in our plots); (2) percent cover of all sedges; and (3) percent cover of all understory vegetation.

We assessed whether restoration treatment had direct and indirect effects on egg and juvenile survival using generalized linear mixed models (GLMMs) with the function glmer from the lme4 package. The numbers of eggs or juveniles that survived to the end of the experiment were treated as binomial responses. In all analyses, tree removal, damming, predation treatment, and their interactions, as well as flight period for egg survival, were treated as fixed effects; block and plot were treated as crossed random effects. We used Wald Z tests to assess the statistical significance of the fixed effects.

To assess direct effects, we tested for effects of restoration treatments and their interaction on survival using only the predator-free treatments. For egg survival, we began with a model that included the three-way interaction between tree removal, damming, and flight period (plus all lower-order terms) to test whether the main and interactive effects of the restoration treatments differed between flight periods. Because this three-way interaction was not significant ($P = 0.14$), we fit a model with all two-way interactions between tree removal, damming, and flight period. We used the same model (without flight period) to assess the direct effect of restoration treatments on juvenile survival. To assess the net effect of restoration treatments (i.e., direct and indirect effects combined), we used the same models as for direct effects, but only used data from the predator-accessible treatment.

Indirect effects of restoration mediated through predation were investigated by comparing the survival in predator-free and predator-accessible treatments as a function of restoration treatment. An effect of restoration treatment on predation intensity would be indicated by a significant tree removal × predation treatment, damming × predation treatment, or tree removal × damming × predation treatment interaction. For egg survival, the four-way interaction between tree removal, damming, predation treatment, and flight period was not significant ($P = 0.57$); therefore we dropped the four-way interaction from the model but included all three-way interactions. For juvenile survival, the three-way interaction between the tree removal, damming, and predation treatments was not significant ($P = 0.76$), so we fit a model with all two-way interactions. To estimate the mortality of eggs and juveniles due to predation, we calculated a mortality response ratio by dividing the survival rate in the predator accessible treatment by the survival rate in the predator-free treatment and subtracting this value from 1.

3.2.4 Documenting predator community

During different stages of their life cycles, St. Francis' satyrs are subject to predation by a host of predators including spiders, dragonflies, ants and birds. Thus, the abundance and distribution of predators is a significant determinant of habitat quality for St. Francis' satyrs. In 2013, we measured the species richness and abundance of dragonflies and ants in each of our restoration plots as part of our ongoing research comparing the quality of different restoration treatments.

To survey dragonflies, we walked through all restoration sites for 15 minutes noting abundance and species of all dragonflies observed. When possible, we recorded dragonfly sex and distance observed from transects. We surveyed on a total of seven days between June 5 – August 12.

To survey ants, we placed nine ant traps at locations spaced out within each plot at the same sites. For each plot, traps were set out on each of two mornings (June 26 and 27) and two afternoons (July 11, 15 and 16). Traps consisted of a 3x5 index card with approximately 50 g of tuna and honey placed in its center. The traps were left in the plots for two hours, after which all ants attracted to the traps were collected. Ants were organized into vials of ethanol for further identification and numeration in the laboratory.

3.2.5 Refine measurements of vital rates, trends and abundance

ABB and SFS caterpillar behavior and survival methods

Caterpillar host use and survival

We measured St. Francis' satyr caterpillar survival in the field by releasing a known number of first instar caterpillars into experimental arenas, allowing them to develop in the arenas, and then counting the adult butterflies that emerged from arenas. We used experimental arenas composed of a 57cm tall X 37cm diameter ring of a polyethylene food grade drum buried approximately 10 cm into the ground (Aschehoug et al. 2015). These arenas were installed in 2012 around naturally occurring *C. mitchelliana*. When preparing arenas in 2016, we chose existing arenas that already contained *C. mitchelliana* so we would not need to supplement larval diets. Because we were limited in our study by our federal permit to using a small number of endangered caterpillars, we only measured caterpillar survival in the control and tree removal/dam implementation treatments in two blocks of the original restoration experiment, releasing caterpillars into two arenas per plot for a total of 8 arenas. We released 7 first instar caterpillars into each arena over two days. Two arenas, one in each treatment, were invaded by ants after the first day of releases, so no additional caterpillars were released into them and they were dropped from the experiment. We left arenas open to predation and counted caterpillars daily. Once we observed pupae, we enclosed the arenas with mosquito netting. We continued to visit arenas daily, recording and releasing all adults that emerged. By releasing St. Francis' satyr caterpillars into arenas, we were able to observe larval feeding and host choice in the wild for the first time. In addition to simply counting caterpillars daily, we recorded the species of sedge on which each caterpillar was feeding.

We tested whether larval survival differed among treatments between St. Francis' satyr and Appalachian Brown (data from Aschehoug et al. 2015). To do this, we used a general linear model with a binomial response variable, including a species*treatment interaction main effect. We conducted this analysis using the glm function of the lme4 package, and Anova function of the car package in R.

Caterpillar behavior

We measured Appalachian brown and St. Francis' satyr caterpillar behavior using captive individuals. These originated from wild-caught females brought into the greenhouse to lay eggs and then released back into the wild as adults. When the eggs hatched, we allowed first instar caterpillars to crawl onto potted *C. mitchelliana* plants in screened captive rearing enclosures. We measured the height above soil level for 20 caterpillars of each species twice a week for four weeks. To test for differences in foraging behavior height, we used a two-way ANOVA with a species*date interaction term to account for differences in foraging behavior as caterpillars develop. Caterpillar heights were square-root transformed to meet ANOVA assumptions. These experiments were done in the greenhouse at Ft. Bragg which is programed to replicate outside environmental conditions.

Caterpillar microhabitat

We measured the sedge canopy above captive St. Francis' satyr and Appalachian brown caterpillars in arenas as a measure of how likely a caterpillar is to be shaded by sedges. We did this by dropping a pin through the sedges to the location of each caterpillar and counting the number of sedge blades that contacted the pin above the caterpillar's location. As with height data, we collected sedge canopy on 20 caterpillars of each species twice a week for four weeks. To compare sedge canopy above the two species, we totaled the number of individuals counted with zero, one, two, three, and four hits above them on the pin for each species across all eight surveys. We used a chi-square test to test for differences between sedge canopy cover experienced by St. Francis' satyrs and Appalachian browns.

Appalachian Brown Population Surveys

We began counting Appalachian Brown butterflies mid-summer 2014. Appalachian Brown counts were recorded alongside Saint Francis Satyr counts during daily surveys in the second flight period. Surveys occurred at both historic and restoration sites for Saint Francis Satyr and consisted of transect walks through each 30x30m plot of each site. The daily counts were converted into Pollard-Yates counts by summing the weekly average of the daily counts.

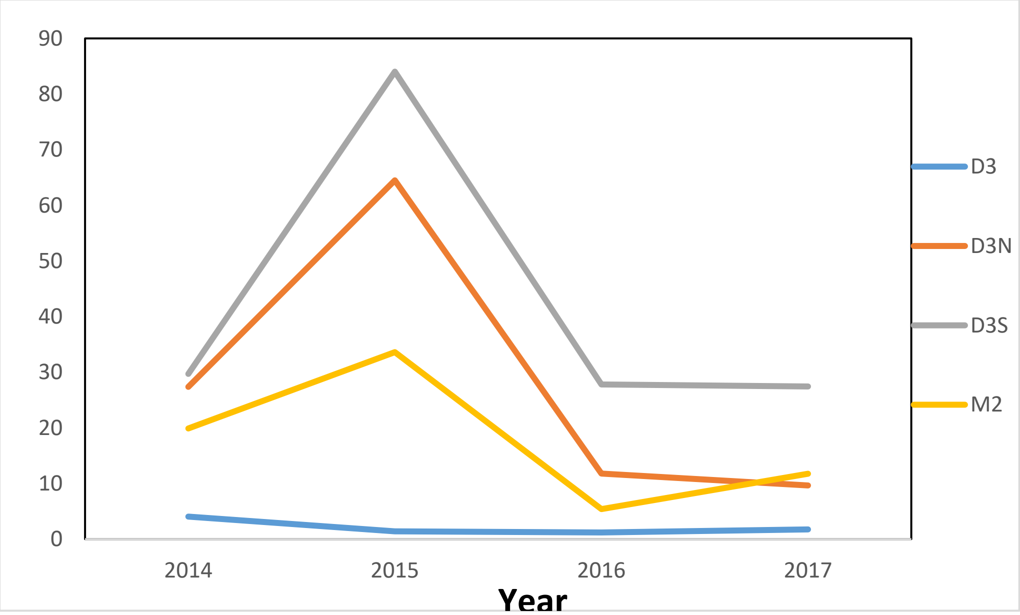


Figure 3.2.5-1 Second flight period Pollard-Yates counts for Appalachian Brown butterflies from 2014-17 at a historic Saint Francis Satyr site (D3) and three habitat restoration sites (D3S, D3N, M2). Because the area of the sites surveyed expanded over time due to habitat restoration, the PY counts have been standardized to an area equivalent to 3 30x30m plots.

Refining ABB egg survival and population growth rate

In summer 2015, we measured population growth rates in the four treatments by releasing female Appalachian browns into field arenas, allowing their offspring to develop in arenas, and collecting the adult offspring that emerged from arenas. Each arena consisted of a 35cm tall section of a 57cm diameter polyethylene drum sunk 10cm into the wetland around naturally occurring *Carex mitchelliana*. A 1.5-meter tall PVC frame allows us to enclose arenas with mosquito netting while maintaining space around the plants for butterfly flight. Female butterflies were kept in areas for two days before they were released back to the site from which they were collected. We then opened all arenas while eggs and caterpillars developed, closing them again once pupae were observed. We then visited arenas daily, recording and releasing all adults that emerged. In each experimental treatment, we deployed four arenas for a total of 16 per site. We did this at both M2 and D3S.

To estimate egg survival, we followed the fate of individual eggs laid by female butterflies in the field arenas. To do this, we searched for eggs at the time of the female's release, inspecting the plants without moving the vegetation and making detailed notes on the position of each egg we could find. We then re-visited arenas daily, recording the status of each of these eggs until they had all hatched, disappeared, or it was obvious they would never hatch. This strategy allowed us to estimate egg survival in-situ without having to transport eggs from the greenhouse to the field. It also had the advantage of allowing females to choose egg locations, although this was somewhat constrained by the enclosure and the vegetation contained within.

To analyze egg survival, we used generalized linear mixed models with binomially distributed errors. We included site (2 levels), the two restoration treatments, and flight period as fixed effects and considered plot and corral as random factors, to account for the repeated measures across flight periods for the same plots and corrals (nested within plot). A model with site and a three-way interaction between flight period, cut treatment, and dam treatment and both random factors failed to converge, so we next tried a model with site plus all two-way interactions between flight period and cut and dam treatment; none of the two-way interactions were significant, and the variance among plots was close to zero. Hence our final model contained main effects of site, flight period, cut treatment, and dam treatment, and a random effect of corral.

3.2.6 Implementation of SEIBMS hardwood removal/ inundation

For the rare and federally endangered Saint Francis satyr (*Neonympha mitchellii francisci*) butterfly, sedge-dominated wetlands at intermediate successional stages are known source habitat that support robust growing populations (Kuefler et al. 2008, Cayton et al. 2015). These wetlands typically occur within riparian forest corridors, which contain some of the same sedge species found in source wetland habitat, and upon which St. Francis satyrs rely for oviposition and larval food sources. But these sedge species occur at lower densities in riparian forest corridors than in source wetland habitat. While butterflies may oviposit eggs on the sedges within riparian forest, our observations indicate that these forest habitats are unable to sustain populations. Thus, if oviposition does occur within riparian forests, it would be considered sink habitat for St. Francis satyrs. Since the primary management strategy for recovering St. Francis satyr populations is to use tree removal and stream damming within the riparian corridor to restore or create new wetland habitat (Cayton et al. 2015), understanding how riparian habitats might impact populations occupying adjacent wetland habitat, whether they act as sinks or not, is important for the success of restoration efforts. In addition, since riparian corridors often connect wetland habitats to each other, understanding the role they play in facilitating connectivity and contributing to range expansion, will be critical to the effort to rebuild a viable interconnected SFS metapopulation that is resilient to disturbance and changing climatic conditions.

Much theoretical work has been done to assess the role sink habitat plays in population dynamics, but the findings indicate divergent roles depending on a wide variety of factors, demonstrating the context-specific effects of sink habitat (Himes Boor et al. in prep). To explore the specific role of sink habitat for St. Francis satyrs on Fort Bragg, we developed a spatially explicit individual-based model (SEIBM) using Netlogo v.5.2.1 (Wilensky 1999) and parameterized it using a combination of empirical data movement and demographic data and pattern-oriented modeling (see section 3.2.7 below). The SEIBM simulates movement and demography of individual SFS over multiple generations within a landscape representative of the areas on Ft. Bragg occupied by two sub-populations of SFS.

The simulated landscape in the SEIBM is composed of 30m x 30m grid cells characterized as one of the following habitat types: wetland, riparian forest, upland forest, and open areas (including grasslands and developed areas). Open and upland forest are matrix habitat through which butterflies move but do not reproduce (i.e., do not oviposit eggs) due to the absence of sedges. Wetland patches serve as source habitat in which reproduction occurs and populations are generally stable or growing. Riparian forest is, depending on the simulation, either matrix habitat with no reproduction, or sink habitat in which reproduction can occur but at non-self-sustaining levels.

3.2.7 Model validation and simplification hardwood removal/inundation

The SFS SEIBM is parameterized using empirical demographic and movement data gathered from SFS, and a surrogate species. Because of St. Francis satyr’s endangered status and rarity, direct handling and experimental manipulations are generally precluded. Therefore, when no SFS data were available to parameterize the model, we used data from the Appalachian brown butterfly (ABB), which occupies similar habitats, has a similar life history, and has been shown to be a suitable surrogate species for St. Francis satyr movement (Hudgens et al. 2012). Details on parameter values used in the model and their empirical source can be found in Hudgens et al. 2012 and Himes Boor et al. (in prep).

To parameterize the butterfly movement portion of the SFS SEIBM we used data from multiple empirical studies that estimated flight distances, turn angles, and resting frequency and duration primarily from ABB. As simulated butterflies move around the landscape, they encounter habitat boundaries where they must choose to cross out of one habitat into another. Inclusion of boundary crossing behavior has previously been found to be an important element in the accuracy of SFS SEIBMs (Hudgens et al. 2012). To parameterize the habitat boundary crossing probabilities, we used a combination of empirical data from one study of St. Francis satyr movement that measured the likelihood of butterflies crossing from wetland habitat into forest habitat (Hudgens et al. 2012 Appendix), and another study of Appalachian brown butterfly (Kuefler et al. 2008) for all other boundary crossing probabilities. Similarly, empirical oviposition rates were not available for SFS or ABB, so we adjusted the oviposition rates used in the model until we achieved growth rates in each colony that matched empirical growth rates. In this way, our model is able to emulate empirical individual behavioral patterns (e.g., colony wetland residence times) and empirical population-level patterns (e.g., growth over time). Previously conducted model simplification exercises revealed that models that included detailed movement behavior (e.g., turning angles and move distance) and boundary crossing behavior performed better than simpler models parameterized solely with mean dispersal distances (Hudgens et al. 2012). The benefit of the increased complexity was especially pronounced when simulations were conducted over broader spatial extent that included more varied habitat. As a result, our final model included the full complexity of fine-scaled movement behavior and boundary-crossing behavior.

3.2.8 Scenario Analysis hardwood removal/ inundation

We used the model to compare five primary metrics with and without the possibility of butterfly reproduction in riparian forests (i.e., presence and absence of sink habitat) in two areas of Fort Bragg that currently support SFS populations. The metrics included total population abundance and variability, population growth rate, mean and maximum dispersal distances. In those scenarios with sink habitat, oviposition occurred in extant colony wetland habitat at empirically based rates, and at lower levels within riparian forest habitat. We tested two levels of oviposition rate in riparian habitat, one based on an assumption of 10% sedge cover in riparian habitats and the other on an assumption of 5% sedge cover. We determined the oviposition rate at these sedge cover levels by fitting a second-degree polynomial function to the oviposition rates at the eastern and western colonies, which have 30$ and 15% sedge cover respectively, and assuming zero oviposition probability at 0% sedge cover. We confirmed via simulation that the estimated oviposition rates in riparian habitat produced declining populations in the absence of source (wetland) habitat. In those simulations in which no sink habitat was present, riparian forests acted as matrix habitat and oviposition was only allowed within extant colony wetland habitat.

In addition to presence and absence of sink habitat, we also varied the total amount of wetland to the landscape by adding restored habitat in two sizes and at two distance from extant colony wetland habitat. At each extant colony on Fort Bragg we ran simulations with no additional restored wetland, and additional restored habitat at 60% and 100% of extant habitat. The restored wetlands were placed within the riparian corridor adjacent to or at 600m away from extant wetland colony habitat. Empirical growth rates at the two extant colonies (East and West) are markedly different; thus by conducting simulations at the two colony sites, we were also able to assess how the presence and absence of sink habitat impacts a population under different source population conditions. The eastern population is growing rapidly, and our simulated populations mimicked this rapid empirical growth. The western population has been slowly declining over multiple years; we simulated populations that mimicked this slow decline (thus, he "source" population was not technically a "source"), but we also ran simulations in which we increased oviposition rates in the western wetland colony patches to produce slow growth within the source population (see Table 3.2.8-1 for a summary of all scenarios assessed).

Table 3.2.8-1. Scenarios explored in the SFS SEIBM

Aspect of Model Varied in Different Scenarios	**Variation 1**	**Variation 2**	**Variation 3**
Sink Habitat	Present (oviposition allowed in riparian habitat)	Absent (oviposition not allowed in riparian habitat)	
Source population growth rate	Rapid growth (Eastern colony - empirical)	Slow decline (Western colony - empirical)	Slow growth (Western colony – not empirical)
Sink Habitat oviposition rate	Moderate (assuming 10% sedge cover)	Low (assuming 5% sedge cover)	
Amount of Source Habitat	Extant	Extant + 60% more restored	Extant + 100% more restored
Contiguity of source habitat	Contiguous	Extant and restored separated by 600m	

3.3 Taylor’s Checkerspot/ Baltimore Checkerspot hostplants & herbicides

3.3.1.1 Monitoring movement and demography: hostplants

We conducted fieldwork on the Baltimore checkerspot butterfly at an ~11.5-ha study site of conservation land in the town of Harvard, Massachusetts, USA (Figure 3.3.1.1-1). This site included ~2 ha of host plant habitat, and ~8 ha of open meadows with nectar plants. In our population, butterflies regularly oviposited on both host plant species, and nectared on a variety of wildflowers in open meadows.

<u>Demography: Larval survival</u>

We measured post-diapause (i.e., spring) larval survival to eclosion as adults on each host plant by collecting individuals in the early spring 2012 and 2013 and rearing them in 60 × 60 cm insect enclosures set-up over unoccupied *C. glabra* or *P. lanceolata* (four post-diapause larvae in each of 10 *C. glabra* and 12 *P. lanceolata* enclosures in 2012, and five post-diapause larvae in each of 14 *C. glabra* and 14 *P. lanceolata* enclosures in 2013). In 2012, the population was very small and all larvae were originally found in host plant patches of *C. glabra*; enclosures depleted of host plant were removed from the study. In 2013, larvae were moved to enclosures from patches of both *C. glabra* and *P. lanceolata* in a crossed design, following Bowers et al.’s design for estimating larval survival in the laboratory (1992). Enclosures at risk of depletion were supplemented with the host plant over which they were placed. We estimated overwinter survival from winter 2013 to spring 2014 on each host plant by setting up cages of wire and tulle fabric around inactive pre-diapause nests in mid-fall 2013 (9 *C. glabra* cages and 10 *P. lanceolata* cages). We monitored cages two-three times per week in spring 2014, counting and removing post-diapause larvae when they were at about the same stage as the start of post-diapause larval monitoring the previous years. All cages contained sufficient host plant growth so no supplementation was necessary.

Demography: Female daily adult survival, population size, and individual mass

We used a capture-mark-recapture study of adult butterflies to estimate daily survival of females eclosed from *C. glabra* or *P. lanceolata* insect enclosures in 2012 and 2013, and to estimate population size of wild-caught adult females in 2012, 2013, and 2014. We marked the wings of adults with a unique color combination of 3–5 dots using metallic gel pens, and surveyed the entire site for new individuals and recaptures several times per week from the late June until no more butterflies were observed in the field (mid-July to early August depending on the population size). As a proxy for fecundity, we used a digital scale to measure body mass of all adult females upon removal from insect enclosures in 2012 and 2013.

Demography: Number of nests, nest size

In the late summer/early fall of 2013 and 2014, we estimated the number of nests laid by adult females on *C. glabra* and *P. lanceolata* using a mark-resight study. We searched for nests on both host plants across the entire site on five occasions, marking newly sighted nests close to the ground with an inconspicuous tag, and recording resights of already marked nests. We estimated the number of prediapause larvae per nest in the late summer/early fall 2013 and 2014 by making a small opening in a portion of nests (63 in 2013, 92 in 2014) and counting the number of individuals in each nest to the nearest ten from 2 to 5 times (to minimize nest disturbance) over 5–10 occasions.

Movement

We quantified movement behavior by mapping individual flight paths in low and high quality habitat cover classes and in open and forest matrix, and by releasing butterflies at forest edges. For all movement studies, we marked butterflies' wings with unique combinations of colored dots to avoid observing the same individual twice. We followed only mated female butterflies, identified by a mating plug on the ventral side of the abdomen (Dickinson and Rutowski 1989). Prior to mapping flight paths, we netted butterflies and held them in spacious, shaded net cages. Upon release in different land cover types, we recorded location and behavior (e.g., basking, flying) every 15 s for 90 min or until 40 unique locations were recorded; these data were used to calculate move lengths (distance in meters), turning angles, and move times (see Turchin 1998). For edge-release experiments, we followed Schultz (1998) and Kuefler et al. (2010) and released mated female *E. phaeton* butterflies at seven forest–meadow interfaces with straight edges. We recorded the location of each released butterfly as forest or meadow once it had moved >15 m from the release location. In addition, we measured host plant preference at the 'soft' edge boundary between open habitat and matrix patches to determine if the presence of host plants was likely to influence movement at structurally similar edges. We released 26 butterflies at the edge between a 10 × 2 *C. glabra* patch and open matrix, and recorded whether the butterflies moved towards or away from the host plant patch once they had moved >2 m from the release point.

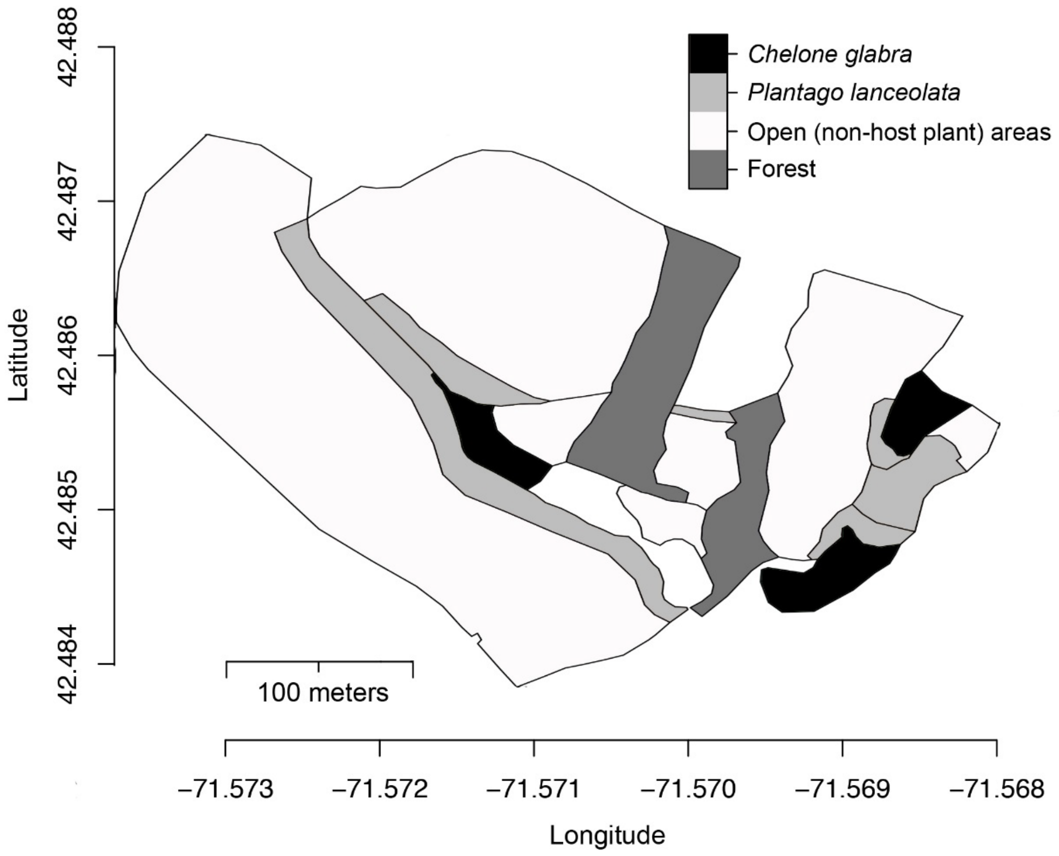


Figure 3.3.1.1-1. Map of site and areas covered by *C. glabra* and *P. lanceolata*.

3.3.1.2 Statistical analysis: hostplants

We conducted all statistical analyses using in R (R Core Team 2015), JAGS (Plummer 2003), and Program MARK (White and Burnham 1999), and using the R packages ‘lme4’ (Bates et al. 2015), R2jags (Su and Yajima 2015), and unmarked (Fiske and Chandler 2011).

<u>Hostplant-specific demography</u>

We estimated demographic parameters for calculating host plant-specific population growth rates using generalized linear models and mixed effects models (GLMs and GLMMs; including a random effect of enclosure to account for variation in microsite or other effects that might influence larval survival estimates), and using methods for analyzing capture-mark-recapture/resight and unmarked population data (Table 3.3.1.2-1). From these models we obtained the host plant-specific values for post-diapause survival, ϕ_1, overwinter survival, ϕ_2, larvae per nest, l, female adult mass, m, and female daily adult survival, ϕ_3, and population-level values for the number of nests, n, and number of adult females, N (Figure 3.3.1.2-1). We inferred population-level oviposition preference for *C. glabra* or *P. lanceolata* by testing whether the proportion of nests found on each type of host plant differed from the proportion of area occupied by a given host at our site, i.e., ~0.3 for ~30% host plant cover of *C. glabra* (*C.g.*) and ~0.7 for ~70% of host plant cover of *P. lanceolata* (*P.l.*). We used the upper and lower confidence intervals (CIs) of the number of nests estimated to estimate upper and lower confidence intervals of the proportions (e.g., $C.g.^{\mathrm{uppCI}}=C.g.^{\mathrm{uppCI}}/(C.g.^{\mathrm{uppCI}}+P.l.^{\mathrm{lowCI}})$ and $C.g.^{\mathrm{lowCI}}=C.g.^{\mathrm{lowCI}}/(C.\ glabra^{\mathrm{lowCI}}+P.l.^{\mathrm{uppCI}})$.

We used parametric bootstrapping of parameter values obtained as shown in Table 3.3.1.2-1 to estimate host plant-specific population growth rates as $\lambda = \phi_1 \times \phi_2 \times \frac{n}{N} \times l \times m^*$. Here, a value of $\lambda = 1$ indicates an annually stable (not growing or declining) population, $\lambda = 2$ indicates a population doubling annually, and $\lambda = 0.9$ indicates a population declining by 10% annually (see Gotelli 2001). In our formula, m^* is a body mass correction for n/N, assuming fecundity is proportional to body mass to allocate the proportion of total nests per adult relative to the body mass of adults reared on *C. glabra* (*C.g.*) versus *P. lanceolata* (*P.l.*), where $m^*_{C.g.} = \frac{2\times m_{C.g.}}{m_{C.g.}+m_{P.l.}}$ and $m^*_{P.l.} = \frac{2\times m_{P.l.}}{m_{C.g.}+m_{P.l.}}$. Given that post-diapause larval survival and the number of nests per adult varied across years, we estimated host plant-specific population growth rates (λ_{hp}, corresponding to parameters for *C. glabra* or *P. lanceolata*) as:

$$\lambda_{hp} = \left[\left(\phi_{1_{hp2012}} \times \phi_{2_{hp}} \times \frac{n_{2013}}{N_{2013}} \times l_{hp} \times m^*_{hp}\right)\left(\phi_{1_{hp2013}} \times \phi_{2_{hp}} \times \frac{n_{2014}}{N_{2014}} \times l_{hp} \times m^*_{hp}\right)\right]^{\frac{1}{2}}$$

The equation above distributes all nests equally among females reared on both hosts. Because adult survival differed somewhat among hosts (albeit non-significantly at the 0.05 level; Table 3.3.1.2-1), an alternative assumption could be that oviposition probability is proportional to life span, and therefore increases with survival. Therefore, we estimated an alternative $\lambda_{C.g.}$ and $\lambda_{P.l.}$ by correcting for differences in survival of adult females reared on the two host plants. We converted daily survival rate into mean days (d) survived as $d_{C.g.} = \frac{1}{1-\phi_{3_{C.g.}}}$ and $d_{P.l.} = \frac{1}{1-\phi_{3_{P.l.}}}$, survival corrected for fecundity as $\phi^*_{3_{C.g.}} = \frac{2 \times d_{C.g.}}{d_{C.g.}+d_{P.l.}}$ and $\phi^*_{3_{P.l.}} = \frac{2 \times d_{P.l.}}{d_{C.g.}+d_{P.l.}}$, and λ^*_{hp} as:

$$\lambda^*_{hp} = \left[\left(\phi_{1_{hp2012}} \times \phi_{2_{hp}} \times \frac{n_{2013}}{N_{2013}} \times l_{hp} \times m^*_{hp} \times \phi^*_{3_{hp}}\right)\left(\phi_{1_{hp2013}} \times \phi_{2_{hp}} \times \frac{n_{2014}}{N_{2014}} \times l_{hp} \times m^*_{hp} \times \phi^*_{3_{hp}}\right)\right]^{\frac{1}{2}}$$

We estimated confidence limits for host-specific population growth rates by parametric bootstrapping. To do so, we generated 10,000 values of each host plant-specific or population-level component of λ by sampling from a normal distribution with the mean and standard deviation of the transformed estimates (Table 3.3.1.2-1), and back-transforming these 10,000 values to calculate λ. We estimated means and confidence intervals for λ_{hp} and λ^*_{hp} from their respective 10,000 estimates.

We evaluated how respective differences in post-diapause larval survival, overwinter larval survival, number of larvae per nest, adult female mass, and adult survival on the native host plant, *C. glabra*, versus the nonnative host plant, *P. lanceolata*, affected population growth rates. To do so, we recalculated λ values for the native host plant, *C. glabra*, by replacing each of the above vital rates on *C. glabra* in turn with the value estimated for *P. lanceolata* (i.e., a Life

Table Response Analysis, LTRE; Caswell 2001). We did not do this for number of nests on *C. glabra* versus *P. lanceolata* per adult since the total number of nests per adult was combined in our formula. For consistency, we evaluated the results of these substitutions for values of both λ (without including differences in adult survival) and λ^* (including differences in adult survival).

Movement: Parameter estimation for minimum patch size model

To estimate movement parameters for our analytical calculation of minimum patch size, we bootstrapped over individual flight paths with at least 4 moves (N_{paths}=22, mean moves=28, max. moves=39) to calculate the average move length, squared move length, cosine of turning angle, and time per move, following Turchin (1998). We calculated the asymptotic per-move increase in squared displacement, $\bar{R}_n^2$, and the diffusion coefficient, D, using the standard correlated random walk approach (Kareiva and Shigesada 1983, Schultz 1998, Turchin 1998). We calculated confidence limits for $\bar{R}_n^2$ and D by sampling entire paths with replacement for 1000 iterations. We sampled paths rather than moves to account for variation among individuals while maintaining correlation among parameters within individuals. We compared predicted $\bar{R}_n^2$ to observed displacements by calculating the mean squared displacement for all pairs of steps within each path, back-transforming to net displacement and taking the mean and standard deviation across individual butterflies (Turchin 1998).

We evaluated the assumption that movement followed a correlated random walk in our population with our capture-mark-recapture data. We compared the distance and time between relocations of marked adult females, with the expectation that squared distance should increase linearly with time (Turchin 1998; $d^2=4Dt$), where d^2 is the squared distance between sequential capture locations and t is the time interval between captures (in days). We regressed d^2 against t

to test the expectation that the intercept of this relationship did not differ from 0 and used the slope coefficient of a 0-intercept model as an estimate of 4*D*. We used flight time per day to convert *D* in square meters per day to square meters per second. Our observations indicated that butterflies flew mostly from the hours of 1000-1500, as these were the earliest and latest times we could collect flight path data. About 80% of days had suitable conditions for flight—others were too rainy or very hot and humid—yielding an estimated 4 flight hours/day. We used 5 flight hours/day as an upper limit (i.e., movement on all days including rainy ones) and 2 flight hours/day as a lower limit (i.e., the time needed to make observations from flight paths and mark-recapture match exactly).

Host-plant specific movement: Parameter estimation for SEIBMs

To estimate movement parameters for SEIBMs, we estimated mean move length, m, cosine of the turning angle, ρ, probability of resting, P, and time spent resting, τ (e.g., if a transition between two points took more than 15 seconds, the interval at which the movement data were collected, any additional time beyond the 15 seconds is time that was spent resting at the first of the two points), using GLMMs. We included individual butterfly ID as a random effect in all models. For models estimating the time spent resting, we also included a unique identifier for each move (pooled across all butterflies) as a random effect to account for overdispersion (Elston et al. 2001); this model fit the data better than a model with butterfly ID alone as a random effect (χ^2=7576, df=1, p<0.001).

In mixed-effects models, the back-transformed fixed effect coefficients are a biased estimate of the true population means (Jensen's inequality; Ruel and Ayres 1999, Bolnick et al. 2011, Crone 2013). We estimated ‘unbiased’ means of back-transformed parameters by sampling from a normal distribution with the link-function scale MLE coefficient and among-individual standard deviation from GLMMs (described in Crone 2013). We back-transformed the samples and calculated means, variances, and coefficients of variation of the back-transformed values. We estimated preference at forest edges initially by fitting GLMMs with open habitat or matrix land cover type as a fixed effect, final location (open vs. forest) as the dependent variable, and release location as a random effect. Given non-significant effects of the different open cover types, we tested whether the overall proportion of butterflies entering the forest versus meadow differed from 50% using an intercept-only binomial GLMM (i.e., to compare the mean proportion with 0.50, or 0 on a logit scale). We tested for host plant preference at 'soft' edges between host plants and open matrix and using a binomial GLM.

Table 3.3.1.2-1. Parameters used to calculate habitat-specific growth rates, and models for estimating parameters from data collected between 2012 and 2014.

Parameter; dates collected	Statistical model	Means, standard errors, confidence intervals *Chelone glabra*	 *Plantago lanceolata*
Post-diapause (spring) larval survival, ϕ_1; spring 2012 & 2013	Binomial GLM with post-diapause host plant and year as factors: effect of enclosure location (χ^2=4.89, *df*=1, p<0.05) and year (χ^2=17.16, *df*=1, p<0.0001); including larval origin (i.e., host plant from which larvae were collected) as a fixed effect or enclosure ID as a random effect in a GLMM did not fit the data better (Bates *et al.* 2014; Brown & Crone 2016)	2012 Logit-link mean (SE): -0.000 (0.316) 2012 Back-transformed mean (95% CI): 0.500 (0.349-0.651)	2012 Logit-link mean (SE): -0.423 (0.295) 2012 Back-transformed mean (95% CI): 0.396 (0.266-0.537)
		2013 Logit-link mean (SE): 1.386 (0.299) 2013 Back-transformed mean (95% CI): 0.800 (0.646-0.882)	2013 Logit-link mean (SE): 0.588 (0.249) 2013 Back-transformed mean (95% CI): 0.643 (0.527-0.749)

Overwinter (fall to spring) larval survival, ϕ_2; fall 2013-spring 2014	Poisson GLMM with post-diapause larval count as response, and offset of log-transformed pre-diapause nest count (Brown & Crone 2016); including enclosure ID as a random effect was a better fit to the than a Poisson GLM	Log-link mean (SE): -1.292 (0.288) Back-transformed mean (95% CI): 0.275 (0.147-0.492)	Log-link mean (SE): -0.587 (0.265) Back-transformed mean (95% CI): 0.556 (0.318-0.971)
Adult female daily survival, ϕ_3; summer 2012 & 2013	CJS model implemented in R2jags, best model for estimating survival on both host plants included effect of year on recapture but not survival probability (recapture rate was higher in 2012 when the population was smaller; Kéry & Schaub 2012; Brown & Crone 2016)	Mean (SE, 95% CI): 0.780 (0.040, 0.697-0.853)	Mean (SE, 95% CI): 0.845 (0.034, 0.773-0.907)
Adult female population size, *N*; summer 2012, 2013 & 2014	Gross population estimates (N*-hat) from POPAN module in Program MARK; in models for all years, recapture probability differed by capture occasion, entrance parameter was constant; in 2012 best model, survival declined linearly with time in best model; in	Means (SEs, 95% CIs) 2012: 45 (5, 36-57) + 20 females from insect enclosures = 65 total (wild caught + enclosure reared) 2013: 222 (30, 171-289) + 34 females from insect enclosures = 256 total (wild caught + enclosure reared) 2014: 1202 (95, 1030-1402) (all wild caught)	

	2013 and 2014 best models, survival was constant across time (White & Burnham 1999)		
Adult female body mass, *m*; summer 2012 & 2013	LM with weak effect of post-diapause larval host plant on adult mass ($\chi^2=2.83$, $df=1$, $p<0.10$); no effect of larval origin or year; including enclosure ID as a random factor in a LMM did not improve model fit (Bates *et al.* 2014)	Mean (SE, 95% CI): 0.328 (0.010, 0.309-0.347)	Mean (SE, 95% CI): 0.304 (0.011, 0.282-0.326)
Number of nests, *n*; late summer 2013 & 2014	Closed population model with memory effects implemented in R2jags, where probability of finding a next in time *t*+1 differed if the nest was seen in time *t* (Kéry & Schaub 2012; Brown & Crone 2016)	2013 Mean (SE, 95% CI): 26 (1, 25-28) 2014 Mean (SE, 95% CI): 34 (4, 28-45)	2013 Mean (SE, 95% CI): 50 (8, 40-70) 2014 Mean (SE, 95% CI): 248 (28, 203-313)
Number of pre-diapause (fall) larvae per nest, *l*; late summer/early fall 2013 & 2014	Open population model, 'unmarked' package in R, with 0 recruitment and constant dynamics; best model included varying detection by plant and by year; including survival effect in model fit the data better than a closed model that only estimates abundance and detection (Fiske & Chandler 2011)	Log-link mean (SE): 4.54 (0.033) Back-transformed mean (95% CI): 94 (88-100)	Log-link mean (SE): 4.96 (0.027) Back-transformed mean (95% CI): 143 (135-150)

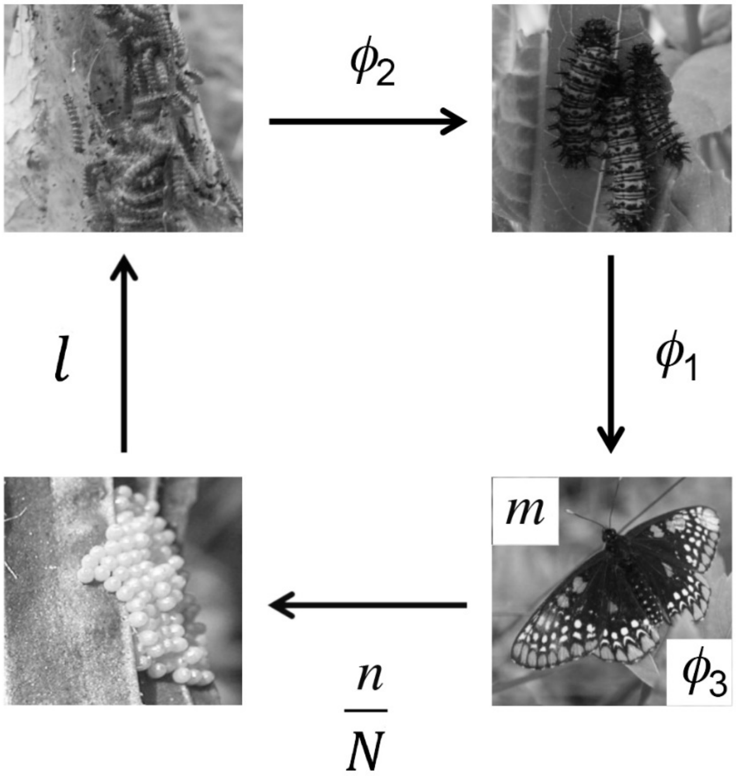


Figure 3.3.1.2-1. Life cycle of *E. phaeton*, illustrating parameters used to estimate population growth rates: post-diapause (spring) larval survival, ϕ_1, overwinter (fall to spring) survival, ϕ_2, adult female survival, ϕ_3, adult female mass, m, adult female population size, N, number of nests, n, and number of pre-diapause (fall) larvae per nest, l.

3.3.2 Experimental tests & analysis: herbicides

Study Species and System

Euphydryas species are mostly univoltine (Pyle 2002; James and Nunnallee 2011); and oviposit in spring and summer, depending on the species and location (White and Singer 1974; Moore 1989). Eggs hatch after 10 to 14 days and the gregarious larvae build webbed nests and feed through three to four instars before entering diapause. Larvae diapause as large groups in webbed nests, in small groups in leaf litter, or solitarily in leaf litter. Post-diapause larvae feed through additional instars in small groups or solitarily, after which they pupate briefly and eclose (Bowers et al. 1992; Singer and McBride 2010; James and Nunnallee 2011).

We used *E. phaeton, E. colon* and *E. editha colonia* to investigate consequences of graminicide-based management. We chose these species to represent a range within the genus, and as surrogates to advise habitat management of federally-listed *Euphydryas* species in North America. Both *E. e. colonia* and *E. colon* reside in the same region as endangered *E. e. taylori* and use the same native larval hostplants as other *E. editha*, as well as other *Euphydryas* in western North America (Pyle 2002; James and Nunnallee 2011). Our third proxy, *E. phaeton*, is a well-studied species from eastern North America (e.g. Stamp 1981; Bowers et al. 1992; Brown and Crone 2016). Like the three western at-risk species, *E. e. bayensis*, *E. e. quino* and *E. e. taylori* (Severns and Warren 2008) some populations of *E. phaeton* have switched from a native pre-diapause hostplant to non-native *Plantago lanceolata* (Bowers et al. 1992; Severns and Warren 2008).

Euphydryas larvae use hostplants from several families within the superorder Lamianae, all of which synthesize iridoid glycosides (Bowers 1991; Rimpler 1991). These include plant families in the order Lamiales (Families: Boraginaceae, Buddlejaceae, Orobanchaceae, Plantaginaceae, Scrophulariaceae) and Dipsacales (Families: Caprifoliaceae, Dipsacaceae, Valerianaceae). North American hostplants include non-native species in these plant families including the genera *Lonicera* and *Plantago*, in which *P. lanceolata, P. major* and *L. japonica* are hosts for larval *Euphydryas* (White and Singer 1974; Singer et al. 2008; MDNR 2014; Robinson et al. 2016). Iridoid glycosides are secondary plant compounds that often reduce herbivory in non-adapted insects (Bowers 1991); however, these compounds serve as feeding stimulants in some specialists, such as *Euphydryas*, and, when sequestered, may deter predators (Bowers 1983; Bowers 1991; Wahlberg 2001).

Graminicides

Three post-emergent graminicides are used regularly by land managers for prairie restoration in the Pacific Northwest; fluazifop-p-butyl, clethodim and sethoxydim. These chemicals systemically target active meristematic sites by inhibiting acetyl coenzyme A carboxylase and thus constrain lipid synthesis (Walker et al. 1988). Larval stages of the butterfly life cycle may be most susceptible to direct and indirect non-target herbicide effects through dermal contact, ingestion of herbicide, or reduction in hostplant nutritional quality. For experiments, we used the herbicide formulations most commonly chosen by land managers in Pacific Northwest prairies: fluazifop-p-butyl as Fusilade DX® (24.5% fluazifop-p-butyl, Syngenta Crop Protection LLC, Greensboro, North Carolina), sethoxydim as Poast® (18% sethoxydim, BASF Corporation, Research Triangle Park, NC) and clethodim as Envoy Plus® (12.6% clethodim, Valent Corporation, Walnut Creek, CA). These chemicals are applied in combination with a "sticker-spreader" to increase efficacy. In all graminicide treatments, we use adjuvant NuFilm IR ® (96% poly-1-p- menthene, Miller Chemical and Fertilizer Corporation, Hanover, PA).

Experiments

To test for the effects of graminicides on *Euphydryas* larvae, we conducted two investigations in the Washington State University Vancouver greenhouse. In the first experiment (the "*Graminicide*" experiment), we examine effects of different graminicides on larval survival and chemistry of *E. colon* reared on *Plantago lanceolata*. Although *P. lanceolata* is a non-native hostplant, it is the lone hostplant species used by all three *Euphydryas* species. In the "*Species x*

Hostplant” experiment, we measured a number of demographic and behavioral responses to a single graminicide for three *Euphydryas* species reared on different host plants. In this second experiment, we used microcosms constructed of 37.8 litre nursery containers potted with either native hostplants (*Chelone glabra* for *E. phaeton*, *Castilleja hispida* for *E. e. colonia* and *E. colon*) or novel hostplant *P. lanceolata*. We used *Eriophyllum lanatum* [Compositae] as a host for hemiparasitic *C. hispida* and therefore we included it in novel host (*P. lanceolata*) microcosms for *E. colon* and *E. editha* to control for its presence.

For both experiments, we collected eggs from females caught in the wild from montane areas of Washington State for *E. colon* and *E. editha* (Yakima County, WA, 46.71 N, -121.11 W), and from egg clusters collected in the wild in Massachusetts (Worcester County, MA, 42.48 N, -71.57 W) for *E. phaeton.* In both experiments, we reared caterpillars to second instar on *P. lanceolata* to ensure all larvae received the same nutritional opportunity prior to treatment. On treatment day, we weighed each larva and randomly assigned to a treatment. Given that colonies often merge in the wild, and benefits of gregariousness seem based primarily on group size rather than relatedness (Moore 1989; Costa and Ross 2003; Ehrlich and Hanski 2004), mixing families is unlikely to influence experimental outcome. We sprayed plants and larvae using a Precision backpack sprayer (RandD Sprayers, Opelousas, Louisiana) with a flat fan 8002VS nozzle and CO_2 propellant (276kPa) at the manufacturer’s recommended field rates. Larvae were given unlimited food until they entered diapause, which was determined by absence of feeding for two days.

Graminicide Experiment

In the *Graminicide* experiment, we applied five treatments to 200 2nd instar *E. colon* larvae (40 individual larvae per treatment) on August 12, 2014. Treatments included three graminicides each combined with NuFilm adjuvant: fluazifop-p-butyl, sethoxydim and clethodim. In addition, we conducted a water treatment and a treatment with just NuFilm. Graminicides were applied per manufacturer recommended rates: 7.5 mL fluazifop-p-butyl with 3.9 mL NuFilm per 1000 mL distilled water; 15.0mL sethoxydim with 3.1mL Nufilm per 1000 mL distilled water; and 5.04 mL clethodim with 2.25mL Nufilm per 1000 mL distilled water. In the NuFilm only treatment, we mixed 3.9 mL of NuFilm per 1000 ml distilled water. Larvae were exposed individually and separately from the hostplant, with the same equipment and rate. Larvae were weighed prior to experimental treatment, and then placed in individual 60 ml rearing containers for the duration of the experiment. Larvae were fed fresh *Plantago* from the appropriate treatment until they stopped feeding and entered diapause, at which time the date of diapause initiation was recorded and larvae were weighed. Larvae were placed in diapause containers in September following protocols with related diapausing species (Linders, *E. e. taylori*, pers. comm. and Saastomoinen, *M. cinxia*, pers. comm). Five individuals from each treatment were sent to University of Colorado for quantification of iridoid glycosides in December 2014.

Aucubin and catalpol (the iridoid glycosides found in *P. lanceolata* (Bowers and Stamp 1992) are known to be sequestered by *Euphydryas* (Bowers et al. 1992). These were extracted from freshly frozen caterpillars (methods in Bowers et al. 1992) and quantified by gas chromatography (methods in Gardner and Stermitz 1988; Bowers et al. 1992). Quantification was based on calibration with pure aucubin and catalpol coupled with the internal standard phenyl-β-D-glucopyranoside (PBG, Sigma Aldrich) (0.500 mg/sample), that was added to each sample. Wet weights of frozen larvae were converted to dry weights using a separate set of caterpillars that were weighed wet and then dried at 50°C for 48 hours and re-weighed.

Species x Hostplant Experiment

In the second experiment, we applied fluazifop-p-butyl mixed with NuFilm (at the same rates as the *Graminicide Experiment*) to larval three *Euphydryas* species and their hostplant species. All treatments were initiated in August and September 2013, when sufficient numbers of larvae reached 2nd instar to conduct a trial, such that *E. colon* were treated on August 26th, *E. editha* were treated on August 1st and 5th, and *E. phaeton* were treated on August 10th, 31st, Sept 1st and 3rd. Larvae were placed in groups of 20 in each experimental microcosm. We allowed larvae to feed gregariously as they do in the wild; each microcosm contained ample plant biomass to support a cohort of 20 larvae. We replicated the four treatments (graminicide vs control by native vs novel hostplant) six times (except for *E. colon*, which had five replicates) with a 20-larva cohort per treatment group (microcosm). We positioned microcosms randomly in the greenhouse to mitigate unintended biases. We noted survival and made the following behavioral observations daily: (1) how many larvae were solitary or group size if not solitary, (2) whether each larva was actively feeding or not. Larvae were considered part of a group if they were in, on, or within one nest-width from the webbed nest. Because nest sizes were never > 20, we could visually inspect all individuals without damaging webbing. Larvae that stopped feeding and remained within the webbing for more than 48 hours were noted as 'in diapause.' We weighed larvae to determine final (diapause) mass.

Statistical Analysis

We used generalized linear models with mixed effects where appropriate to analyze experimental data. Data were analyzed using 'lme4' package (Bates et al. 2015) in R using (g)lm and (g)lmer functions for models without and with random effects, respectively (R Core Team 2015).

In the *Graminicid*e experiment, we assessed survivorship to diapause using a general linear model with a binomial distribution, logit link and a single fixed effect of Treatment (one of three graminicides, NuFilm, or control). We analyzed development time from treatment date to diapause with a Poisson distribution, a log link and a fixed effect of Treatment. Survivorship and development time did not show evidence of overdispersion in this experiment. We analyzed change in mass from initial to final using a linear model with fixed effects of initial vs final size. We analyzed percent dry weight of aucubin and catalpol using linear models with Treatment as a fixed effect. For analyses in the *Graminicide* experiment, we report χ^2 from Likelihood Ratio Tests for type II χ^2 tests from analysis of deviance. In addition, to test if each treatment was different from the control, we report P-values from Dunnett contrasts for multiple comparisons using R package ‘multcomp’ (Hothorn et al. 2008).

For the *Species x Hostplant* experiment, Exposure (i.e., use of graminicide or not), Species (*Euphydryas* species) and Host (host plant species) and their interactions were included as fixed effects. Treatment date, observation date and microcosm were included as random effects. Microcosm, as a random effect, takes repeated observations of larvae per microcosm into account (experimental block) and observation date, when applicable, accounts for repeated measures (in time). We analyzed survivorship to diapause using a linear model with a binomial distribution and logit link. We analyzed development time from treatment date to diapause with a Poisson distribution and log link; this model included an observation-level random effect to account for possible overdispersion (Elston et al. 2001). For effects of herbicides on change in mass, we used a Gaussian family, identity link effect model with an additional fixed effect of observation date (initial vs. final size). We analyzed gregariousness and feeding behavior using a binomial distribution and logit link. We analyzed the number of larvae per group using a Poisson distribution and log link; we used the total number of grouped larvae as the response variable and the log- transformed number of groups as an offset to estimate the model ratio. This model included an observation-level random effect to account for overdispersion.

3.3.3 Minimum patch size and connectivity

Minimum patch size estimation

The idea of minimum patch area, first proposed by Skellam (1951) and Kierstead and Slobodkin (1953) (collectively KSS's model) provides a mechanistic framework for estimating MAR as a function of movement and demography. In KSS's framework, minimum patch area is modeled using reaction-diffusion equations that describe the change in population density over time and movement is modeled according to a random walk (Cosner 2008). Individuals diffuse out of patches and if a patch is too small, they will leave before reproducing. Accordingly, there is a threshold critical minimum patch size, below which a population cannot persist (Crone & Schultz 2003). Because large patches have lower emigration rates than small patches as a function of size and edge-to-area ratio, patch size predicts residence time (days spent in the patch, sensu Schultz & Crone 2001) and subsequent population growth (Fahrig 2007). We combined KSS's theoretical notion of minimum patch area with field-collected movement and demographic data to analytically estimate the minimum patch size for the Baltimore checkerspot butterfly (*Euphydryas phaeton*, Nymphalidae).

We modified KSS's model to reflect the temporal dynamics of butterfly life histories. Specifically, butterflies move, die, and lay eggs throughout their lives as they encounter host plants, and eggs hatch into relatively immobile larvae that mature over the course of a year (Crone & Schultz 2003). Movement and survival can be modeled with an equation identical to KSS's model, where *r* is the distance of individuals from the patch center, *D* is the diffusion coefficient, and the instantaneous population growth rate is replaced with the instantaneous rate of mortality, μ:

$$\frac{\partial n}{\partial t} = -\mu n + D\frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial n}{\partial r}\right). \qquad [1]$$

The solution for Eq. 1 becomes

$$\frac{n(r,t)}{n(r,0)} = \exp\left[-\left(\mu + D\left(\frac{\beta_1}{R}\right)^2\right)t\right], \qquad [2]$$

where *R* is the patch radius, $\beta_1 \approx 2.41$ (the first 0 of a Bessel function; see derivation in Kot 2001), and *n*(*r*,*t*) describes the population size at time *t* and location *r* (cf. Kot's [2001] Eqs. 16.69-16.70). Equation 2 represents the proportion of animals left in a patch of radius *R* at time, as a function of loss from mortality (*m*) and movement ($D\left(\frac{\beta_1}{R}\right)^2$). The expected residence time as a function of patch radius is

$$\frac{1}{\left(\mu+D\left(\frac{\beta_1}{R}\right)^2\right)} \qquad [3]$$

(i.e., the reciprocal of the rate of loss). The ratio of expected residence time in a patch of radius *R* to the organism's lifespan in an infinitely large patch is

$$\frac{\mu}{\left(\mu+D\left(\frac{\beta_1}{R}\right)^2\right)}. \qquad [4]$$

Reproduction is proportional to the amount of time spent in the patch, so the realized annual population growth rate becomes

$$\lambda = b_{\max}\left[\frac{\mu}{\left(\mu+D\left(\frac{\beta_1}{R}\right)^2\right)}\right], \qquad [5]$$

where $b_{\max}$ is the per capita number of offspring that survive to reproduce in unlimited habitat. The population persists in isolation if $l \geq 1$, and the radius (in meters), R_c, of the CMP is

$$R_c = \beta_1 \sqrt{\frac{D}{\mu(b_{\max} - 1)}} \quad [6]$$

(Kot's [2001] Eq. 16.75).

As in KSS's continuous-reproduction model, R_c increases with D and declines with $b_{\max}$. In our model, R_c also declines as mortality, m increases because we assumed maximum reproductive output is independent of adult mortality. Hence, a species with a shorter lifespan and the same reproductive output reproduces more quickly, allowing it to persist in smaller patches. The model is a conservative assessment of CMP because individuals do not return to a patch after leaving (see mathematical explorations of effects of edge behavior in Ovaskainen 2004, Schultz and Crone 2001 and Xiao et al. 2013). From Eq. 6 the CMP in hectares is $\frac{\pi}{10{,}000} {R_C}^2 = \frac{\pi {\beta_1}^2 D}{(10{,}000)\mu(b_{\max} - 1)}$.

We estimated vital rates and population size estimates from data collected 2013-2014 as described in Section **3.3.2**, but estimated across values for both host plants rather than separately. These values were post-diapause larval survival, ϕ_1 population size, $\hat{N}$, and survival rate, ϕ_3, of adult females; number of larval nests, $\hat{n}$; larvae per nest, $\hat{l}$; and overwinter survival, ϕ_2 (Table 3.3.4-1). We calculated the observed maximum population growth rate as the product of post-diapause survival × overwinter survival × nests per adult × larvae per nest:

$$b_{\max} = \emptyset_1 \emptyset_2 \frac{0.5 \hat{n} \hat{l}}{\hat{N}}, \quad [7]$$

where the 0.5 accounts for an approximately even sex ratio (female offspring per adult female). We calculated confidence limits for $b_{\max}$ with parametric bootstrapping (i.e., sampling over normal distributions defined by the means and standard errors of each model parameter).

Equation 7 is a conservative estimate of $b_{\max}$ because we estimated nests per female in a finite patch. Alternatively, we could assume that the probability of reproduction is proportional to the amount of time spent in a patch; in this case, the observed number of nests, $\hat{n}$, would be the actual maximum lifetime number of nests, $\hat{n}^*$, multiplied by the proportion of an individual's lifespan spent in the patch (from Eq. 4):

$$\hat{n} = \hat{n}^* \left[\frac{\mu}{\left(\mu + D\left(\frac{\beta_1}{R}\right)^2\right)}\right]. \qquad [8]$$

Here, m is the instantaneous (per second) mortality rate of adult females calculated from flight time per day and the daily survival rate, ϕ_3, D is the diffusion coefficient, and R is the patch radius. We used R=183 m for our ~10.5-ha study site and all other parameters as estimated above. We solved for $\hat{n}^*$ with Eq. 8 and calculated $b_{\max}$ and all other derived variables twice, once using $\hat{n}$ as our estimate of nests produced and once using $\hat{n}^*$. Parametric bootstrap confidence limits of variables calculated using $\hat{n}^*$ included sampling distributions for D and ϕ_3 (Table 3.3.3-1).

We evaluated the estimated growth rate by comparing predicted population growth rates (Eq. 5) with changes in abundance at our study site (2012-2014). We calculated the expected population growth rate as $b_{\max}$ (Eq. 7) multiplied by the proportion of time spent in the patch (Eq. 4).

SEIBM implementation

We calculated landscape-scale metrics, specifically residence time of Baltimore checkerspot butterflies in their natal patch and dispersal to [i.e., connectivity] and time spent in a new patch using a spatially-explicit individual-based simulation model built in Netlogo (Wilensky 1999). To do so, we first created a habitat-nonhabitat only simulation model to estimate growth rates, mean residence time (days in patch) and mean dispersal distance. For this habitat-nonhabitat model, we used parameter estimates from GLMMs for demography averaged across host plants as shown in Table 3.3.3-1. In addition to these values, we also estimated the probability of oviposition, *o*, as $\hat{n}/(\widehat{N} \times L)$, where L is the expected lifetime in days. The logit-transformed survival on any given day, *d*, starting at $d = 0$, is $\beta_0 + \beta_1 \times d$. We defined the expected lifetime, L, as the number of days for the inverse-logit transformed daily survival, $\frac{\exp(\beta_0+\beta_1 \times d)}{\exp(\beta_0+\beta_1 \times d)+1}$, to decline to 0.5, i.e., solving for L such that $\prod_{d=0}^{L} \frac{\exp(\beta_0+\beta_1 \times d)}{\exp(\beta_0+\beta_1 \times d)+1} = 0.5$. We re-estimated movement parameters across host plants using GLMMs as described in Section 3.2.2; Table 3.3.3-2).

For our habitat-nonhabitat SEIBM, we ran 1000 5-year simulations for circular habitat patches of 0.1, 0.2, 0.5, 1, 2, 4, 8, 12, 16, 20, 24, 28, 32, 36, and 40 hectares, each with a starting population size of 50; within 5 years, populations either went extinct or grew exponentially. We assumed a season of 28 days based on the earliest to the latest days butterflies were seen at our site in 2012 and 2013, and assumed that individuals were active ~4-flight-hours/day (see Section **3.3.2**). At each time step, individuals in the model lived or died, layed eggs or did not, and moved or rested. The only difference in this model between habitat and nonhabitat was that oviposition occured only in habitat. The logit-transformed survival on any given day and the probability of oviposition were converted to 15-s intervals, the time step at which the model proceeded. Nest size was chosen from a Poisson distribution with a mean of $\hat{l}$, the number of larvae per nest estimated from the field, and multiplied by overwinter survival, post-diapause survival, and 0.5 to model only adult females.

For each individual that lived and was not already resting at a particular time step, we used the per-move probability of resting to determine if it moved or rested. If it rested, the time spent resting was drawn from a Poisson distribution at the beginning of each resting bout, and the individual returned to the “not resting” pool at the end of that bout. For individuals that moved, we modeled movement as a correlated random walk (i.e., the direction, θ, of a move at time t is correlated with the direction at time t–1). We simulated movement direction from a wrapped Cauchy distribution defined as $\theta_t = \theta_{t-1} + 2\arctan\left(\frac{1-\rho}{1+\rho} tan\{\pi[U(-0.5,0.5)]\}\right)$, where the initial direction is randomly chosen from 0 – 2π, and ρ is the mean cosine of the turning angle (Barton et al. 2009). We simulated move lengths from a gamma distribution with parameters α (scale) = μ^2/σ and λ (shape) = μ/σ, where μ and σ are the back-transformed mean and variance of move length (everywhere else in this paper, λ refers to the population growth rate, not the shape parameter).

We calculated statistics based on years 2-5 of simulations because the first year (and resulting population growth rate) was affected by the initial random placement of adults on the landscape. We estimated the annual population growth rate, λ, for each patch size by regressing the population size, N, across model iterations for a particular patch size at time t+1 against the intercept, with an offset of the population size at time t, using a Poisson GLM. We obtained dispersal distances in two ways. First, we recorded the mean dispersal distance across individuals in each of the 1000 simulations per patch size to estimate the distribution of average distances moved across replicate simulations. Second, we quantified the net distance dispersed in a single year by 5000 homogeneous individuals and 5000 individuals with heterogeneity in movement in a 2-Ha patch to describe variation across individuals within a single population.

To add landscape-specific metrics to our habitat-nonhabitat model, we created base maps of structural variation in land cover across our study site from aerial photographs available in ArcMap (2013–2014 orthoimagery from MassGIS 2014). We used aerial photographs to separate forest and open areas on the landscape and manually traced and digitized these areas in ArcMap. We ground-truthed maps by walking the perimeters of open areas on the landscape, and checked that the recorded areas of GPS points based on ground observations matched those of the digitized landscape. We divided open land cover types into habitat and open matrix by estimating the relative density of native and non-native host plants across our site. We surveyed all non-forested land in a regular 50 × 50 m grid, using a compass to follow straight lines. We stopped every ~10 m, and chose a sampling location offset from the main grid by walking a randomly chosen 0–5 paces in a randomly chosen direction (following Holl and Crone 2004). We recorded the distance of the three closest individuals of *C. glabra* up to five meters from the sampling location, and the three closest individuals of *P. lanceolata* up to one meter from the sampling location. The search area for *C. glabra* was larger than for *P. lanceolata* because *C. glabra* are less dense and more conspicuous, so we would not have obtained reasonable estimates of the relative density of *C. glabra* had we restricted the search area to one meter. It would not, however, have been feasible to search for *P. lanceolata* within a five-meter radius from each point in tall grass without trampling butterfly habitat. We estimated relative host plant density *ad hoc* by converting the distance, *d*, of each individual from each sampling location into the area of a circle with radius *d*, taking the reciprocal of the area (defined as zero for cases where there were no additional plants within the search area), and averaging the three numbers for the three individuals of each host plant species. We used spatial interpolation (kriging) of ln-transformed density indices to create a map of plant densities (Figure 3.3.3-1; Kriging tool, ArcMap 10.3, ESRI 2015).

We divided the study area into discrete patches based on estimated host plant densities, and classified these into five land cover classes: (1) high quality *C. glabra* habitat [mean (SD) = 0.03 (0.09) plants/m^2], (2) high quality *P. lanceolata* habitat [mean (SD) = 76.3 (211.1) plants/m^2], (3) low quality habitat, typically areas with at least ~1/10 of the *P. lanceolata* density found in high quality habitat [mean (SD) = 4.9 (32.8) plants/m^2; note there was no low quality *C. glabra* habitat in our study area], (4) open matrix, i.e., non-forested areas lacking host plants, and (5) forest matrix. We created an ~1 km buffer from the central-most point of our ~11.5 hectare study region, and classified most areas outside of our study site as open or forest matrix using aerial imagery as described above. The only exception was a wetland separated by forest ~0.2 km from our study site containing *C. glabra*, that we classified as low quality habitat because preliminary observations suggest that *C. glabra* density in this patch is noticeably lower than in our main study site. This patch has not recently been occupied by Baltimore checkerspots (E. Crone, *pers. obs*) and is the only wetland in the area with *C. glabra* according to our observations and those of local naturalists (members of the Massachusetts Butterfly Club, see Breed et al. 2013, and the local town conservation committee).

We programmed movement parameters in SEIBMs to differ among specified land cover classifications across a landscape representing our study area. Although there was no low quality *C. glabra* habitat within our study area from which to estimate movement in the new patch, we programmed movement in this patch as low quality based on our measurements from low quality *P. lanceolata* habitat, which is reasonable given the similarity in movement parameters between the two host plants in high quality habitat. We included edge behavior at forest boundaries by programming individual butterflies predicted to cross from open to forest areas in simulations to instead randomly turn back with probability 1 – (z/0.5), where *z* is the observed proportion crossing the edge (following Hudgens et al. 2012). Note that this relationship defines the proportion of simulated crossing events that are *not* allowed, not the proportion of crossing events, i.e., the proportion is 0 when z = 0.5. We assigned new moves to butterflies that turned back at edges until a move was generated in which the individual remained in the meadow. There was no preference for the host plant at ‘soft’ boundaries between patches with host plants versus open matrix—the observed preference was exactly even—so we did not include edge behavior at non-forest edges in our simulations. To simplify this SEIBM, and because we were not using it to estimate population growth rates, we excluded demography. All other model assumptions were identical to the simpler habitat-nonhabitat model described above.

We evaluated the consequences of different land cover classification decisions for residence time of Baltimore checkerspot butterflies in their natal patch and dispersal to [i.e., connectivity] and time spent in a new patch by simulating movement based on combinations of four decisions: (1) combined or separate estimates for move lengths and turning angles in high and low quality habitat; (2) combined or separate estimates for move lengths and turning angles in open and forest matrix; (3) combined or separate estimates for resting parameters across habitat/non-habitat types, and (4) inclusion or not of edge behavior. In other words, we separately evaluated the effects of (A) separating movement and resting parameters for all land cover classes versus separating them only when parameters differ significantly, (B) dividing landscapes into only habitat and matrix versus finer categorization within each category, and (C) including preference at patch edges. We based these decisions on several factors. First, we combined or separated movement and resting parameters based on the results of our statistical analysis of movement across land cover classes. Second, classic movement studies often consider only differences among move lengths and turning angles, and assume resting behavior is constant across land cover types (e.g., Kindvall 1999; Schultz and Crone 2001). Finally, edge behavior is not straightforward to estimate from many common kinds of movement data such as GPS tracking and capture-recapture data, so its consequences are not always considered.

For each of 16 movement scenarios, we recorded residence time in the natal patch, the proportion of butterflies that entered the new patch, and residence time in the new patch. For each scenario, we simulated movement in 10,000 adult butterflies randomly placed across the study site within high quality *C. glabra* habitat, high quality *P. lanceolata* habitat, and low quality habitat; 100% of nests in which the gregarious larvae reside occurred in these areas. Preliminary simulations in which adults only emerged from high-quality patches led to qualitatively similar results (*unpubl. data*). We chose 10,000 as a population size large enough to capture the expected range of expected dispersal distances. We treated simulation edges as 'absorbing,' whereby individuals cannot return once they reach the simulation edge (e.g., Reeve et al. 2008) because we observed that fewer than ten percent of simulated butterflies reached the edge of our simulated landscape, and those that approached the edge did not return to our focal study site or the unoccupied patch within the simulation period.

We summarized simulation results using Gamma family inverse-link GLMs for residence times and binomial family logit-link GLMs for the probability of finding the new patch. Individual butterfly was the unit of replication in all models. We summarized data by (1) comparing models in which only one of each of four modeling decisions were altered to results from a 'reference' model based on statistical analysis, and (2) calculating the average value of response variables across all simulation scenarios with or without each of the four decisions.

Table 3.3.3-1. Estimated parameters and derived variables used to evaluate critical minimum patch size for Baltimore checkerspot butterfly persistence.

		95% CI limits		Model for error
Parameter	Estimate[a]	lower	upper	propagation[b]
Flight paths				
m_1, average move length	3.19	2.42	4.06	bootstrap over individual flight paths
m_2, average squared move length	24.7	14.3	38.4	bootstrap over individual flight paths
ψ, average cosine of turning angle	0.331	0.250	0.404	bootstrap over individual flight paths
τ, average time per move	128	89	188	bootstrap over individual flight paths
Demographic model				
$\phi_{\square}$, post diapause larval survival	0.722	0.644	0.806	logit normal, mean (SE) = 0.954 (0.106)
$\phi_{\square}$, overwinter survival	0.500	0.476	0.526	logit normal; mean (SE) = 0.000 (0.026)
$\widehat{N}$, number of adult females	235	195	296	number of wild adults is log normal, mean (SE) = 5.303 (0.122); $\widehat{N}$ is number wild + 34 from bug dorms

$\hat{n}$, number of nests	69	63	78	log normal, mean (SE) = 4.234 (0.027)
$\hat{l}$, number of pre-diapause larvae per nest	150	138	162	log normal, mean (SE) = 0.954 (0.106)
Other parameters				
$\phi_{\square}$, daily survival of adult females	0.844	0.751	0.906	logit normal, mean (SE) = 1.689 (0.297)
s, seconds of flight time per day	4×60×60 = 14,400	2.5×60×60 = 9,000	5×60×60 = 18,000	rough upper and lower bounds (see Results)
β_1, first 0 of Bessel function	2.405	NA	NA	NA
Derived variables				
D, diffusion, calculated from m_1, m_2, ψ, and τ	0.069	0.035	0.116	bootstrap over individual flight paths; approx. as $\sqrt{D}$ ~ normal; mean (SE) = 0.266 (0.039)
μ, mortality per second of flight time, $\mu = 1 - \exp\left(\frac{\ln \phi_3}{s}\right)$	1.178×10^5	0.682×10^5	1.983×10^5	calculated from distribution of ϕ_3, and point estimate of s
$\hat{n}^*$, expected number of nests if patch size not limiting, calculated from $\hat{n}$, s, μ, and D.	137	99	220	calculated over samples of $\hat{n}$, μ, and D, and point estimate of s.
b_{max}, b_{max}^*, maximum population growth rate, calculated from $\phi_{\square}$, $\phi_{\square}$, $\hat{N}$, $\hat{l}$, and $\hat{n}$ or $\hat{n}^*$	7.96, 15.74	2.65, 5.17	11.60, 29.16	calculated over samples of all parameters with point estimate of s for $\hat{n}^*$

λ, λ^*, expected annual population growth rate in 10.5 ha patch, calculated from D, μ, and b_{max} or b_{max}^*	3.96, 7.82	1.21, 2.65	6.63, 11.60	calculated over samples of all parameters with point estimate of s for b_{max}^*
R_c, R_c^*,critical minimum patch radius, calculated from D, μ, and b_{max} or b_{max}^*	68.8, 47.2	44.1, 35.0	154.5, 89.2	calculated over samples of all parameters with point estimate of s
CMP, CMP*, critical minimum patch size; R_c and R_c^*, converted to hectares	1.49, 0.70	0.61, 0.38	7.50, 2.50	back-transformed samples of R_c and R_c^*.

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[a] Median of bootstrap samples for movement parameters; maximum likelihood estimate for demographic model parameters and adult female survival; calculations from the above parameters for derived variables.

[b] Parameters for sampling distributions are shown on the link function scale (e.g., the expectation of ln[x] for a log normal, logit[x] for logit normal, etc.).

Table 3.3.4-2. Movement parameters estimated using generalized linear mixed-effects models in R. All models included individual butterfly as a random effect. For all parameters except time spent resting, the ‘unbiased’ (i.e., corrected for Jensen’s inequality) back-transformed means were used in SEIBMs. For time spent resting, back-transformation was done within SEIBMs.

	Description	Family (link function)	MLE Estimate	Residual standard deviation	Individual variance
m	Mean move length	Gamma (log)	$\mu = 0.952$	$\sigma_{\text{resid}} = 0.983$	$\sigma^2_{\text{ind}} = 0.380$
ρ	Mean cosine of the turning angle	Normal with scaled (from -1 -1 to 0-1), logit-transformed cosines	$\mu = 1.248$	$\sigma_{\text{resid}} = 2.802$	$\sigma^2_{\text{ind}} = 0.361$
P	Probability of resting in any 15-sec interval	Binomial (logit), where successes are moves >15s (indicating an individual rested)	$\mu = -0.810$	NA	$\sigma^2_{\text{ind}} = 0.379$
τ	Time spent resting	Poisson (log), for all moves >15s, including a unique ID for each >15-s move as a random effect to account for overdispersion[†]	$\mu = 1.533$	$\sigma_{\text{over}} = 1.929$	$\sigma^2_{\text{ind}} = 0.923$

[†] See Elston et al. 2001; the “residual” standard deviation used here is actually the standard deviation estimated from overdispersion.

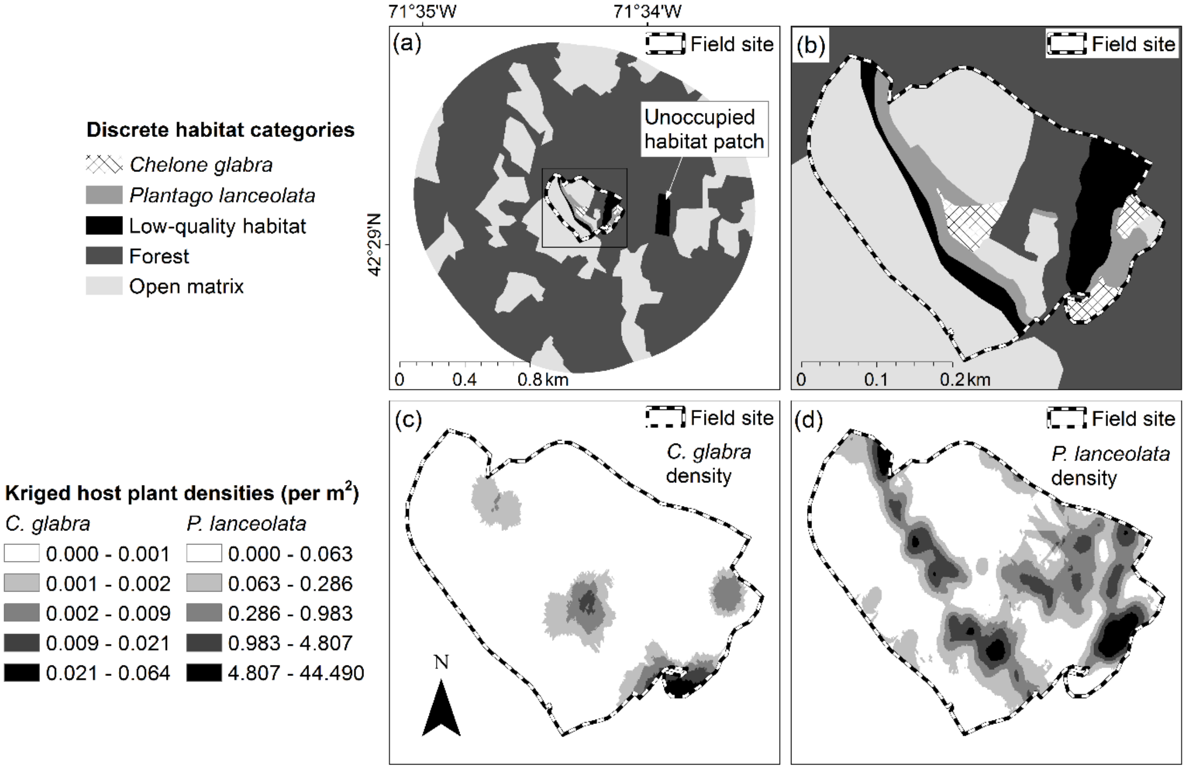


Figure 3.3.3-1. (a) Landscape for Baltimore checkerspot movement models, with field site and surrounding 0.8 km buffer in Harvard, Massachusetts, USA, (b) field site with land cover types based on host plant densities (*Plantago lanceolata* and *Chelone glabra*), (c) kriged host plant densities for *Chelone glabra* based on 2013 survey data, and (d) kriged host plant densities for *Plantago lanceolata* based on 2013 survey data.

3.3.4.1 Implementation of SEIBMs

Taylor's and Baltimore checkerspots exhibit boom-bust dynamics, with their abundances fluctuating dramatically over time. It is currently unclear whether these dramatic fluctuations are caused primarily by exogenous, e.g., environmental stochasticity, or endogenous, e.g., over-compensatory, density dependence. Perhaps more importantly, it is also unclear whether the best strategy for restoring habitat across a landscape differs under exogenously versus endogenously driven boom-bust dynamics. We used spatially explicit individual-based models (SEIBMs) to assess how butterfly populations governed by the two mechanisms would respond to habitat restoration strategies that varied in the level of resource patchiness – from a single large patch to multiple patches spaced at different distances.

We developed two SEIBMs that reflected the Taylor's checkerspot life cycle, one simulating exogenously driven dynamics and the other emulating one type of endogenously governed dynamics. In both cases, populations have the capacity for rapid growth and decline (i.e., boom-bust dynamics) and are limited by some form of density dependence. In the exogenous model, we assume the population is regulated by abrupt density dependence (via a population ceiling) and that environmental stochasticity is responsible for inter-annual fluctuations in population size. In the endogenous model, we simulate a resource-consumer dynamic that results in over-compensatory density dependence producing large fluctuations in population size even in the absence of environmental stochasticity.

Both SEIBMs were built using Netlogo software (Wilensky 1999), and simulated the movement of adult female butterflies in the same way. Parameter values and sources are provided in Table 3.3.4-1. Many of these are taken from field research with Baltimore checkerspot, and details regarding data collection and parameter estimation can be found in Brown and Crone (2016) and Brown et al. (in review).

We simulated female movement and demography in 15-second time steps to match empirical movement data. Every 15 seconds, a female could move or rest (according to an empirically estimated binomial probability of initiating a rest or move). The duration of rests (in number of time steps) was drawn from a Poisson distribution with log normal mean. If the female moved, we modeled her movement as a correlated random walk, drawing the move length from a gamma distribution, and the turn angle (relative to the current heading) from a wrapped Cauchy distribution. At each time step, whether resting or moving, females could oviposit a clutch of eggs with a per-time-step probability converted from lifetime fecundity, and with clutch size drawn from a Poisson distribution. Individuals also had a chance of dying at each time step, based on empirically estimated daily survival probabilities scaled to the 15-second time-step, but maximum possible lifespans were limited to four weeks. Once all adult butterflies had died, an empirically estimated combined egg and larval survival probability dictated how many of the eggs and subsequent pre-diapause larvae survived the summer and early winter to become post-diapause larvae the following year. We assumed a 50% sex ratio, only retaining females for subsequent years.

Demographic stochasticity is an emergent property of the models as a result of the above stochastic demographic and movement parameters and finite population size. While movement, adult longevity, and egg and larval survival were the same in the two models, the relationship between oviposition and host plant biomass differed, as follows.

Endogenous model: The endogenous model was designed to emulate negative density dependent feedback by linking the total number of eggs that could be oviposited to the available biomass of the principal host plants (*Castilleja* and *Plantago* spp.) in a given year, which was affected by the amount consumed by post-diapause larvae (Fig. 3.3.4-1A). Each post-diapause larva consumed one host plant (if available), based on laboratory estimates of feeding rates (M. Linders pers. comm.; Barclay et al. 2009). If insufficient biomass of the principal host plants was present to feed all post-diapause larvae, we assumed that they were able to exploit alternative food sources (Dunwiddie et al. 2016) and that their survival was not adversely affected by the available biomass. Those that survived (based on empirical post-diapause survival probability) metamorphosed into adult butterflies. During the adult life stage, oviposition was restricted to the principal host plants since oviposition on other plants (even those that can support post-diapause larvae) has been found to be lethal to newly hatched larvae (Bowers and Schmitt 2013), and was limited to a maximum of 130 eggs per 10 plants. Thus, consumption of host plants in late winter/spring by post-diapause larvae had the potential to negatively impact the number of eggs that could be oviposited by those same individuals once they became adults. Once the total number of eggs in a patch exceeded the maximum capacity (maximum per plant multiplied by the number of plants remaining per patch), the probability of oviposition was set to zero for all adults in the patch. If no host plant biomass remained after the post-diapause larval stage, no oviposition was allowed during the adult phase; if this occurred in every patch, the population went extinct. We made the simplifying assumption that consumption of host biomass by (successively) post- and pre-diapause larvae in one year did not affect plant biomass in the following year (and therefore we did not explicitly track consumption by pre-diapause larvae). Given that the host plants are short-lived perennials that are capable of rapid compensation for herbivory, the assumption that plant biomass at the start of each growing season is independent of the amount of feeding in the previous year is reasonable. Simulations ended after 30 years or when the population went extinct, whichever came first. Extinction occurred if no eggs were oviposited in a given year or if no adults emerged in the spring because all individuals failed to survive the egg and larval stages.

Exogenous model: The exogenous model was designed to simulate a population with abrupt density dependence imposed at a population ceiling, with the primary driver of population fluctuations being random environmental variation in the height of the ceiling. In the exogenous model, we did not consider the interaction between Taylor’s checkerspot and its host plants. When post-diapause larvae metamorphosed into adults, if the resulting adult count exceeded the ceiling, the adult population was reduced to the ceiling; otherwise, it remained unchanged (Fig.

3.3.4.1-1B). Adults behaved as in the endogenous model, except that no limits on oviposition were imposed. In the absence of environmental stochasticity, populations grew to the ceiling and remained at that level indefinitely. To achieve population fluctuations similar in magnitude to those in the endogenous model, in each year we multiplied the per-patch ceiling value by a lognormal random deviate (log $\mu = 0$, log $\sigma = 0.5$), such that the ceiling value fluctuated annually and these fluctuations were perfectly correlated among patches. The mean total population ceiling was 31,000 adult females (to match the expected number of individuals that would be supported by the available plant biomass in the endogenous model), and the mean per-patch ceiling was the total population divided evenly among the patches.

Landscape:

The landscape used in the SEIBMs represents an area within the Puget Trough prairies in WA that includes Glacial Heritage Preserve, where restoration efforts have been underway for Taylor’s checkerspot for more than a decade, and Mima Mounds Natural Area Preserve, where future restoration efforts have been proposed (Fig. 3.3.4.1-2). We ran simulations at both the Glacial Heritage and Mima Mounds sites, but given their similarity, no significant differences were found between the two sites, so we only present results from the Mima Mounds site. The simulated landscape consisted of four habitat types among which butterfly demography or movement differed: restored prairie, harboring a concentration of Taylor’s checkerspot host plants; nectar prairie, representing areas with nectar food sources for adult butterflies but no host plants (high quality matrix); fields and exurban areas, with no host or nectar plants for butterflies (low quality matrix); and forest, representing a partial barrier to butterfly travel. Oviposition only occurred within restored host prairie habitat, and thus larvae were restricted to this habitat type. Adult movement characteristics, including step length and turning angle distributions, differed among the four habitat types, but resting characteristics, including resting probability and rest duration distributions, were the same in all habitats. We did not model movement of the relatively immobile larvae.

In our simulated landscape, distinct boundaries existed between each habitat type, but, with the exception of the forest boundary, our simulated butterflies did not respond directly to habitat boundaries. At forest edges, butterflies crossed into forest habitat with binomial probability 0.3 which is somewhat more often than observed for upland prairie butterflies (Schultz et al. 2012, Brown et al. in review), but is less than wet meadow butterflies at forest edges (Kuefler et al. 2010). They crossed all other boundaries without restriction or modification of their flight trajectory. Butterflies may exhibit some level of attraction to areas of concentrated host or nectar plants or repulsion from non-preferred habitat (Schultz and Crone 2001), but we have not observed attraction to host plants in Baltimore checkerspots (Brown et al. in review).

Table 3.3.4.1-1 Parameter values used in the Taylor's checkerspot SEIBM.

Category	SEIBM Parameters	Value	Units	Distribution	Source	Species Source	Notes
General & Initial Conditions							
	Time Step (tick)	15	seconds		Brown and Crone 2016a	Baltimore checkerspot	
	Daily flight period	4	hours/day		Brown and Crone 2016a	Baltimore checkerspot	
	Initial total number of adult females	10,800	adults/1.44 ha				Experimentally determined to allow allow growth within the first few simulation years before density dependent factors
Landscape					Center for Natural Lands Management; USGS; J. Smokey; R. Lundergan		
	Landscape size	6.84x10.96	km			Taylor's checkerspot	
	Number of habitat-types	5				Taylor's checkerspot	Host (Castilleja & Plantago), nectar field (high quality matrix), field (low quality matrix), forest, exurban (low quality matrix)
	Total host patch size	1.44	ha			Baltimore checkerspot	About twice the critical minimum patch size from Brown & Crone 2016b
Butterfly Movement							
	Probability of resting (per tick)	0.385		Binomial	Brown et al. (in review)	Baltimore checkerspot	
	Move distance mean						
	Host (Chelone + Plantago)	4.8	meters	Gamma	Brown et al. (in review)	Baltimore checkerspot	
	Nectar (High Quality Matrix)	6.7	meters	Gamma	Brown et al. (in review)	Baltimore checkerspot	
	Field & Exurban (Low Quality Matrix)	12.5	meters	Gamma	Brown et al. (in review)	Baltimore checkerspot	
	Forest	8	meters	Gamma	Brown et al. (in review)	Baltimore checkerspot	
	Move distance variance						
	Host (Chelone + Plantago)	48.9	meters	Gamma	Brown et al. (in review)	Baltimore checkerspot	
	Nectar (High Quality Matrix)	91.4	meters	Gamma	Brown et al. (in review)	Baltimore checkerspot	
	Field & Exurban (Low Quality Matrix)	327.4	meters	Gamma	Brown et al. (in review)	Baltimore checkerspot	
	Forest	131.7	meters	Gamma	Brown et al. (in review)	Baltimore checkerspot	
	Rest time log mean	1.63	ticks	Log Normal*	Brown et al. (in review)	Baltimore checkerspot	*Individual rest times drawn from Poisson with mean equal to expoentiated log-normal deviate (determined from GLM by Brown & Crone 2016a)
	Rest time log standard deviation	1.79		Log Normal*	Brown et al. (in review)	Baltimore checkerspot	*Individual rest times drawn from Poisson with mean equal to expoentiated log-normal deviate (determined from GLM by Brown & Crone 2016a)
	Turn angle mean cosine						
	Host (Chelone + Plantago)	0.292		Wrapped Cauchy	Brown et al. (in review)	Baltimore checkerspot	
	Nectar (High Quality Matrix)	0.318		Wrapped Cauchy	Brown et al. (in review)	Baltimore checkerspot	
	Field & Exurban (Low Quality Matrix)	0.479		Wrapped Cauchy	Brown et al. (in review)	Baltimore checkerspot	
	Forest	0.378		Wrapped Cauchy	Brown et al. (in review)	Baltimore checkerspot	
	Boundary crossing probabilities						
	Matrix to forest	0.3		Binomial	Brown et al. (in review) & Kuefler et al. (2010)	multiple	Intermediate between estimates from Brown et al. (in review) and Kuefler et al. (2010)
	All other boundaries	1		Binomial	Brown et al. (in review)	Baltimore checkerspot	
Butterfly Demography							
	Adult daily survival intercept coefficient (β_0)	3.704		Binomial*	Brown and Crone 2016a	Baltimore checkerspot	*The logit-transformed survival probability (binomial) = $\beta_0 + \beta_1 * d$, where d = day
	Adult daily survival slope coefficient (β_1)	-0.196		Binomial*	Brown and Crone 2016a	Baltimore checkerspot	*The logit-transformed survival probability (binomial) = $\beta_0 + \beta_1 * d$, where d = day
	Egg & pre-diapause larvae overwinter survival	0.5		Binomial	Brown and Crone 2016b	Baltimore checkerspot	
	Post-diapause survival	0.722		Binomial	Brown and Crone 2016b	Baltimore checkerspot	
	Maximum allowed lifespan	4	weeks	Fixed	Brown and Crone 2016a	Baltimore checkerspot	
	Probability of ovipositing	0.0000306	per tick	Binomial	Brown and Crone 2016a	Baltimore checkerspot	Only in host patches
	Mean nest size	150	eggs	Poisson	Brown and Crone 2016b	Baltimore checkerspot	
Plant Biomass							
	Plant density in host patches	5	plants/m^2	Fixed	M. Linders pers. comm. & Dunn & Fimbel 2012	Taylor's checkerspot	Based on target outplanting density for Taylor's checkerspot restoration of 10-15 plants/m^2 within 4m^2 plots, adjusted for realized densities at broader spatial scale
	Post-diapause larvae consumption rate	1	plants/year	Fixed	M. Linders pers. comm. & Barclay et al. 2009	Taylor's checkerspot	Based on consumption volume from captively bred larvae converted to number of plants based on an estimated total conusmption of about 15 leaves/larvae and about 15-20 leaves/plant
	Maximum eggs allowed per unit biomass	13	eggs/plant	Fixed	Model testing		Experimentally determined using endogenous model runs in the single patch scenario to produce sustained boom-bust dynamics that matched empirical checkerspot population patterns

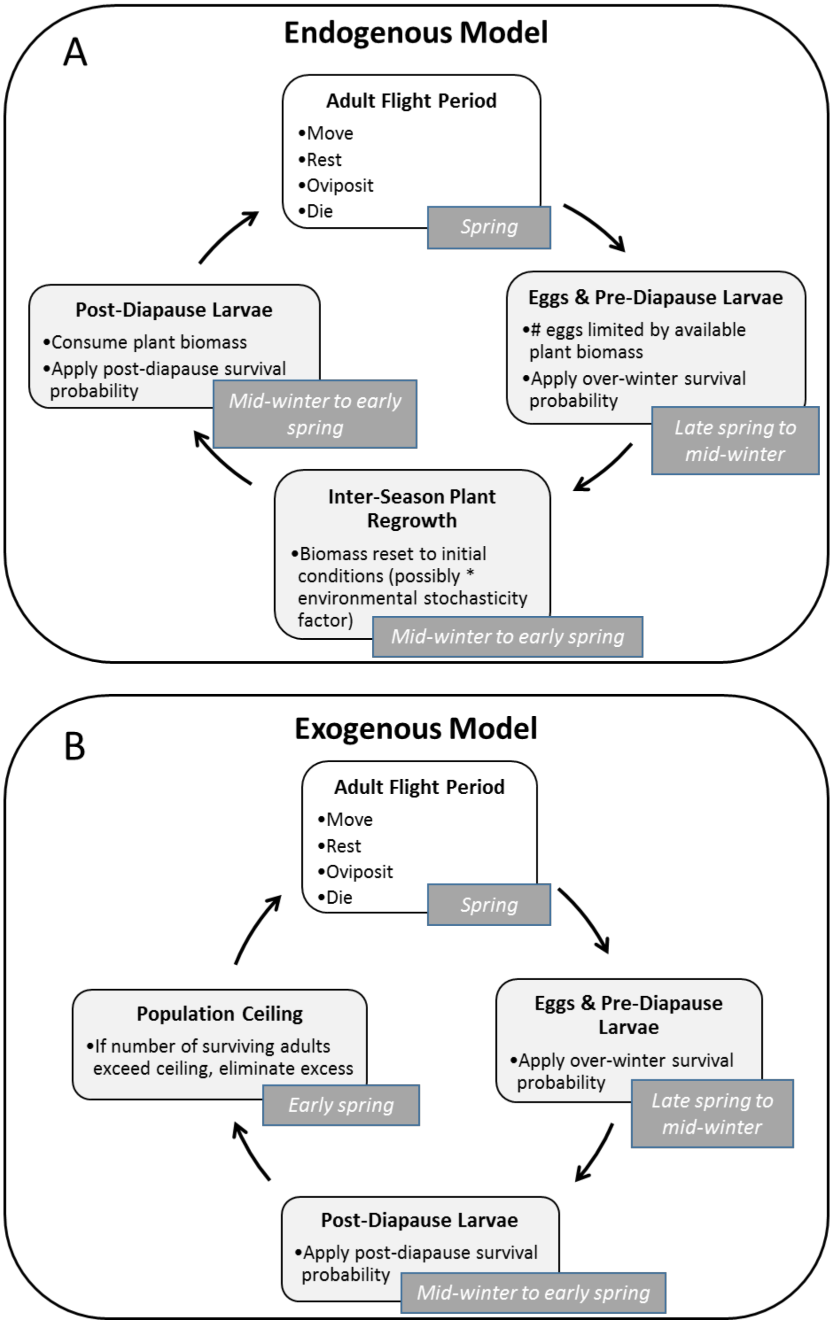


Figure 3.3.4.1-1 Taylor's checkerspot spatially explicit individual-based model diagrams for A) the endogenous model and B) the exogenous model. White boxes depict spatially and temporally explicit modeled actions, and light grey boxes depict aspects of the model that were applied instantaneously and non-spatially. Dark grey boxes indicate the time of year in which each model phase would be happening.

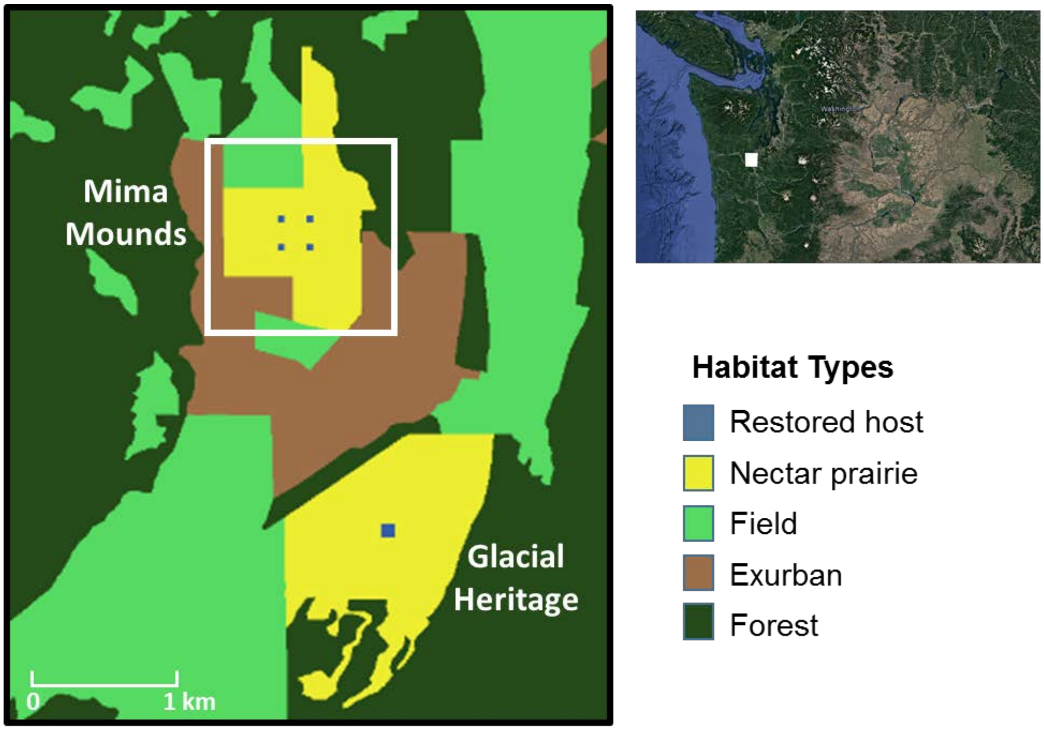


Figure 3.3.4.1-2 The South Puget Trough study area of western Washington, including the Mima Mounds Natural Area Preserve and Glacial Heritage Preserve. The blue squares represent potential host plant restoration areas, with the configurations at the two sites representing 2 of the 21 habitat scenarios tested in our models. The Glacial Heritage site shows a single contiguous host patch of 1.44ha, and the Mima Mounds site shows four patches of 0.36ha each, spaced at 200m apart.

3.3.4.2 Model validation and simplification

While population estimates for Taylor's checkerspots are relatively sparse, like other checkerspot butterflies (e.g., Hellmann et al. 2004), Taylor's checkerspots appear to exhibit boom-bust cycles within the few remaining extant populations (Fig. 3.3.4-1). Given the paucity of long-term abundance data for Taylor's checkerspot, in our model, we did not try to emulate observed population trajectories precisely, but instead, compared our model population trajectories with natural populations to ensure that the general magnitude and pattern of fluctuations was similar.

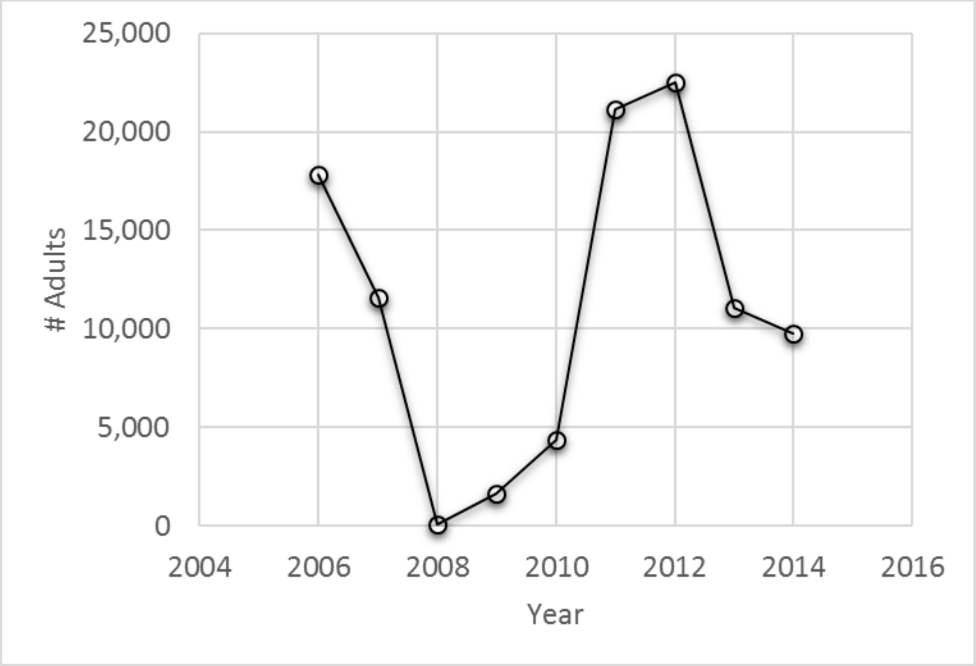


Figure 3.3.4.2-1 Estimated Taylor's checkerspot butterfly abundance at a single locale in Washington state. To derive these estimates, we used raw field count data obtained from Washington Department of Fish and Wildlife (G. Olson & M. Linders), and applied insect population estimation software INCA (Longcore et al. 2003).

3.3.4.3 Scenario Analysis

Restoration scenarios:

We used our SEIBMs to measure how the size, number, and spacing of restored host plant patches impacted population dynamics under the two mechanisms responsible for population fluctuations. Specifically, we added patches of host plants to the base landscape but fixed the total restored area at 1.44ha, about twice the estimated minimum critical patch size (0.7ha) needed by Baltimore checkerspots (Brown and Crone 2016) and which we would expect to yield about a two-fold growth per year. The restoration scenarios differed in the number (and therefore size) of host patches and the distance between adjacent patches. We simulated 1, 2, 4, 6, and 8 patches, varying from 1.44 to 0.18ha per patch, and for scenarios with 2 or more patches, we varied the distance between patches (20, 50, 100, 200, 400m), for a total of twenty-one unique restoration scenarios (e.g., Fig. 3.3.4-2).

Environmental Stochasticity

Correlated. We compared output from the exogenous model (marked by high stochasticity correlated among patches) with output from the endogenous model with no environmental stochasticity. In addition, because environmental stochasticity may also have some impact on endogenously governed populations (Stamp 1984), we also compared the exogenous model output with endogenous output impacted by two levels of stochasticity (moderate and high). With no environmental stochasticity, in the endogenous model, the plant biomass in each patch was reset to the same base level at the start of each year. Under moderate and high stochasticity, the level of biomass in each patch was reset to the base level multiplied by a lognormal random deviate ($\log \mu = 0$; $\log \sigma = 0.25$ or $\log \sigma = 0.5$ respectively), such that, as in the exogenous model, annual environmental variation was perfectly correlated among patches.

Uncorrelated. As has been shown with Bay checkerspots, micro-climatic differences can cause demography to differ even at relatively small distances (Ehrlich and Hanski 2004). To assess the potential impact of variation in habitat quality and micro-climate among patches, we also applied environmental stochasticity to patches in an uncorrelated fashion in both models. To do so, we generated a different lognormal deviate for each patch each year, multiplying the deviate by the per-patch ceiling value (in the exogenous model) or by the per-patch base biomass level (in the endogenous model). We did not include any between-year auto-correlation in the environmental stochasticity.

Simulations and Output

We ran each simulation for 30 years and produced 100 simulations for each combination of model, restoration scenario, and environmental stochasticity (i.e., 2 models, 21 scenarios, and 5 possible environmental stochasticity combinations). For each simulation, we tracked total population size through time starting at 10,800 individuals, which was chosen to generally allow populations to grow for 2-3 years before density dependence was invoked. We compared model output using the following metrics: extinction risk, mean population size, intrinsic growth rate, and temporal coefficient of variation of population size. We calculated extinction risk as the proportion of simulations that ended in extinction (total population size of zero) within the 30-year time horizon for each model-restoration-stochasticity scenario. We calculated the mean population size as the average number of adults produced each year over all years and all simulations ($\bar{N}$). For the mean intrinsic growth rate ($\bar{r}$), we averaged over all simulations the natural log of the annual growth over the first two years:

$$\bar{r} = \frac{\sum_{i=1}^{n} \ln\left(\frac{N_{i,2}}{N_{i,0}}\right)}{2n}$$

where $N_{i,0}$ is the starting adult population size in simulation i, $N_{i,2}$ is the adult population size in the second year of simulation i, and n is the number of simulations (100). We calculated the population size coefficient of variation (CV) as the standard deviation of adult population size over all years and all simulations divided by the mean population size ($\bar{N}$).

To understand the role that metapopulation dynamics (e.g., extinction-recolonization and the rescue effect) plays in creating the population-level patterns in our two models, we also assessed the following patch-level dynamics: extinction rates, patch population variability, patch recolonization rate, and the level of dispersal among patches. We calculated mean per-patch extinction rates as the total number of patch extinctions (defined as zero adults present in a patch at the beginning of a year) over all patches, years, and simulations in a given scenario divided by the number of patch-years (i.e., number of patches multiplied by number of years and number of simulations). For patch population variability, we calculated the CV as above using the standard deviation and the mean patch population size across all patches and simulations. We calculated the mean recolonization rate as the total number of patch recolonizations (adults present at the beginning of an annual cycle following an extinction in that patch in a previous year) divided by the total number of patch extinctions over all patches, all years, and all simulations. To minimize model run time, we did not record individual dispersal events between patches, but instead recorded the proportion of time individuals spent in all host patches relative to their lifespan, and the time spent in their non-natal host patch relative to time spent in all host patches. The latter metric provided an indirect measure of dispersal among patches.

3.4 Transition Activities

3.4.1 Review of management actions for TERS

SEIBMs are potentially useful tools for guiding resource management decisions. However, they are complex models with heavy data requirements, and not appropriate for all management scenarios. To better understand the types of habitat management and restoration being conducted on Department of Defense (DoD) installations and the capability of managers to build SEIBMs using available monitoring data, we conducted an informal survey of DoD natural resource managers. This information helps us to assess the practical applicability of SEIBMs for guiding habitat management on DoD lands, and to better understand managers' perceptions and needs, so we can provide them with useful information and tools.

Contact information for 90 DoD installations potentially conducting habitat management or restoration for threatened, endangered, or rare species (TERS) were identified using the National Military Fish & Wildlife Association website (www.nmfwa.net), Breuer (2016), reports (Rubinoff et al. 2006, Balbach et al. 2010), and word of mouth. We sent e-mails to 115 natural resource managers at these installations, inviting them to participate in a survey on the utility of SEIBMs for managing habitat for wildlife. Those who agreed were asked to read a paragraph on SEIBMs and complete a three part, multiple choice questionnaire. In the first part, managers were asked questions about how habitat management is conducted on their installation. They were also asked whether the questions commonly addressed by SEIBMs would be important for managing their species. In the second part, managers were asked to provide information on the types of monitoring data collected for at least one species whose habitat is being restored or managed on the installation. They were asked whether they collect the types of data required to build an SEIBM, namely habitat, survival, fecundity, movement, and population size data. In the third part, managers were asked about whether they felt SEIBMs would enhance their ability to manage species on their installation, and what factors would limit them from using SEIBMs.

3.4.2 Develop user guide to SEIBMs

Based on results of the informal survey of DoD natural resource managers (see section 4.4.1), we found that SEIBMs could address questions relevant to the management of habitat for TERS on military installations, and that managers are open to using them. However, if these models are to be more generally applied, managers need a better understanding of how SEIBMs are constructed and what they can do. When asked what information would help them evaluate whether SEIBMs would be a practical tool for management, 26% of the managers surveyed stated that they would like to see examples of SEIBMs that were used successfully to guide habitat management. They also wanted to know what types of survey work are needed to collect the appropriate data, what information SEIBMs could provide that habitat assessments don't, and whether SEIBM results would be accepted by federal regulatory agencies like the U.S. Fish and Wildlife Service and U.S. Forest Service. Guided by these requests, we wrote a user guide that covers SEIBM construction, data collection, limitations, and how SEIBMs perform relative to simpler habitat and demographic analyses. We used examples from the scientific literature to illustrate how SEIBMs have performed in various contexts.

To provide managers with a more concrete example of the amount and types of data required to build an SEIBM, and to assess the extent of DoD managers' limitations in building SEIBMs with current data sets, we also reviewed the data sets for 9 working SEIBMs used to guide habitat management. This set of studies was compiled by searching Google Scholar for papers published between 2000-2015 using the terms “spatially explicit individual based model” or “spatially explicit population model”. In addition, we included unpublished data sets for the Fender's blue butterfly and St. Francis' satyr SEIBMs developed for this SERDP project. Criteria for selection of studies were that SEIBMs were applied to decision-making for an actual habitat restoration project, and that the authors provide documentation or references for the data used to parameterize the model. We summarized the amount and types of data collected on habitat, population size, survival, fecundity, and movement behavior.

3.4.3 Apply tools to additional case studies

3.4.3.1 Diffusion and Density

Study Area and Environments

We conducted our study at 19 field sites in Israel along a climatic gradient from the arid Negev desert to Mediterranean regions of northern Galilee (Fig. 3.4.3.1-1a). Each site was located at the intersection of an agricultural field and a semi-natural area. Butterfly densities and movement behaviours were recorded in four land cover classes: wheat fields, olive groves, semi-natural grasslands or scrublands, and field margins.

The first two land cover classes, wheat fields and olive groves, were common agricultural crop field types that differ greatly in their structure. Wheat fields (Fig. 3.4.3.1-1b) were open monocultures, most of which were intensively managed with agrochemicals and mechanical disturbance. Olive groves (Fig. 3.4.3.1-1c) were structurally heterogeneous environments, with rows of mature trees (> 4m height) separated by areas of open habitat, and typically less intensively managed than wheat fields. Butterfly host and nectar plants were patchily found in the open microhabitats of olive groves, and butterflies used the trees for shade, perching or roosting.

The third and fourth land cover classes were the semi-natural grasslands and scrublands outside the agricultural fields (Fig. 3.4.3.1-1d), and the margins of the fields themselves. The grassland/scrubland areas were open areas containing a diversity of plants not occurring in other areas. Although grazed by goats and cattle, these sites were otherwise undisturbed. The “field margin” land cover class (Fig. 3.4.3.1-1e) included linear elements such as unpaved roads, fences, or paths that separated agricultural fields from the surrounding semi-natural environment. Field margins were characterized by a heterogeneous mix of vegetation that resulted from elevated nutrient levels, agrochemical use and mechanical disturbances. Ruderal species were often abundant, offering resources including nectar and host plants. The field margin also attracted perching or “ravining” species that establish territories along linear features (Tennent 1995). Field margins ranged in width from 1.5-21 m (average 9.6 m) between sites (for further details see Pe'er *et al.* 2011b).

Butterfly surveys and movement data

We conducted surveys along transects established in sites containing one of the two agricultural field types (olive or wheat), field margin, and the surrounding semi-natural grassland/scrubland area. Each transect consisted of three lines perpendicular to the field margin, starting 50 m within the semi-natural area, traversing the width of the field margin, and extending 100 m into the agricultural field. Transect lines were connected by two 50 m lines parallel to the field margin, one in the semi-natural area and one in the field margin (Fig. 3.4.3.1-2a, see also Pe'er *et al.* 2011b). Additionally, a 100 m transect was sampled along the length of the field margin. Semi-natural areas were only sampled to a depth of 50 m because the topography in most sites tended to change beyond this depth, rendering the environment no longer homogeneous.

We completed 2-3 surveys along transects at each site from March to May 2006, the peak of butterfly activity in Israel, and the period in which wheat fields and olive groves received minimal treatment. We used standard Pollard Walk methods to conduct surveys between 09:00 and 16:00, under conditions of <50% cloud cover, temperatures of 18-33˚C, and wind speeds <10 km/hr. Pollard-Yates indices correlate well with population size in many studies (Thomas 2005; Collier, Mackay & Benkendorff 2008). For each survey, two observers walked at a constant pace of 1 km/hr, searching for butterflies within 5 m of the transect line (i.e., a 10 m wide survey width), and recorded a GPS location for each individual butterfly observed. In addition, we recorded short movement paths for as many butterflies as possible during the surveys. Observer pairs recorded butterfly movement paths from when an individual butterfly was first located, following the butterfly at > 1.5 m distance and registering locations at which the individual landed or changed direction until one of the following conditions was met: 20

seconds, 6 turns, 40 m distance, or the butterfly disappeared from view. Observer pairs recorded total observation time and resting time of each followed individual. After completion of the observation, one of the two observers recorded the GPS location of each stopping or turning location. We noted land cover class (semi-natural area, field margin, and wheat field or olive grove) for each marked point. When we encountered two butterflies simultaneously, we followed the path of the less common species. For common species, we recorded up to 20 observations per site on a given sampling day. Examples of movement paths are provided in Fig. 2. We conducted our study within a single season because observed differences in diffusion rates between land cover classes are generally much larger than differences between years (e.g. Schultz, Franco & Crone 2012).

Diffusion Rates

We calculated diffusion coefficients (D) for each species × land cover class combination using the equation $D = \frac{M+2\psi\mu^2}{4\tau(1-\psi)}$, where μ is average move length, M is average squared move length, ψ is mean cosine of the turning angle, and τ is the average duration per move or move time (Turchin 1998, page Box 5.3 and page 102). For each individual, we partitioned the movement path into moves made in each land cover class. Each move consisted of a move length, measured as the distance between turning or stopping points i and i+1, and a turning angle θ_i, measured as the angle between move i-1 and i. If the movement path contained only two points (i.e., a straight line with no landing behaviours observed), we assigned a very small angle (<1 degree) for the turning angle. This non-zero value was introduced to prevent the calculated diffusion rate from being estimated as infinity (i.e., because a mean turning angle, ψ, of 0 has a mean cosine of 1, reducing the denominator in the above equation for D to 0, and any fraction with a denominator of 0 = infinity). Because flight time was measured for the entire path rather than for each move, we estimated the average speed [meters per second] as $\bar{s} = \frac{total\,path\,length}{total\,time\,in\,flight}$, and the duration for each move as $t_i = \frac{l_i}{\bar{s}} + r_i$, where l_i is the move length preceding stop i and r_i is the resting time at stop i. We averaged move lengths, move durations, and turn angles over the pooled moves in each species × land cover class combination (following Schultz and Crone 2001). We estimated diffusion coefficients for combinations for which at least 5 complete moves were recorded, i.e., 5 move lengths, 5 move times, and 4 turn angles. To separate between edge-mediated behaviour and movement behaviour within semi-natural areas, olives groves and wheat fields, we used only data that were collected at least 10 m away from the field margin, i.e., far enough from boundary within semi-natural areas, olives or wheat. The 10 m buffer was based on various studies demonstrating a shift in movement behaviour close to structural habitat boundaries (Haddad 1999; Schultz & Crone 2001; Ovaskainen & Cornell 2003; Ovaskainen 2004; Schultz, Franco & Crone 2012; Zurita *et al.* 2012). We also visually inspected the data to corroborate that this buffer width was consistent with our data. We used all movement behaviour within field margins as this area is, by definition, a boundary-influenced habitat type. For each move within each species × land cover class combination, we used bootstrapping to create 1000 sample sets of the 4 movement parameters μ, M, τ and ψ. From these we calculated expected net squared displacement, $E(R^2) = \frac{M+2\psi\mu^2}{(1-\psi)}$ for a single move, and diffusion rate, D, for each species × land cover class across these 1000 sample sets. We based analyses below on the median of bootstrapped estimates of D, $E(R^2)$, μ, τ and ψ.

Density

We used survey data to estimate the density (abundance divided by area) of each species in each land cover class. We estimated abundance for each species at each site using the survey date with the highest count for that species at that site. We calculated the sampling area as the length of the survey transect × transect width (10 m). We only used density data from each of the four primary land cover classes (semi-natural areas, field margin, olive groves and wheat fields) and excluded all observations within the 10 m boundary zone for olive groves, wheat fields and semi-natural areas for consistency with the treatment of movement data above.

Statistical Analysis

We determined the relationship between density and diffusion using linear mixed models (lme4 package in R, Bates, Maechler & Walker 2015) with diffusion, wingspan, and diffusion × wingspan as fixed effects, and butterfly species as a random effect (to account for repeated measures of species, and supported by an initial test of the best model for the random effects structure, Zuur *et al.* 2009). We did not detect phylogenetic signal in our data (Table 3.4.3.1-1 and Figure 3.4.3.1-3), so we did not use phylogenetic regressions because the lme4 package allows greater model flexibility, including the ability to weight models by confidence in the data. We included wingspan estimated to the nearest 0.5 cm using published keys and field guides (Table 3.4.3.1-1) as an index of body size because it is a potential correlate of density (e.g., Gaston & Lawton 1988) that could influence the relationship between density and diffusion. Because densities may differ among species and among land cover classes, e.g., species for which semi-natural areas whereas versus olive groves are higher quality habitat, we ran an additional analysis with land cover class as a fixed effect in addition to diffusion, wingspan, and diffusion × wingspan. We used models with land cover as a fixed effect to evaluate the importance of land cover class relative to diffusion for predicting density, and to estimate densities in each habitat type evaluated at median values of wingspan and diffusion. We calculated 95% confidence limits of expected densities by parametric bootstrapping, i.e., taking 0.025 and 0.975 quantiles of 1000 sampled values sampled from a multivariate normal distribution defined by model coefficients and sampling error variance-covariance matrix of fixed estimates (vcov() function in R).

In all models, we log+0.5-transformed diffusion rate and density for each species × land cover class combination to improve normality in the residuals. Because sample sizes were highly variable, with common species having many more movement paths than rare species (Fig. 4.4.3.1-1), we weighted models by the inverse of the 95% bootstrap confidence interval standardized to a mean of one (to keep the total error degrees of freedom constant). For standardization, we used the confidence interval of the diffusion rate, expected net square displacement, or flight path parameter (μ, ψ, *and* τ) estimate, as appropriate for the predictor variable in each model.

In addition to testing diffusion as a predictor of density, we tested whether parameters measured directly from flight paths were sufficient predictors of density. For example, does move length sufficiently predict variation in density? We repeated the analyses above with move length, cosine of turning angle and time per move (μ, ψ, *and* τ, $E(R^2)$, above), in turn, as fixed effects (again with wing span and land cover class as covariates). We log+0.5-transformed move lengths and times per move and logit-transformed cosines of turning angles that were scaled to range from 0 to 1. As a second test of possible independent drivers of density, we quantified the relationships between body size and diffusion, and body size and density, for all species in our data set. Specifically, we calculated median diffusion rate and density for each species. We used linear models to test whether body size was a significant predictor of either diffusion rate or density. This analysis differs from the models above in that we evaluated the relationship among species, averaged across land cover classes, rather than within species, among land cover classes.

Table 3.4.3.1-1 Comparison of coefficients of phylogeny model, model with species as a random effect (best fit model, see Table S2) and species + family as a random effect. To compare these models, the latter two models were run without weighting by confidence intervals and thus are not directly comparable to results in Tables 1 and 2. Model with fixed effect of diffusion and wingspan on density (a), and model with fixed effects of diffusion, land cover class and wingspan on density (b).

a)

	MCMCglmm	lme4 species	lme4 species + family
(Intercept)	1.50	1.48	1.48
log(Dif + 0.5)	0.16	0.17	0.18
wingspan	0.03	0.03	0.03
log(Dif + 0.5):wingspan	-0.01	-0.01	-0.01

b)

	MCMCglmm	lme4 species	lme4 species + family
(Intercept)	-0.13	-0.45	-0.45
log(Dif + 0.5)	0.59	0.56	0.56
wingspan	0.22	0.13	0.13
Location - nature	0.41	0.94	0.94
Location - olive	-0.47	-0.46	-0.46
Location - wheat	-15.10	-15.23	-15.24
log(Dif + 0.5): wingspan	-0.03	-0.02	-0.03
log(Dif + 0.5): Location - nature	-0.26	-0.56	-0.56
log(Dif+ 0.5) : Location - olive	-0.04	0.09	0.09
log(Dif+ 0.5) : Location - wheat	6.97	6.45	6.45
Wingspan: Location - nature	-0.04	-0.05	-0.05
Wingspan: Location - olive	-0.08	-0.09	-0.09
Wingspan: Location - wheat	0.18	0.18	0.18
log(Dif + 0.5): Wingspan: Location - nature	0.01	0.02	0.02
log(Dif + 0.5): Wingspan: Location - olive	0.02	0.02	0.02
log(Dif + 0.5): Wingspan: Location - wheat	-0.01	-0.09	-0.09

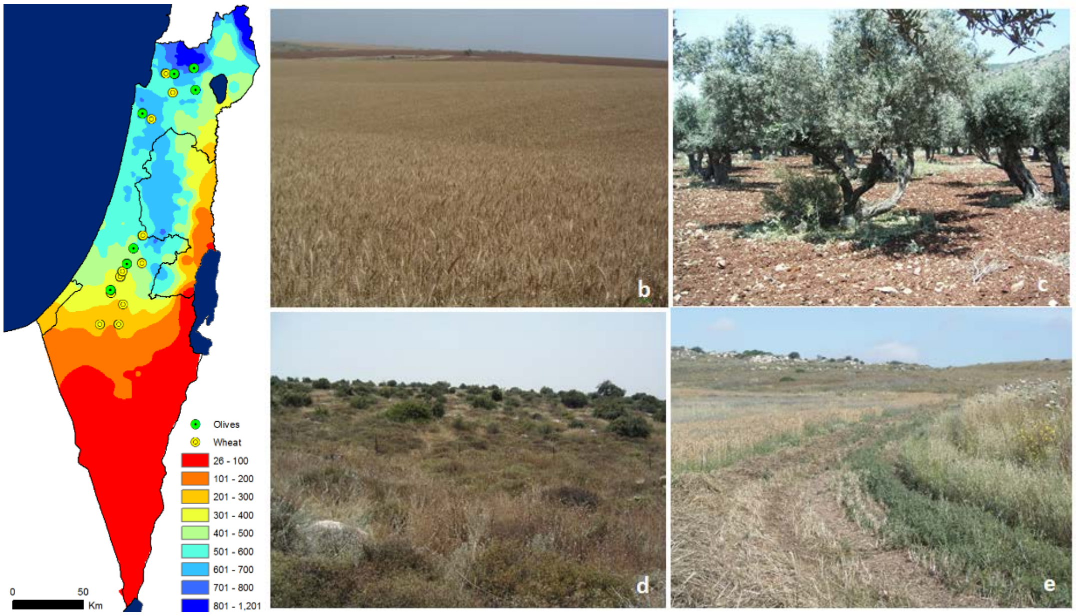


Figure 3.4.3.1-1: Location of field sites in Israel (a) and examples of the sampled land cover classes: (b) wheat fields, (c) olive groves, (d) semi-natural area, and (e) field margin (here, at the edge of a wheat field). Color in (a) represents the rainfall gradient (see Pe'er et al. 2011).

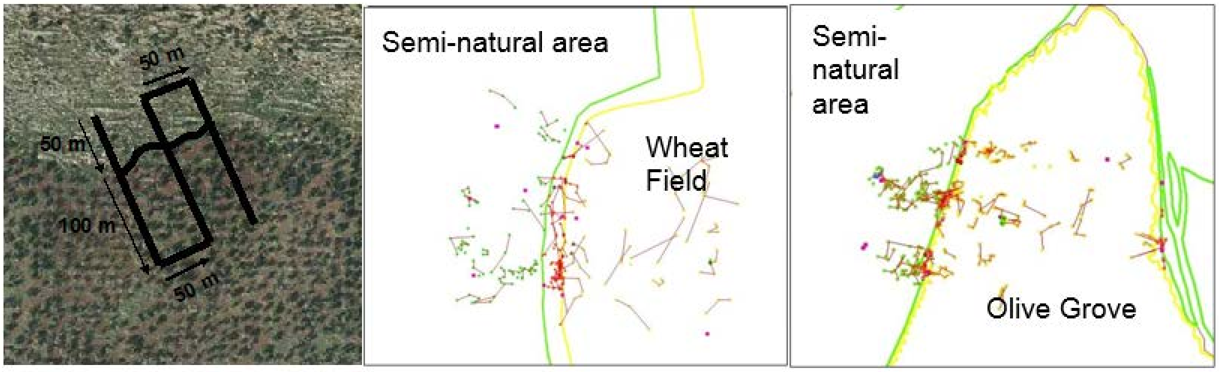


Figure 3.4.3.1-2: a) The sampling transect protocol (example) and example of flight paths b) in wheat and c) in olive sites. Each series of linked points representing one movement path of an individual. Note the clear difference in path structure in semi-nature vs. within the wheat field. Yellow line is edge of agricultural area, green line is edge of semi-natural area; area in between these is the field margin.

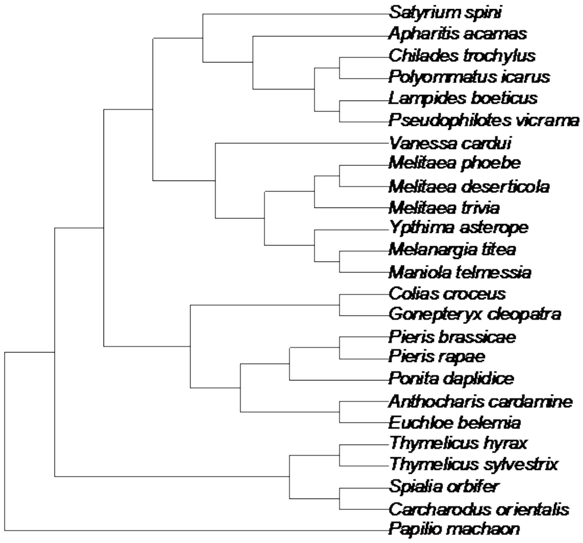


Figure 3.4.3.1-3. Phylogenetic tree of species included in the statistical analyses.

3.4.3.2 Edge behavior mini meta analysis

Studies of edge preference are less common that studies of movement in high- vs. low-quality habitat. Nonetheless, a number of studies have released butterflies at habitat patch edges, and recorded habitat preference, as quantified by the side at which they left the habitat interface.

We compiled these studies by searching for studies that had cited two of the first papers in this area (Schultz 1998, Kuefler et al. 2010), and searching forward and backwards from paper citing these studies. In all, we found 9 studies including data edge responses of 9 prairie butterfly species. We divided the edge responses into three categories: (1) preference at host plant patch edges, in which habitat was structurally similar, and differed primarily in the presence/absence of larval host plantsl; (2) structural habitat boundaries, typically open / forest boundaries; and (3) boundaries between open natural areas and developed habitat, typically roads or parking lots, but sometimes including developed suburban areas. Not all studies included all interfaces (Table 3.4.3.2-1).

Table 3.4.3.2-1. Edge types studied for each butterfly species

Butterfly species	Edge type		
	Host	Forest	Pavement
Appalachian Brown		1	
Baltimore Checkerspot	1	1	
Crystal Skipper		1	1
Fenders Blue	1	1	
Monarch		1	1
Pearl Crescent		1	
Regal Fritillary	1	1	1
Scarce Large Blue	1	1	1
Taylors Checkerspot		1	1

We used binomial family, logit link generalized linear mixed models (GLMMs) to evaluate edge preference. For each study, the number of trials (butterflies released at each edge type) and the number choosing habitat vs. matrix were extracted from the original raw data. We included the logit-transformed expected proportion of butterflies choosing matrix habitat as an offset. Thus, the test of whether there is a significant cross-study preference for habitat over matrix is the p-value testing whether the intercept coefficient for each model differs from 0. Species was included in each model as a random effect, which makes the standard deviation of that random effect the expected among-species standard deviation in edge preference.

3.4.3.3 Movement in high quality vs low quality habitat meta analysis

We compiled a long list of 267 studies related to movement in heterogeneous environments by searching forward for papers that cited several classic studies of movement in heterogeneous environments. We then screened these papers for studies that included both estimates of the rate of net displacement (net distance moved per time) in at least two habitat types, and independent estimates of habitat quality (indicated by demographic rates such birth or death rates, food density, and/or population growth rates) for these habitat types. Hereafter, we refer to “net displacement per time” as “movement”. Studies were excluded if they did not have both movement and habitat quality measurements in at least two environment types, if habitat quality was assumed but not documented (e.g., assuming suburban vs. natural areas represent “high” and “low” quality), or habitat quality was inferred from movement behavior (e.g., foraging behavior of pelagic birds as an indicator of prey density). Studies were also excluded if the measure of movement confounded net displacement with other aspects of behavior, such as preference at patch boundaries, e.g., studies of residence time in patches were not used because longer residence times could reflect slower movement or higher preference at patch boundaries. Studies were retained in the data base if they included a response variable that related in a monotonic way to movement, even if they were not sufficient to predict net displacement, e.g., studies were retained if they included measures of speed or tortuosity but not both.

Of the original set of studies, 64 included clear, independent measures of habitat quality and the rate of net displacement. 14 studies were ambiguous, and their inclusion was decided by consultation among three co-authors (Schultz, Hodgson, and Crone when needed as a tie-breaker). This led to a final set of 78 studies. For analysis, we used each species within each study as the unit of observation. Of 78 studies, 71 included one species, four included two species, two included three species, and one included four species. Conclusions changed only slightly if we randomly chose one species from each study for inclusion in the analysis.

We used a simple vote-counting meta-analysis, because studies included several different metrics of movement in different units (e.g., speed, tortuosity, diffusion coefficients), and because we were primarily interested in the qualitative direction, not the magnitude of the response. We divided studies into three categories: studies in which movement (net displacement per time) was faster in lower-quality habitat, studies in which movement was slower in lower-quality habitat, and studies in which the pattern was unclear. Unclear patterns could reflect statistically nonsignificant relationships, or studies in which multiple measures of movement led to different conclusions (i.e., different sets of habitat conditions, or different metrics, such as speed and tortuosity, that had relationships in different directions and were not combined into a net metric of movement). We also compiled taxonomic data (Phylum, Class, Order, Family, Genus, Species).

We analyzed the relationship between habitat quality and movement using binomial family, logit link, generalized linear mixed models (GLMMs) with various metrics of taxonomy as random effects. In general, these were nonsignificant, so final conclusions were based on a GLM (generalized linear model with no random effects). We used intercept-only models to compare the proportion of studies with faster vs. slower movement in lower quality habitat. We tested whether the proportion of "faster" studies differed significantly from 0.5 (note that 0.5 equals 0 on a logit scale, so this is the default p-value included in the summary() function). We repeated analyses using ordinal multinomial logistical regression (polr function in R; with no random effects but including the 10 ambiguous studies) to obtain confidence limits for the proportion of all studies in each category, after accounting for ambiguous studies. Confidence limits were obtained by parametric bootstrapping, i.e., 95% quantiles of 1000 simulated data sets obtained with the sim() function, and re-analyzed with the polr() function.

3.4.3.4 Applications of source sink dynamics to bumblebees

Rationale: During the course of this award, the rusty-patched bumble bee (*Bombus affinis*) became the first federally-listed bee species in the continental US. We used available data for common bumble bee species, and the conceptual framework developed for source-sink dynamics of Fenders' blue butterflies, to develop a preliminary model of bumble bee dynamics in heterogeneous source-sink landscapes.

Model Overview

Bumble bees are social insects that live in annual colonies, each founded in the spring by a single reproductive queen. Within each colony, sterile workers collect resources and tend to larvae while the queen produces multiple cohorts of workers throughout the season and new reproductive queens at the end of each season (as well as short-lived reproductive males). Newly produced, mated queens that survive the winter and establish new colonies form the basis for populations in the following year. Because we are interested in predicting long-term population dynamics over several years, we model population dynamics as the number of queens establishing nests in year *t* per nesting queen in year *t-1*. This relationship implicitly includes within-season colony dynamics (cf. Crone and Williams 2016, and see *Demographic and Dispersal Data*, below).

At the landscape level, population dynamics are described by the population projection matrix:

$$\mathbf{A} = \begin{bmatrix} F_{nat}\delta_{nat} & F_{agr}(1-\delta_{agr}) \\ F_{nat}(1-\delta_{nat}) & F_{agr}\delta_{agr} \end{bmatrix}, \qquad (1)$$

where F_i is the per-capita rate of increase in habitat i. In our model of bumble bees, this represents the rate at which queens in habitat i produce new queens that establish colonies the following year, and is the product of multiple processes: survival of new queens over the winter, colony establishment probability the following spring, the probability that an established colony produces any new queens, and the average number of queens produced per successful colony (Crone & Williams, 2016). Queens that successfully establish new colonies remain in the habitat type in which they were produced with probability δ_i, or emigrate from their natal habitat into the alternative habitat type with probability 1- δ_i.

Demographic and Dispersal Data

We used the values for demographic parameters reported in Crone and Williams (2016), as a basis for exploring the population-dynamic consequences of habitat change. These parameters were estimated from data collected by Williams, Regetz, and Kremen (2012), who experimentally placed bumble bee colonies in different landscape types. Crone and Williams (2016) partitioned colony dynamics into effects of local land cover type, floral resources during colony growth, and within-colony demographic parameters, such as initial colony size and growth rate per floral resource unit (cf. Williams and Crone 2016). Annual population growth rate (queens per queen) was higher in natural landscapes than in conventional agricultural landscapes, even after accounting for ambient floral densities (F_{nat} = 1.64, F_{agr} = 0.56). We explore these discrete effects of local habitat type in our models to illustrate the general effects of source-sink dynamics in the familiar matrix model framework. Preliminary exploration of continuous spatial variation led to qualitatively similar dynamics as the discrete model (E. Crone, unpubl. analyses).

To model the dispersal of bumble bee queens from their natal colonies, we derived dispersal kernels using published data for queen dispersal distances in two bumble bee species: *B. flavifrons* (Fig. 4 in Bowers, 1985) and *B. pascuorum* (Fig. 2B in Lepais *et al.*, 2010). Hereafter, we label the best-supported dispersal kernals for the two species k_{long} and k_{short} to distinguish bumble bees capable of relatively long distance queen dispersal (based on the dispersal data for *B. pascuorum*) from those with limited dispersal (*B. flavifrons*).

Landscape Configuration and Movement between Habitat Types

We used a series of landscape simulations to examine the effects of landscape structure and bumble bee dispersal ability on source-sink dynamics. We used Saura and Martínez-Millán's (2000) modified random cluster algorithm to generate a series of heterogeneous landscapes, while independently controlling the amount of remaining natural habitat, denoted by η, and the degree of habitat aggregation, denoted by α (where larger values of α result in less habitat fragmentation; Fig. 3.4.3.4-1). We constructed a range of landscapes from highly agricultural (η = 0.05) to moderately natural (η = 0.50; more than enough natural landscape to facilitate rapidly increasing populations), and from highly fragmented (α = 0.05) to highly aggregated landscapes (α = 0.30).

We estimated δ_{nat} and δ_{agr} in each simulated landscape under each of the two species' dispersal kernels (k_{short} and k_{long}; see results in *4.4.3.4*), by repeatedly placing "newly emerged" queens randomly in each habitat and drawing random dispersal distances from the empirical dispersal kernels. From these simulations, we calculated the probability that individuals remained in their natal habitat (δ_i) or moved into the alternative habitat ($1 - \delta_i$).

Measurement of Long-Term (Asymptotic) Population Dynamics across Landscape Scenarios

For landscapes under each combination of η and α, we used the corresponding estimates of δ_{nat} and δ_{agr} to generate a population matrix model using equation 1. We used standard methods to describe landscape-wide asymptotic population dynamics:

For each population matrix, we calculated the long-term population growth rate (denoted λ) as the dominant eigenvalue of the matrix (Caswell, 2001). For conventional stage-structured populations, λ describes the per-capita rate at which the population (and each life cycle stage) multiplies after the population has converged on its stable structure in the long-term. For our spatially structured model, λ describes the per-capita annual rate at which the entire source-sink population (and populations in each habitat) grows or declines in the long-term. In this way, λ describes the suitability of the landscape for long-term bumble bee persistence; $\lambda > 1$ implies long-term population growth, $\lambda = 1$ implies population stability, and $0 < \lambda < 1$ implies long-term exponential decline.

The corresponding right eigenvector of each population matrix describes the stable population structure. In our spatially-structured matrix models, population structure represents the relative abundance of bumble bee colonies in natural and agricultural habitats in the long-term, analogous to the stable stage distribution in stage-structured matrix models.

Measurement of Short-Term (Transient) Population Dynamics Following Landscape Change

Sudden environmental perturbations (e.g., conversion of natural habitat to agriculture) can generate short-term "transient" population dynamics that differ from asymptotic dynamics (Stott, Townley & Hodgson, 2011). In our source-sink models, transient dynamics are generated when the distribution of colonies among natural and agricultural habitats immediately following a landscape change differs from the eventual stable distribution at equilibrium. Transient population dynamics will occur until the new stable population structure is attained, at which point the population will grow or decline at a constant annual rate (λ) with a constant relative proportion of bumble bee colonies in each habitat type (Caswell, 2001).

We explored transient dynamics for two contrasting and ecologically relevant scenarios. To study the effects of an abrupt loss of natural habitat, we assume a fraction of a completely natural landscape was abruptly converted to agriculture such that λ in the modified landscape was 0.8 (leading to a 20% decrease per year in the long-term). To study the effects of an abrupt restoration of natural habitat, we assume a fraction of a completely agricultural landscape was immediately restored to natural habitat such that λ in the restored landscape was equal to 1.2

(leading to a 20% increase per year in the long-term). These are extreme cases along a potential continuum of disturbance scenarios, but are nevertheless of heuristic value for understanding transient dynamics in source-sink systems and of applied relevance (e.g., the rapid conversion of over 530,000 ha of formerly protected grassland habitat to agricultural land in the midwestern United States from 2010 to 2013; Morefield *et al.*, 2016).

We assumed that initial habitat loss or restoration initially removed all bumble bees from the altered habitat patches; thus, initial abundance in the newly created habitat was set to 0. This assumption is plausible for ground-nesting bumble bees, where soil preparation (either for agricultural land conversion or seeding of native species during restoration) is likely to impose significant disturbance to underground colonies and diapausing queens. For each scenario, we use numerical simulations to plot the resulting transient dynamics and calculate the time required for the population to converge on its new long-term growth rate.

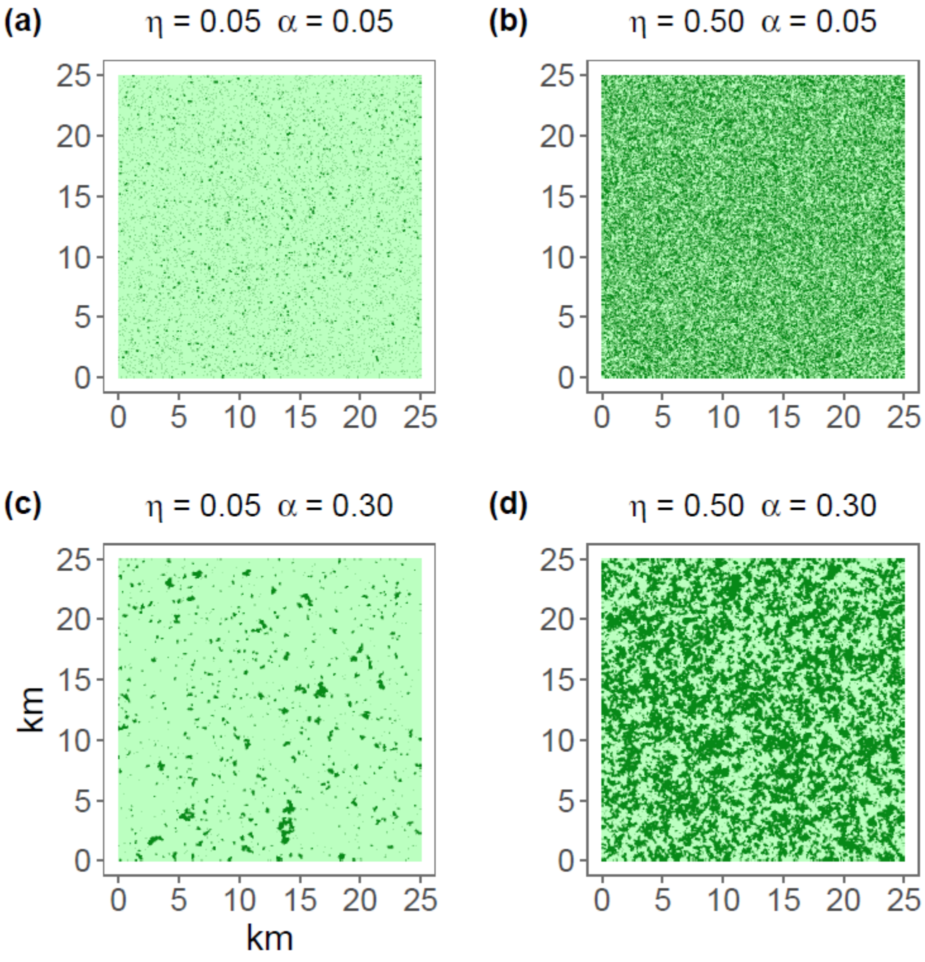


Fig. 3.4.3.4-1. Representative examples of simulated landscapes used to study the consequences of habitat loss, habitat fragmentation, and dispersal ability on source-sink population dynamics. We independently controlled the amount of natural habitat (η; dark green cells) and degree of habitat aggregation (α).

3.4.3.5 Karner Blue & Frosted elfin

For comparison with our Fender's blue work, we conducted more limited studies of demography of ecologically similar at-risk butterflies, frosted elfin, *Callophrys iris*, which is not federally listed but is a species of conservation concern in 11 states (DE, MD, NH, OH, Ct, MI, NJ, NY, WI, MA and RI), and Karner blue (*Lycaeides melissa samueli*) which is a federally-listed endangered species. Both species occur on military lands: The frosted elfin is of concern to at least three DoD and DoE lands in the northeast: Westover Air Reserve Base, MA;

Brookhaven National Laboratory, NY (historic), and the NH State Military Reserve. The Karner blue occurs at Ft. McCoy, WI, and the NH State Military Reserve.

For the frosted elfin, we monitored adult butterfly populations for three summers, 2015-2017, in relation to a management burn that was conducted in 2015 (after the adult flight period) on a private conservation lands. We expected that, if the effects of this particular management burn were similar to the effects of fires used to improve Fender's blue habitat, we might see a drop in population size in 2016 (due to direct effects of fire) but recovery and a possible in 2017 (due to increased habitat quality). We tested this by conducting a mark-recapture study in three years, and estimating the three population sizes using the POPAN module in Program MARK.

For the Karner blue, we worked with NH Fish and Game to estimate dispersal kernels from a mark-recapture program they conducted at the Concord Airfield (adjacent to the NH State Military Reserve) from 2007-2015. We analyzed movement using multi-state mark-recapture models with states defined as sites on the airfield and adjacent lands, and distance-dependent transition probabilities. We also estimated the "resistance" (sensu Ricketts 2001) of different habitat types (open, forest, and pavement) using multistate models with different coefficients for the effect of distance through different habitat types.

3.4.4 End User Work Shop

In May 2016, we convened a workshop with project scientists and DoD Natural Resource specialists to discuss project findings, demonstrate project tools and gain insights into how project tools might be fine-tuned to address resource management needs. The workshop was held at Washington State University's Vancouver campus, within proximity of two of our three focal species, Fender's blue and Taylor's checkerspot.

In the invitation, we described the overall SERDP project goals, including developing Spatially Explicit Individual Based Management Models to guide management on DoD land when concerns about status of habitat as source vs sink may influences natural resource decisions for at-risk species. The goals of the workshop were

- to demonstrate the Spatially Explicit Individual Based Models (SEIBMs) to the managers working most closely with these species, and with related species on Department of Defense Lands,
- to create a venue to demonstrate the value of the approach to managers needing to make short and long-term decisions about how to allocate and manage land for these at-risk species,
- to spark discussions about how biologists and managers from across these systems can learn from each other's work to enhance the work in their own region, and
- to provide us with feedback about how we can direct future research to promote recovery of endangered species in concert with Department of Defense activities as well as other uses of these lands

4 Results and Discussion

4.1 Fender's Blue Butterfly

4.1.1 SEIBMs direct planting

<u>4.1.1.1: Population Responses</u>

We found stable population dynamics among the scenarios with environmental stochasticity independent among patches (uncorrelated; Scenarios 1-12), with only one scenario resulting in population declines (Figure 4.1.1-1). Increasing the number of patches decreased the variability of the population around carrying capacity, but also resulted in slower population growth to carrying capacity. With 25 patches spread through the 100 ha site, population growth was slower. In the 250 ha site with 25 patches, populations generally declined to extinction (Figure 4.1.1-1).

Population dynamics were more variable among the scenarios with environmental stochasticity constant among patches (correlated; Scenarios 13-24). Standard deviation of the mean population size each year was greater when compared with the uncorrelated scenarios (Figure 4.1.1-2). Variability of the population around carrying capacity remained high across all scenarios except for those that tended toward extinction. Increasing the number of patches generally decreased population growth to carrying capacity compared to the uncorrelated scenarios, and the 25 patch planting strategy resulted in population declines in both the 100 ha and 250 ha sites (Figure 4.1.1-2).

4.1.1.2: Residence Time Responses

Residence time per butterfly decreased as the number of patches increased among scenarios (Figure 4.1.1-3a; 4.1.1-3b). In a single six hectare patch, residence time per butterfly was 13 days in both correlated and uncorrelated scenarios. Among the uncorrelated scenarios, increasing the number of patches to 9 dropped residence time to 9.5 days and 7.9 days at the 25 ha and 250 ha sites, respectively. Further increasing the number of patches to 25 resulted in a residence time of 8 days at the 25 ha site and 5.5 days at the 250 ha site (Figure 4.1.1-3a). Residence times did not differ when compared to the correlated scenarios (Figure 4.1.1-3b). When edge behavior was removed from the model, residence time per butterfly dropped to 2.9

days in a single six hectare patch and to 0.6 days in the 250 ha site with 25 patches (Figure 4.1.1-3c).

4.1.1.3: Intrinsic Rate of Increase among Scenarios

Increasing the number of patches generally decreased the intrinsic rate of increase (*r*) among all scenarios (Figure 4.1.1-4a; 4.1.1-4b). Populations grew fastest within a single six-hectare lupine patch, up to *r* = 1.21 (95% CI: 1.05 – 1.40) with correlated environmental stochasticity and up to *r* = 1.18 (95% CI: 1.02 – 1.37) with uncorrelated environmental stochasticity. Among the uncorrelated scenarios, increasing both the number of patches and the size of the site resulted in lower estimates of *r* (Figure 4.1.1-4a). The 9-patch scenario within the 25 ha site produced *r* = 0.96 (95% CI: 0.92 – 1.00) compared to *r* = 0.53 (95% CI: 0.52 – 0.55) at the 250 ha site. This contrasts with the 25-patch scenarios, with an intrinsic rate of increase of *r* = 0.70 (95% CI: 0.68 – 0.71) at the 25 ha site and *r* = 0.01 (95% CI: -0.03 – 0.04) at the 250 ha site.

We found a similar trend of increasing the number of patches and the size of the site on estimates of r among the correlated scenarios (Figure 4.1.1-4b). Compared to the uncorrelated scenarios, the intrinsic rate of increase was routinely lower as patch fragmentation and site size increase. With the 4-patch scenarios, *r* = 0.98 (95% CI: 0.92 – 1.04) at the 25 ha site for the uncorrelated scenario, and *r* = 0.71 (95% CI: 0.63 – 0.81) for the same site size in the correlated scenario. The correlated 9-patch scenarios resulted in *r* = 0.57 (95% CI: 0.50 – 0.65) at the 25 ha site and *r* = 0.34 (95% CI: 0.29 – 0.39) at the 250 ha site.

4.1.1.4: Discussion

Our study indicates that there is substantial flexibility in planning restoration plantings for Fender's blue. A large range of lupine patch sizes spread across small to medium size sites does well at balancing sufficient habitat area that is close enough for butterflies moving throughout the site to readily locate lupine. However, when sites grow too large (e.g. 250 ha), the patches are too isolated, and butterflies that fly into the matrix do not locate sufficient lupine habitat to have adequate fecundity.

Coupled with these findings, is the overwhelming importance of understanding the behavior of the focal species in relation to habitat structure. The population dynamics in our restoration scenarios would be fundamentally altered if our focal species lacked edge behavior. In this case, instead of having a great deal of flexibility in planning for restoration, the population is likely to decline rapidly to extinction unless significant additional resources are restored. Many species exhibit attraction behavior towards critical resources or structures (Kalarus et al. 2013, Skorka et al. 2013). For example, experimental work by Crammer et al. (2012) in the United Kingdom indicates that bumblebees follow hedgerows as well as artificial linear structures and butterflies also respond to these structures (see also Dover and Sparks 2000). Spatial planning of these elements influences connectivity for these bees and reproductive success of plants which the bees pollinate.

We note that in some species attraction to conspecifics drives behavioral decisions and may be more important than habitat structure or quality, *per se* (e.g. O'Neil et al. 2014). In butterflies, as well as many other taxa, some species show positive density dependent emigration and immigration (e.g Nowicki and Vrabec 2011) and other species show negative density dependent migration (Roland et al. 2000). We do not know the effect of density on Fender's blue migration and these factors are not considered within our modeling efforts here.

We note that it is also the case that for many foraging insects, a correlated random walk without a bias captures the movement behavior and population dynamics of the populations (Kareiva and Shigesada 1983, Brouwers and Newton 2010), and that movement behaviors can lead to persistent populations over the site if the sites are highly heterogeneous with sufficient coverage of key hostplants. For Fender's blue, a correlated random walk without bias would be insufficient to support the population, as evidenced by the rapid decline to extinction in simulation runs with no edge behavior.

Questions we raise are parallel to questions often considered in the context of restoring pollinators to augment ecosystem services. Surprisingly landscape context is rarely considered in the context of pollination services. Hadley and Betts (2012) were stunned to find that only 6 of 303 studies investigating pollinator services considered effects of landscape context and structure as separate from effects of habitat loss. This finding indicates a lack of awareness in considering pollinator behavior in the context of this ecosystem service. In contrast, studies focused on plant insect interactions are increasingly aware of the role of plant spacing in the population dynamics of the herbivores

Integrating behavior into site-based restoration planning leads to scale-sensitive decisions for recreation of habitat structure. For example, Conlisk et al. (2014) find that if habitat restoration for the San Diego cactus wren, *Campylorhynchus brunneicapillus sandiegensis*, is limited to a 20 ha area, restoration efforts should focus on enhancing patch size. In contrast, if restoration efforts include a 200 ha restoration, then connectivity becomes a key consideration.

Rarely is behavior considered as an active component in spatial planning of restoration efforts. A notable exception to this is restoration of tropical forests. In tropical dry forests, Lindell and others (2008, 2013) note that placement of trees as bird-perches influences behavior of avian seed predators, key species to facilitate seed dispersal of tropical trees. Advantageous placement of focal trees results in more rapid and complete restoration of tropical dry forests. Similarly, clusters of restored trees substantially increased recruitment of animal-dispersed tree species in tropical premontane forests (Zahawi et al 2013). For Fender's blue, spatial planning will be important resulting dynamics at sites that are large for the Willamette Valley (250 Ha) but, due to edge behavior, the system is robust to a large variety of planting configurations at smaller sites as long as sufficient resources are restored across the site.

Our approach lends itself to address questions raised by numerous authors on the challenge of defining a "patch." As the field of landscape ecology and conservation planning has exploded over the last two decades, the need to specify patches on a map which have ecological significance has similarly mushroomed. In fields such as conservation planning for rare species, state level conservation plans, or plans which respond to emerging threats from climate change, use of maps with discrete patch boundaries are central. But, often when planners need to demarcate the maps, questions arise about the complexity or lack of ecological understanding and limit our ability to draw lines on maps. In our case, great discussion surrounds the question of boundaries for Fender's blue habitat. Is it the boundary of lupine? Or nectar? Of the meadow? The property line? In addition, when species use multiple resources that do not directly co-occur (e.g. hostplants and nectar resources), demarcating maps is more challenging. Finally, lines might be drawn on maps for multiple purposes. So, for example, one map might include lupine habitat which drives attraction to habitat and thus residence time, and other map might include nectar habitat as areas that include key resources to be managed or conserved to maintain a population. Decisions about where to draw these lines, to create a single map vs. multiple maps for different purposes, or which maps to use for what purpose, are critical to conservation and restoration planning, as well as region-wide conservation initiatives. Our study for Fender’s blue supports flexible planning in which there is a minimum coverage of a key resource, hostplant lupine, across a spatial area of a “patch.” This approach may help with planning for other taxa in which decisions about resource abundance and distribution are critical to restoration success.

We conclude with a few thoughts for advancing restoration work for at-risk species. First, models and approaches such as this are possible because the models are carefully parameterized based on demography and dispersal behavior of the focal species. While less depth may be necessary in some cases, it would be short-sighted to ignore the importance of key behavioral traits, in this case edge behavior, when planning for restoration. In several cases, underestimating the importance of behavioral traits has resulted in ecological traps in which individuals are attracted to sub-optimal habitat. Second, models provide a way to conduct “virtual experiments,” which can save thousands of dollars and decades of time, depending on the type and extent of habitat. Even limited data can be used in a modeling context to construct “what if” scenarios that can help guide on-the-ground efforts. Finally, a combination of data and models can be used to construct “rules of thumb” which can help biologists and planners take next steps in pivotal conservation decisions. In this case, our models help inform DoD, USFWS and other agencies that we have great flexibility in the arrangement of reproductive resources as long as there are sufficient resources and spread within a site of ~ 50-100 Ha. For many planning efforts, this is sufficient precision for planners to take next steps in prioritizing land and selecting areas for purchase.

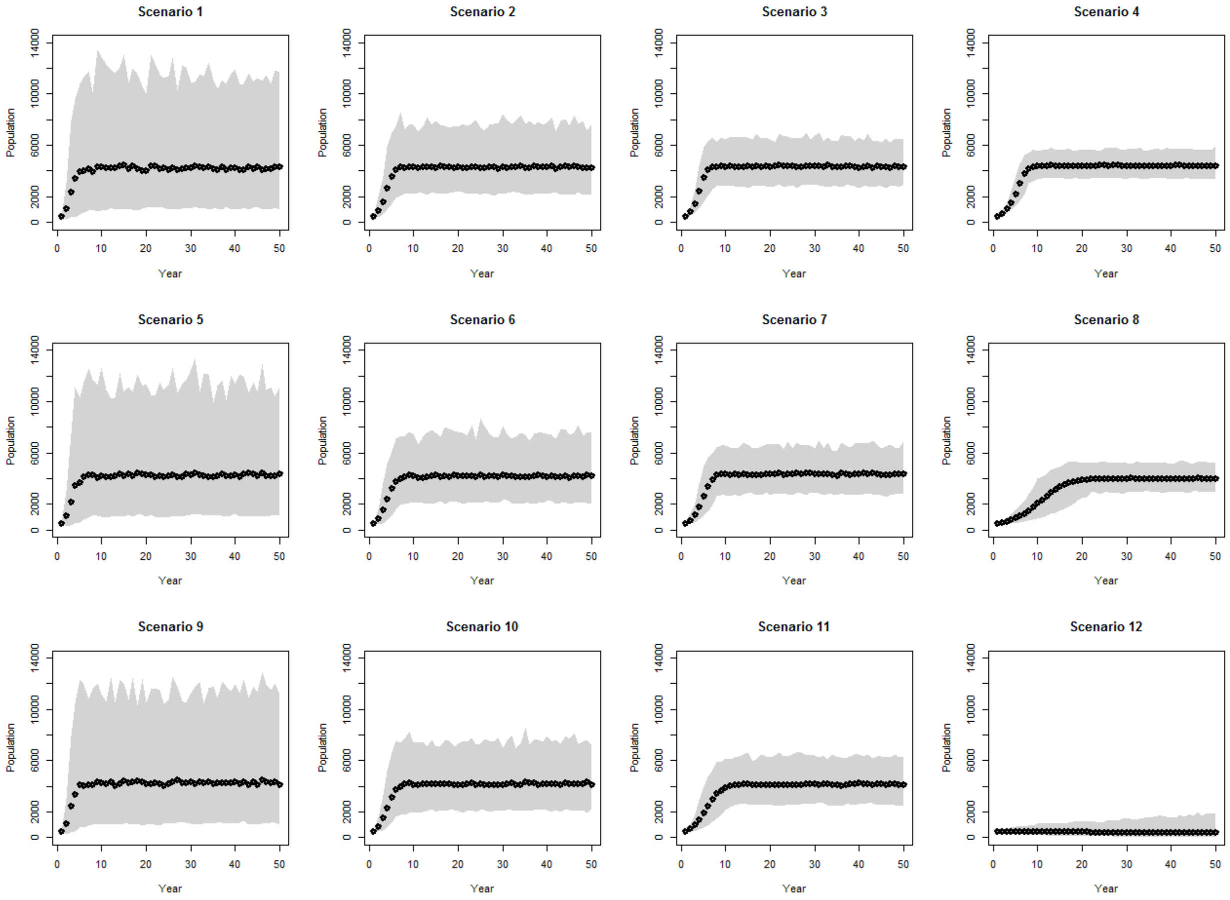


Figure 4.1.1-1. Population trajectories of each scenario with environmental stochasticity uncorrelated among patches. Black dots = mean population size, shaded gray region = 95% confidence intervals.

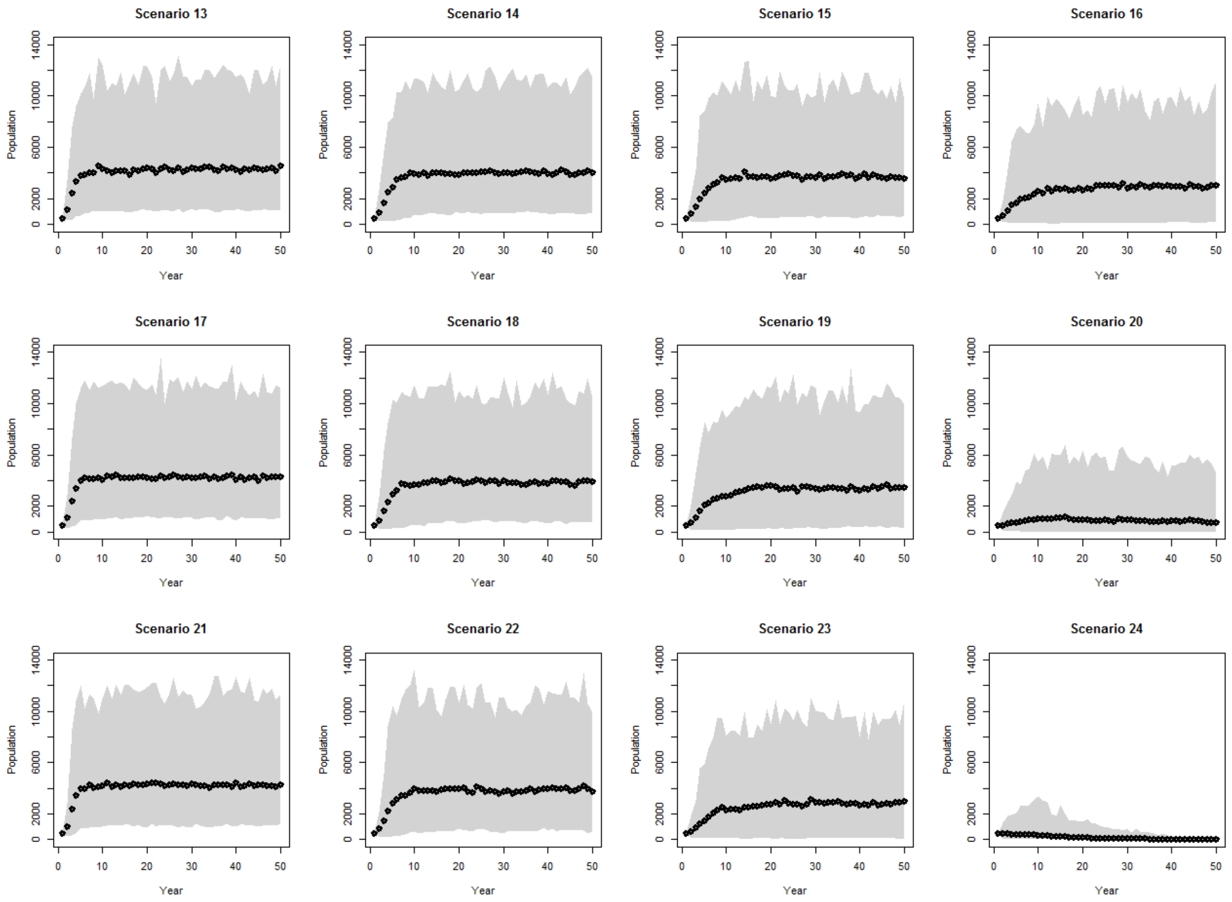


Figure 4.1.1-2. Population trajectories of each scenario with environmental stochasticity correlated among patches. Black dots = mean population size, shaded gray region = 95% confidence intervals.

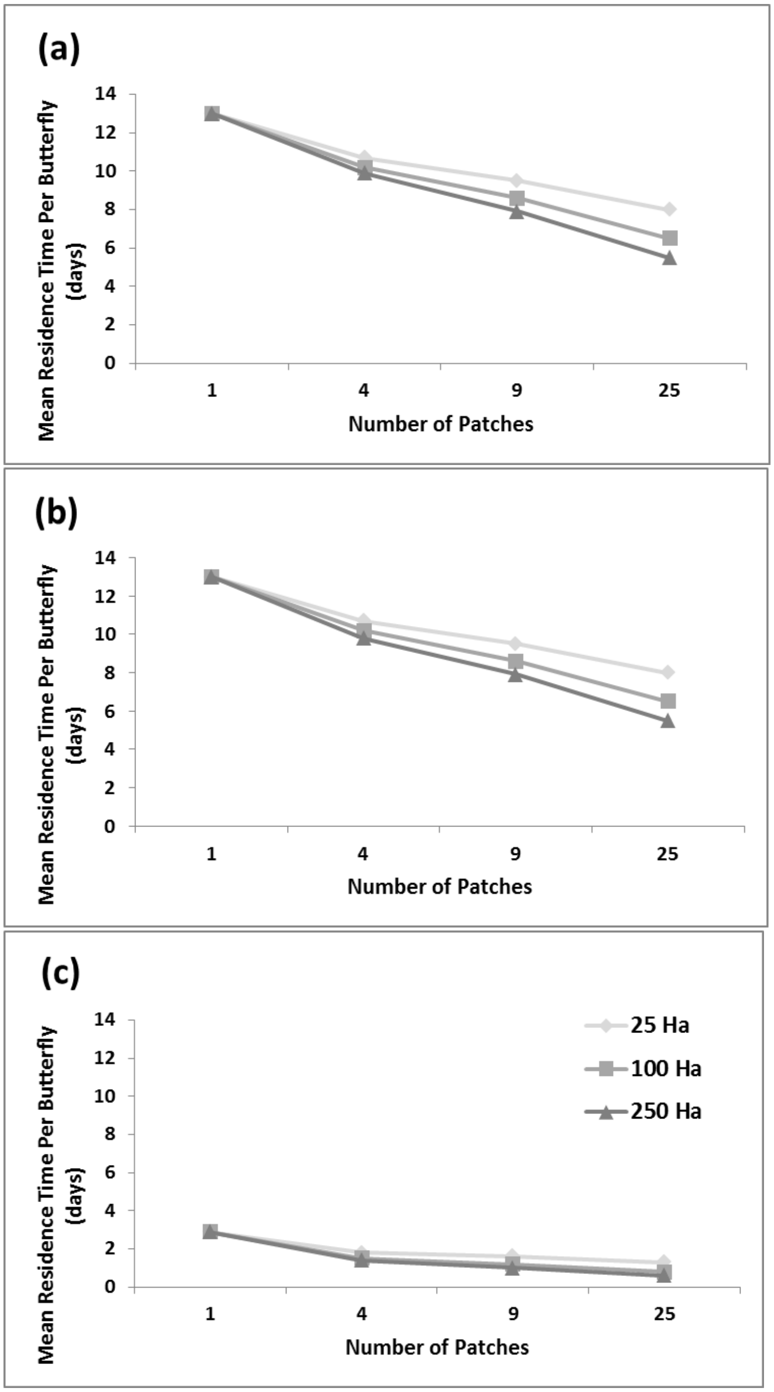


Figure 4.1.1-3. Mean residence time per butterfly for each scenario. (a) shows residence times with environmental stochasticity uncorrelated among patches. (b) shows residence times with environmental stochasticity correlated among patches. (c) shows residence times without edge behavior. Light gray circles = 25 ha site, gray squares = 100 ha site, dark gray triangles = 250 ha site.

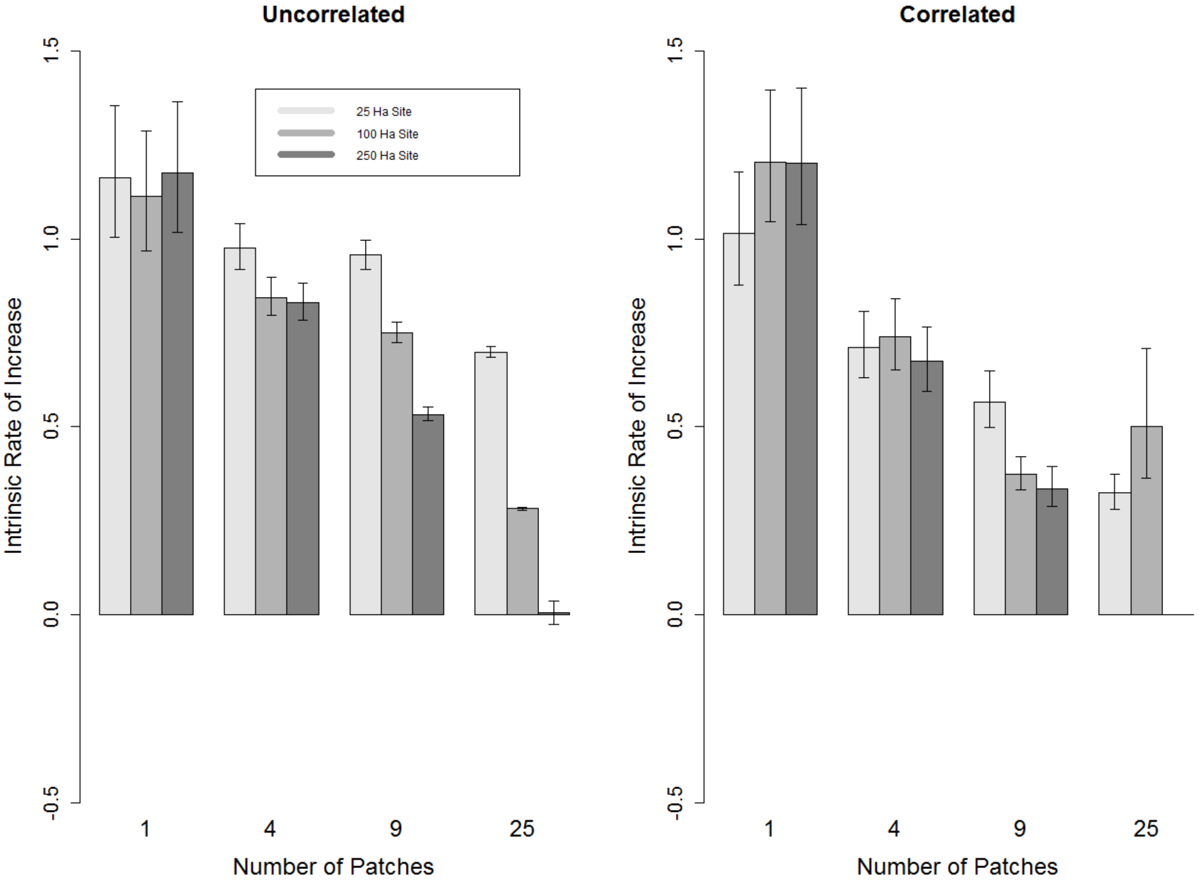


Figure 4.1.1-4. Estimates of intrinsic rate of increase values for each scenario with 95% confidence intervals. (a) Environmental stochasticity uncorrelated among patches. (b) Environmental stochasticity correlated among patches.

4.1.2 Demographic influences of fire

Demographic and behavioral responses

Fire increased eggs per larva (i.e., fecundity) in 2012 and 2013, but not in 2014 (Table 4.1.2-1, Figure 4.1.2-1a). There were 68 eggs/larva in the year of the fire and the year after the fire (2012 and 2013, Table 4.1.2-2) while the control plots had 48 eggs/larva in both of these seasons. In 2014, three years after the fire, both burn and control plots had 25 eggs/larva. Thus, fire influences eggs/larva for two years post fire.

Fire affected larval survival, as measured by leaf damage, with significantly less damage in burn plots in 2012, and significantly more damage in burn plots relative to controls in 2013 (Table 4.1.2-1, Figure 4.1.2-1b). By 2014, damage did not differ between control and burn plots. This pattern implies that there is initial mortality due to fire (2012), followed by a one-year increase in larval survivorship. The following year, larval survival (as measured by larval damage) in treatment plots returns to baseline pre-burn levels.

Movement behavior was not influenced by fire history. In all analyses, movement parameters did not differ significantly between habitat that had been burned in the prior season and habitat that had not been burned ($\chi^2 < 1.2$, $p > 0.27$ for all main effects and interactions of fire history x lupine presence). All movement parameters (move length, turning angle and move time) were influenced by presence of lupine, the larval host plant ($\chi^2 > 3.86$, $P < 0.05$ for all main effects of lupine; Table 4.1.2-3, Table 4.1.2-4). In addition, butterflies did not show habitat preference at the edge of burned areas. The proportion crossing into the burn did not differ from 0.5 ($|z| < 0.6$, $P > 0.56$; Table 4.1.2-5), nor was the probability of entering the burned area affected by the presence of lupine plants ($\chi^2 <1.2$, $P > 0.24$, Table 4.1.2-5) regardless of the distance at which we evaluated crossing distances (1, 2 or 5 m from the release location).

Table 4.1.2-1. Models of comparing model structure with effect of prescribed fire to null model with no effect of fire for eggs, and larvae. Note, damaged leaves used as an index of post-diapause larval survival. See Warchola *et al.* (2015) for additional details. Shown are □^{2}from type II χ^2tests from analysis of deviance.

Model	Year_t	χ^2	df	$P(\chi^2)$
Fecundity				
Eggs_t / larva_t	2012	5.28	1	0.022
	2013	4.80	1	0.029
	2014	0.07	1	0.791
Overwinter survival				
Damaged leaves_t / egg_{t-1}	2012	8.94	1	0.003
	2013	4.31	1	0.038
	2014	0.60	1	0.437

Table 4.1.2-2. Demographic parameters for Fender’s blue in relation to time since fire (fires lit in Fall 2011). Damage is the number of lupine leaves showing characteristic feeding damage (used as a proxy for larval presence as described in text)

Parameter	Control				
	2011-12	2012-13	2013-14	2014-15	
Larvae/damage	0.045	0.029	0.062		
Damage/egg	0.291	0.723	0.337		
Larvae/egg*	0.013	0.021	0.021		
Eggs/larva		48.848	47.573	24.513	
Growth rate (λ)	0.490	1.033	0.999	0.334	
	Burn				
	2011-12	2012-13	2013-14	2014-15	
Larvae/damage	0.045	0.029	0.062		
Damage/egg	0.132	1.223	0.275		
Larvae/egg*	0.006	0.036	0.017		
Eggs/larva		68.147	67.367	25.635	
Growth rate (λ)	0.223	2.437	1.157	0.349	
	Differences due to fire (log-scale)				GLMM average
	2011-12	2012-13	2013-14	2014-15	
Larvae/damage					0.043
Damage/egg	-0.7893	0.5250	-0.2016		0.313
Larvae/egg	-1.1754	0.1789	-0.4505		0.022
Eggs/larva		0.3330	0.3479	0.04478	37.340
Growth rate multiplier	0.4542	2.3584	1.1575	1.0458 ≈1	

*Larva/egg = Larvae/damage x damage/egg

Table 4.1.2-3. Analyses of movement parameters. Shown are χ^2 from type II χ^2 tests from analysis of deviance.

Parameter	Fixed Effect	χ^2	df	$P(\chi^2)$
Move length (m)	Burn	0.45	1	0.5014
	Lupine	31.95	1	<0.0001
	Burn × Lupine	0.11	1	0.7341
Turning Angle (cos, radians)	Burn	1.18	1	0.2767
	Lupine	3.86	1	0.0496
	Burn × Lupine	0.74	1	0.3895
Move time (s)	Burn	0.26	1	0.6078
	Lupine	29.35	1	<0.0001
	Burn × Lupine	0.09	1	0.7608

Table 4.1.2-4. Dispersal parameters from burn experiment.

Parameter	Habitat	Burn mean	95% CI	Control mean	95% CI
Move length (m)	Inside Lupine	2.39	(1.98 – 2.89)	2.19	(1.82 – 2.63)
	Outside Lupine	3.56	(2.91 – 4.37)	3.45	(2.99 – 3.94)
Turning Angle (cos, radians)	Inside Lupine	0.78	(0.71 – 0.84)	0.82	(0.78 – 0.87)
	Outside Lupine	0.76	(0.69 – 0.83)	0.77	(0.72 – 0.81)
Move time (s)	Inside Lupine	21.55	(16.89 – 27.63)	23.13	(18.17 – 29.48
	Outside Lupine	14.64	(11.07 – 18.71)	14.64	(11.80 – 18.21)

Table 4.1.2-5. Boundary behavior, estimated from GLMMs including random effects of experimental blocks ('fingers') and fixed effects of lupine patches. Main effects of burning were evaluated by testing whether intercept terms differed from 0 across habitat types (0 on a logit scale = 0.5 on a back transformed scale), and interactions with lupine were tested by comparing intercept-only models to models with fixed effects of lupine habitat using likelihood ratio tests

Distance from release	Lupine effect (Does proportion entering burn differ with lupine?)		Edge effect (Does proportion entering burn differ from 0.5, across both habitats?)		Proportion which fly towards burned habitat (95% CI)		Among-finger SD
	χ^2	*P*	z	*P*	Inside Lupine	Outside Lupine	
1 meter	0.20	0.651	-0.58	0.564	0.40 (0.15 - 0.71)	0.48 (0.34 - 0.64)	0 (10^{-7})
2 meters	0.02	0.892	-0.35	0.729	0.50 (0.22 - 0.78)	0.48 (0.36 - 0.60)	0 (10^{-8})
5 meters	1.38	0.241	-0.08	0.729	0.69 (0.35 - 0.91)	0.45 (0.30 - 0.63)	0 (10^{-8})

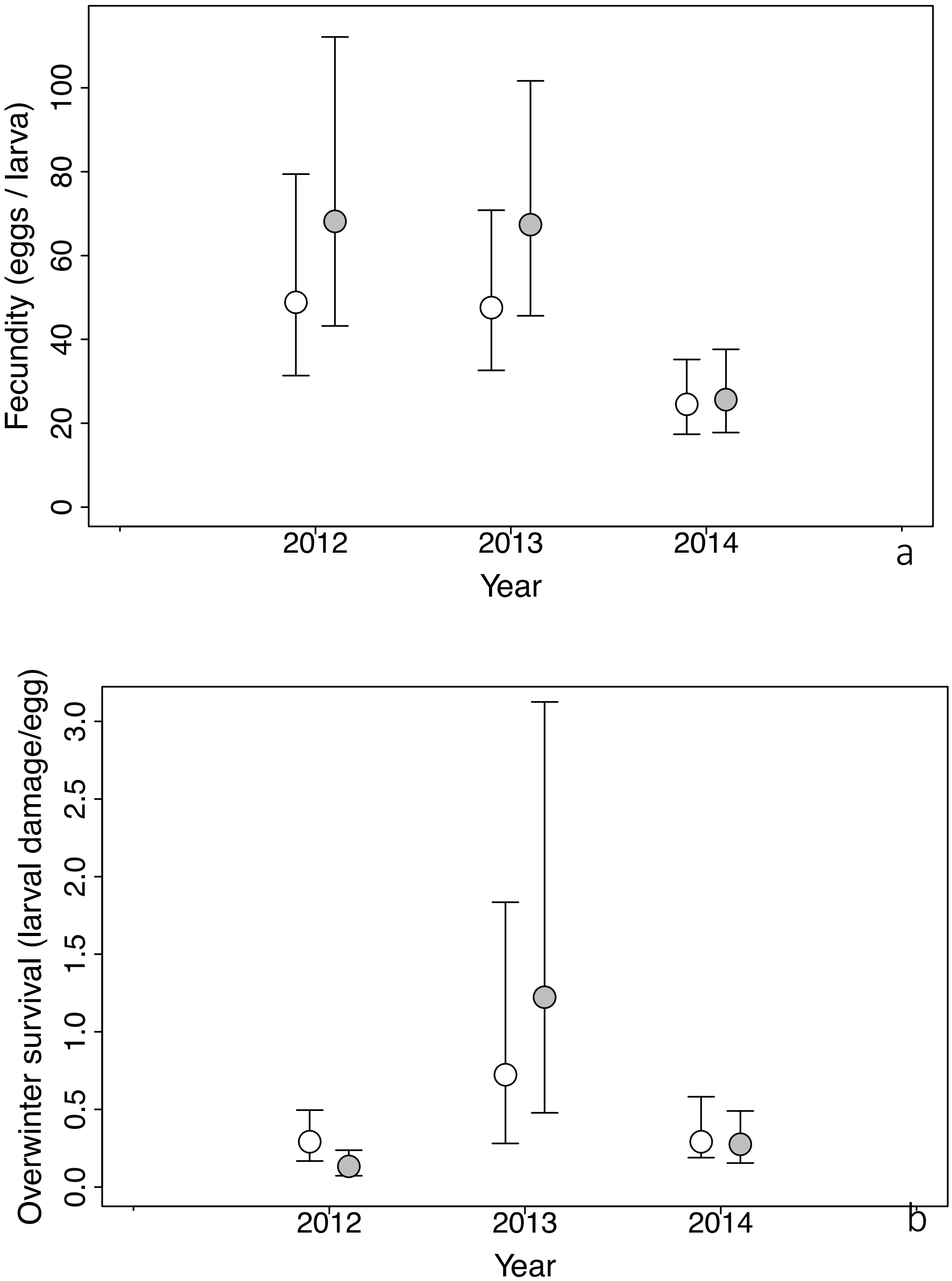


Figure 4.1.1-2. Demographic responses of Fender's blue: a) eggs per larva in 2012, 2013 and 2014 in burn (gray) vs control (white), and b) overwinter survivorship (larval leaf damage per egg). Error bars are 95% confidence intervals.

4.1.3 Time series demographic model of fire effects

Population model

For Scenario 1, i.e., targeted burning of habitat ≥3 years post-burn, the best strategy is to burn as much of this habitat stage as possible, with the optimum at burning 100% of this habitat stage each year, which is 27.03% of the landscape (Figure 4.1.3-1). Directed fire (Scenario 1) is always better than randomly burning without respect to fire history (Scenario 2). However, if targeted fire is not feasible or if a wildfire starts, the best strategy (e.g., the context in which managers might not want to control wildfires) is to burn 19% of the habitat (Figure 4.1.3-1b, max $\lambda = 1.085$ at 19% of the habitat burned when $\delta = 0$, max $\lambda = 1.012$ at 0 of the habitat burned when $\delta = 1$). If more than 42% of the landscape burns in an undirected manner and dispersal is random ($\delta = 0$), then $\lambda < 1$ and fire quickly shifts from a beneficial management strategy to disturbance purely detrimental event. With all local dispersal ($\delta = 1$), population growth rate (λ) drops below 1 with 8% of the habitat burning.

In our models, local dispersal, i.e., reproducing within the same successional stage, is always worse than dispersing throughout the site. With targeted fire management (Scenario 1), $\lambda = 1.2$, with global dispersal ($\delta = 0$) but less than 1.01 with 100% local dispersal (Figure 4.1.3-1a). With undirected fire (Scenario 2), the effect of dispersal strategy on population growth is smaller, especially when a large fraction of the habitat burns (Figure 4.1.3-1b). In addition, local dispersal reduces the optimal proportion of the landscape burned under Scenario 2 (untargeted burning), but not Scenario 1 (targeted burning; Figure 4.1.3-1a & b)

Life table response experiments (LTRE) indicated that the three demographic effects of fire have similar magnitude impacts on population growth rates. In Scenario 1, reduced larval survival through the fire leads to an 18.1% decrease in growth rate, increased fecundity for two years after the burn leads to a 20.5% increase in growth rate, and increased larval survival in the year after the fire, leads to an 18.0% increase in growth rate. Together, these effects result in a 20.5% increase in growth rate, i.e., $\lambda = 1.22$ with targeted burning of 100% of habitat that was burned at least 3 years ago (Figure 4.1.3-2a). In Scenario 2, reduced larval survival through the fire leads to a 13.7% decrease in growth rate, increased larval survival in the year after the fire leads to an increase in 11.1% increase in population growth rate, and increased fecundity for two years after the fire leads to an 11.4% increase in population growth rate. Together, these effects result in a 7.2% increase in growth rate, ie. $\lambda = 1.08$ assuming the optimum proportion of habitat burned with unplanned fire, 19% (Figure 4.1.3-2b).

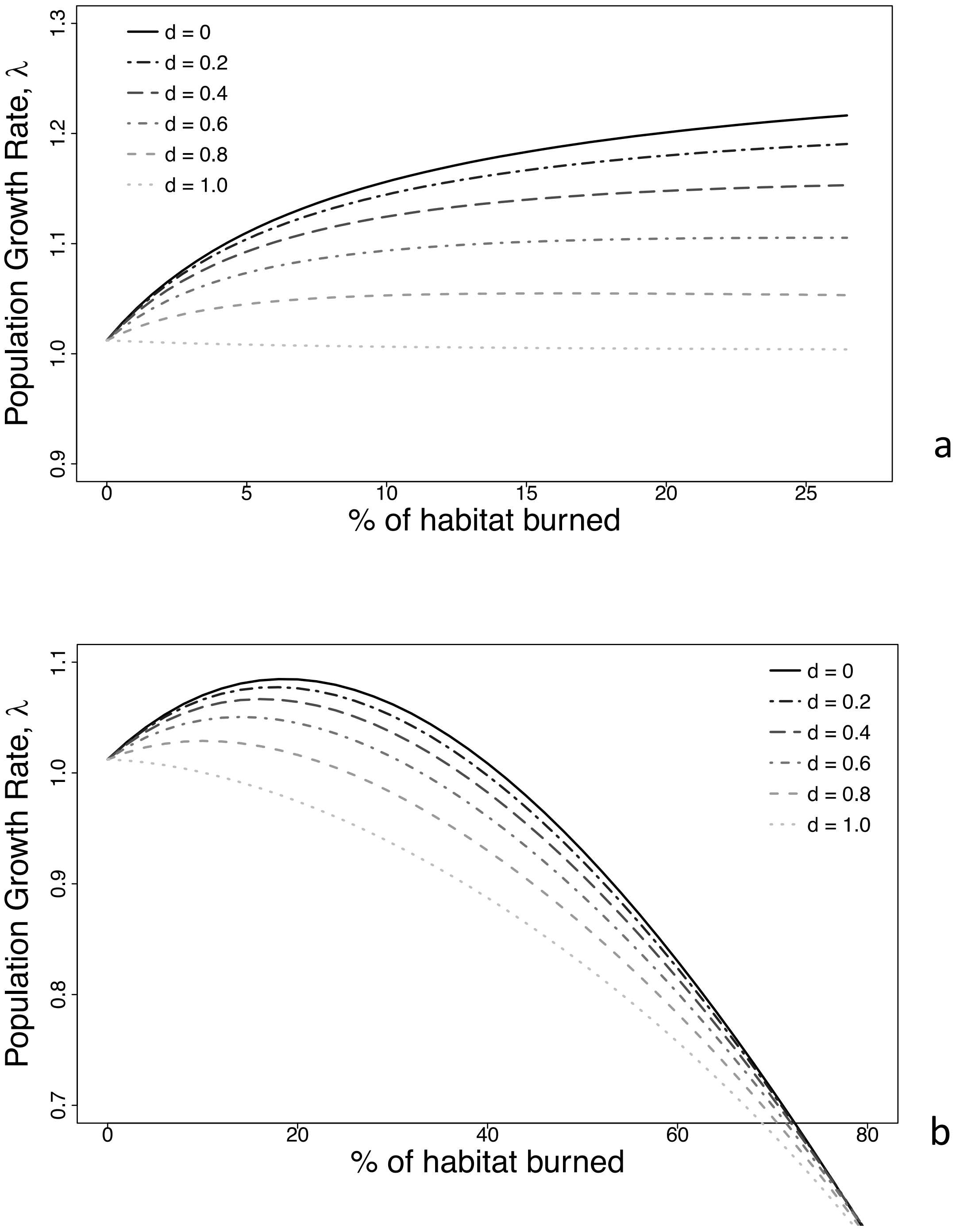


Figure 4.1.3-1. Targeted vs Non-targeted burns as a function of percent habitat burned. a) targeted fire only in habitat 3 or more years since last burn. Note, maximum burn in targeted burn is 27% of the habitat, the stationary amount of stage 3 habitat at equilibrium. b) non-targeted fire. Solid black is 100% random/non-local dispersal (d = 0). Lightest gray dotted line = 100% local dispersal (d = 1).

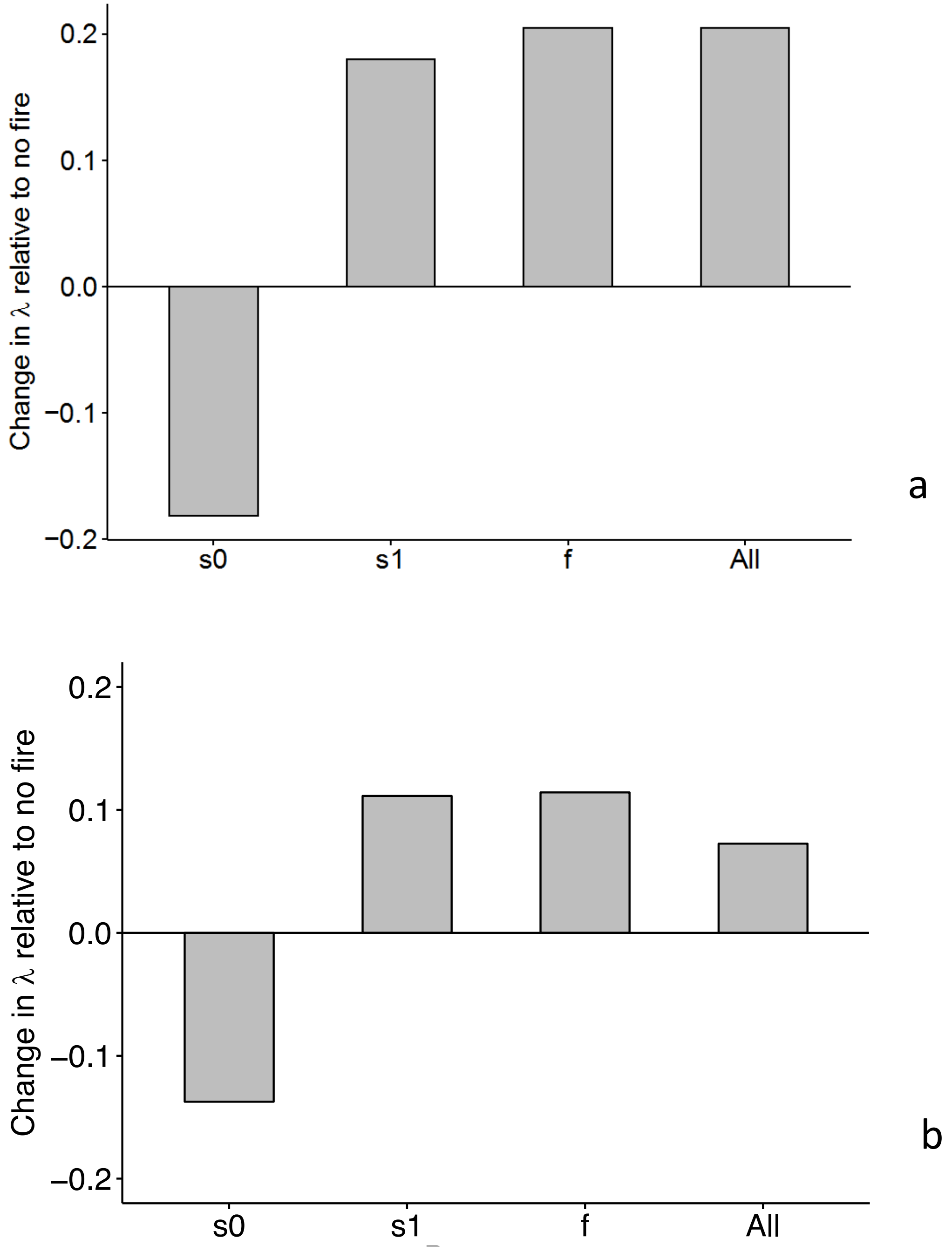


Figure 4.1.3-2. Results of the life table response experiment analysis (LTRE): a) in targeted burn and b) in non-targeted burn. The effects of fire on larval survivorship during a burn (s_0), and the year after the burn (s_1), fecundity after the burn (f , which is the same for f_1 and f_2) and all parameters simultaneously influencing the population (*All*) .

4.1.4 SEIMBs fire management

4.1.4.1: Population Response to Fire

The observed metapopulation growth rate from census data from 1993 – 2015 is λ = 1.28 (95% CI: 1.24 – 1.32), and the metapopulation growth rate from the no fire scenario simulation is λ = 1.15 (95% CI: 1.14 – 1.17). Cool fire under the “whole” scenario reduces metapopulation growth rate to λ = 1.23 (95% CI: 1.21 – 1.25), and hot fire further reduces growth rate to λ = 1.17 (95% CI: 1.15 – 1.19). The “half” scenarios with both hot and cool fire result in metapopulation growth rates similar to the observed growth rate (Figure 4.1.4-1). We found significant increases in metapopulation growth rate relative to the observed growth rate with the “quarter” scenario. Cool fire increases metapopulation growth rate to λ = 1.36 (95% CI: 1.34 – 1.37), and hot fire increases growth rate to λ = 1.55 (95% CI: 1.52 – 1.57). Hot fire under the “quarter” scenario brings metapopulation growth rate to conservation target levels set by population viability analyses (Figure 4.1.4-1).

We found differences between sites in population growth rate response to fire (Figure 4.1.4-2). Fire always decreased growth rates below observed growth rate at the small sites (Shore Lane and Eaton Lane), even with fine-scale burn plans. Under the “whole” scenario, hot fire decreased population growth rate at Shore Lane to λ = 0.68 (95% CI: 0.65 – 0.72), and to λ = 1.10 (95% CI: 1.07 – 1.13) at the largest site, Green Oaks. The “quarter” scenario with hot fire decreased population growth rate to λ = 0.99 (95% CI: 0.97 – 1.01) at Shore Lane, but increased growth rate to λ = 1.51 (95% CI: 1.48 – 1.54) at Green Oaks. Only the “quarter” scenario with hot fire raised population growth rate at the largest site to conservation target levels set by population viability analyses (Figure 4.1.4-2).

4.1.4.2: Proportion of Eggs from Immigrant Butterflies

Under the no fire scenario, 5% (95% CI: 4.98 – 5.13%) of eggs in the landscape are laid by immigrant butterflies. This proportion is not different under the “quarter” scenario in the year after fire (Figure 4.1.4-3). The “whole” scenario with cool fire increases the proportion in the year after fire to 10.2% (95% CI: 9.8 – 10.6%), and nearly doubles the proportion to 18.9% (95% CI: 18.3 – 19.5%) with hot fire. We found the “half” scenario slightly increases the proportion of eggs laid the year after fire by immigrant butterflies compared to no fire (Figure 4.1.4-3).

We found stark differences of post-fire proportions between sites (Figure 4.1.4-4). Under no fire, the proportion of eggs laid by immigrant butterflies at Shore Lane was 66%, but only 1% at Green Oaks. The “quarter” scenario did not significantly change proportions of eggs laid by immigrant butterflies in the year after fire, and tended to slightly reduce proportions compared to no fire. Proportions were significantly higher with hot fire under the “whole” scenario, ranging from 86% (95% CI: 85 - 86%) at Shore Lane to 44% (95% CI: 43 - 45%) at Spires Lane. The “half” scenario slightly increased the proportion of eggs laid the year after fire at each site except for Green Oaks (Figure 4.1.4-4).

4.1.4.3: Extirpation Risk from Management Strategies

Fire management that does not partition sites into burn units tends to increase the frequency of extirpations and increase extirpation risk for small populations (Table 4.1.4-1). Under the “whole” scenario, Shore Lane had an extirpation probability of 20% (95% CI: 17 – 24%) with hot fire. For the same scenario, the largest population had an extirpation probability of 1% (95% CI: 0 – 2%). Both frequency of extirpation and extirpation risk noticeably decrease with the “half” and “quarter” scenarios. We found 0% extirpation risk under the “quarter” scenario with hot fire for all populations except Shore Lane, which showed extirpation under every scenario (Table 4.1.4-1).

4.1.4.4: Life-table Response Experiment without Immigrant Eggs

Metapopulation growth rate with no fire and no immigrant eggs is λ = 1.08 (95% CI: 1.05 – 1.12; Figure 4.1.4-5). Cool fire under the "whole" scenario slightly increases metapopulation growth rate to λ = 1.17 (95% CI: 1.15 – 1.19), while hot fire reduces growth rate to λ = 1.03 (95% CI: 1.00 – 1.06). The "half" scenarios result in increases up to λ = 1.21 (95% CI: 1.19 – 1.23) with cool fire, and the "quarter" scenarios substantially increase metapopulation growth rate up to λ = 1.47 (95% CI: 1.44 – 1.49) with hot fire when compared to no fire (Figure 4.1.4-5). The small populations of Shore Lane and Eaton Lane are routinely extirpated under all scenarios without immigrant eggs, resulting in population growth rates of λ = 0 (Figure 4.1.4-6). For Spires Lane under the "whole" scenario, both cool and hot fire decreased population growth rates to λ = 0.09 (95% CI: 0.08 – 0.10) and λ = 0.02 (95% CI: 0.02 – 0.03), respectively, when compared to no fire. Only the "quarter" scenario with hot fire was able to substantially boost Spires Lane growth rate to λ = 0.73 (95% CI: 0.70 – 0.77). The largest population, Green Oaks, showed increases in population growth rate to λ = 1.26 (95% CI: 1.23 – 1.29) and λ = 1.43 (95% CI: 1.40 – 1.46) for cool and hot fire, respectively, when compared to no fire with the "quarter" scenario. Under the "whole" scenario, cool fire slightly increased Green Oaks' population growth rate to λ = 1.14 (95% CI: 1.11 – 1.17), while hot fire reduced growth rate to λ = 1.01 (95% CI: 0.98 – 1.05; Figure 4.1.4-6).

4.1.4.5: Discussion

We find that fine-scale fire disturbance is better for this Fender's blue metapopulation. Fine-scale fire disturbance increases population growth rates in the landscape relative to no fire simulation, regardless of burn intensity. Hot burns cause greater extremes in population dynamics, and hot burns in combination with fine-scale approaches generate higher population growth rates than cool burns. Extirpation risk is minimized by fine-scale disturbance, similar to results by earlier studies with non-spatial models (Schultz and Crone 1998). Consistent with optimal strategies suggested by demographic matrix modeling approaches (Warchola et al., *in press*), only about a quarter of habitat should be disturbed each year in order to achieve the greatest population boosts.

While many studies infer the importance of dispersing individuals in population recovery after disturbance (e.g., Banks et al. 2011; Harper et al. 2000; Lindenmayer et al. 2009; Panzer 2003), our results clearly illustrate how immigrants are key drivers of population recovery after fire by using a life-table response experiment approach. Through directly removing contributions of immigrant eggs on population growth, we showed decreases in metapopulation growth rate under all management scenarios when compared to simulation including immigrant eggs (Figure 4.1.4-5). Small populations rely on recolonization via immigrant egg contributions for population persistence, and larger populations suffer decreases in growth rate from lack of immigrant eggs even with fine-scale burning (Figure 4.1.4-6). This key result of our modeling is further clarified by our analysis of the proportion of eggs laid by immigrants compared to natal butterflies (survivors) in the year after fire. Large-scale fire leads to higher proportions of eggs from immigrant individuals relative to survivors after disturbance when compared to no fire, with the greatest proportions seen in small populations (Figure 4.1.4-4). By contrast, fine-scale disturbance does not change the proportion relative to no fire.

Thus, when disturbance affects most of a population, the magnitude of population growth rate after fire is largely driven by immigrant eggs. However, this is not uniformly the case across our metapopulation, as demonstrated by the minimal influence of immigrants on population growth at the largest site. Banks et al. (2011) studied response of small mammals to fire, and found that *in-situ* survival from refugia in large habitat patches was responsible for driving population recovery after fire. Their conclusion explains patterns seen in our largest population, where the proportion of immigrant eggs is a negligible driver of population growth rate under all management scenarios. Even with the "whole" fire scenario, enough individuals within the relatively greater lupine extent at Green Oaks are able to survive fire and drive population recovery after disturbance. Because dynamics at our largest population are predominantly driven by residents, it is a reasonable hypothesis that refugia within large habitat patches facilitate population recovery even after large-scale disturbance.

Differences in fire intensity may affect the role of immigrant individuals in shaping population recovery after disturbance. Under our "whole" management scenario, the proportion of immigrant eggs relative to survivors after fire is nearly double with hot burns (Figure 4.1.4-3). This effect can be explained by differences in larval mortality with fire intensity. Butterfly larvae are thought to be able to evade fire mortality by finding refuge at the base of host plants, in leaf litter, and in soil (Thom et al. 2015). For Fender's blue, hot fire kills more overwintering larvae than cool fire, presumably because hot fire penetrates deeper into soil while cool fire leaves refugia in the burn mosaic (Schultz and Crone 1998; Warchola et al., *in press*). Thom et al. (2015) studied the mortality response of the atala hairstreak (*Eumaeus atala* Poey), another fire-adapted butterfly, at different depths of burial. They found that larvae at deeper depths could evade fire mortality, and survival of larvae was correlated with peak fire temperature. Thus, the difference we found in the proportion of immigrant eggs after hot fire compared to cool fire can be attributed to the difference in mortality between fire intensity. Managers sensitive to population losses may find cool burns to be more appealing, since cool burns lessen larval mortality and allow for population recovery to be driven by *in-situ* survivors.

Extinction risk in our model was greatest in large-scale, hot burns with extirpation events driven by small populations (Table 4.1.4-1). Studies investigating population recovery after fire in other systems found similar risk of disturbance on extirpation of small populations of birds and butterflies (van Mantgem et al. 2015). Hermes copper (*Lycaena hermes*), a rare butterfly near San Diego, CA, exists in a historically well-linked metapopulation that is now highly fragmented. Small populations of the butterfly were extirpated after wildfire, leading Marschalek and Klein (2010) to emphasize post-fire recolonization as critical to population recovery. Both Hermes copper and Fender's blue have adequate dispersal capability to move within in their respective metapopulations. Yet, fire-extirpated Hermes copper populations have rarely recolonized, and Marschalek and Klein (2010) cautioned that more frequent fire might reduce the species' ability to recover. Because habitat fragmentation and loss of connectivity generally increase extirpation risk, fine-scale burning can alleviate added risk from disturbance, especially if there is concern whether recolonization will occur in highly fragmented metapopulations.

We were surprised to find hot burns in combination with fine-scale disturbance yielded the highest population growth rates. Fire of higher intensity eliminates more thatch and woody vegetation compared to cool burns, resulting in more nutrient release and better habitat quality for plants after fire (Reinhart et al. 2016). From our experimental burns, fire leads to greater host plant biomass and higher fecundity after disturbance (Schultz and Crone 1998; Warchola et al. 2015; Warchola et al., *in press*). In these studies, we found hot burns result in higher fecundity than cool burns. In our present model, we minimize mortality from disturbance with the "quarter" fire scenarios which generate a higher proportion of surviving butterflies contributing eggs relative to immigrants in years after fire (Figure 4.1.4-3). Because of higher fecundity after hot fire, these surviving individuals and immigrants lay more eggs in areas burned with hot fire than in areas burned with cool fire. Thus, because of higher fecundity, population growth rates in our “quarter” scenarios are highest with hot fire. These growth rate predictions are near downlisting target levels set by population viability analyses with the Fender’s blue (Schultz and Hammond 2003). This strongly suggests hot burns, when applied at finer scales in the landscape, might be the ideal management strategy across the species’ range; but, it is worth emphasizing the option of late-season burns during the cool months, which is cheaper for managers and still gives population boosts at fine scales.

Management Conclusions: In synthesizing our findings, we offer some key points for managers to consider when developing burn regimes to manage fire-sensitive animal populations. If fire is to be used sparingly to minimize impact to the population, cool burns are better, and fine-scale disturbance lowers extinction risk. If fire is to be used to maximize population growth rates, hot burns in combination with fine-scale disturbances are optimal. If constraints limit the frequency of burning, cool burns are cheaper and can be applied at larger scales with less negative impact to populations. The role of immigrants in driving post-fire population recovery can be important, especially for small populations. Since extinction risk is generally driven by small populations, connectivity to larger populations may ensure adequate population recovery after fire and minimize extirpation. In general, connectivity between populations in the landscape could be a critical component to enable post-fire population recovery of many taxa.

Table 4.1.4-1. Site-level extirpation frequency and extirpation risk. Total extirpations are out of 500 replicates of 20 years for each scenario.

Site	Scenario	*Status quo*	Whole		Half		Quarter	
	Fire Intensity	**No Fire**	**Cool**	**Hot**	**Cool**	**Hot**	**Cool**	**Hot**
Shore Lane	Total extirpations	223	118	147	88	55	71	72
	Extirpation Probability (95% CI)	28% (24-32%)	17% (14-21%)	20% (17-24%)	11% (9-15%)	8% (6-11%)	9% (7-12%)	2% (1-3%)
Spires Lane	Total extirpations	8	6	6	5	2	1	0
	Extirpation Probability (95% CI)	1% (0-2%)	1% (0-3%)	1% (0-3%)	1% (0-2%)	0% (0-1%)	0% (0-1%)	0
Eaton Lane	Total extirpations	34	16	30	9	8	4	0
	Extirpation Probability (95% CI)	5% (3-6%)	3% (1-4%)	5% (3-7%)	2% (1-3%)	1% (0-2%)	1% (0-2%)	0
Green Oaks	Total extirpations	6	0	3	1	1	0	0
	Extirpation Probability (95% CI)	1% (0-2%)	0	1% (0-2%)	0% (0-1%)	0% (0-1%)	0	0

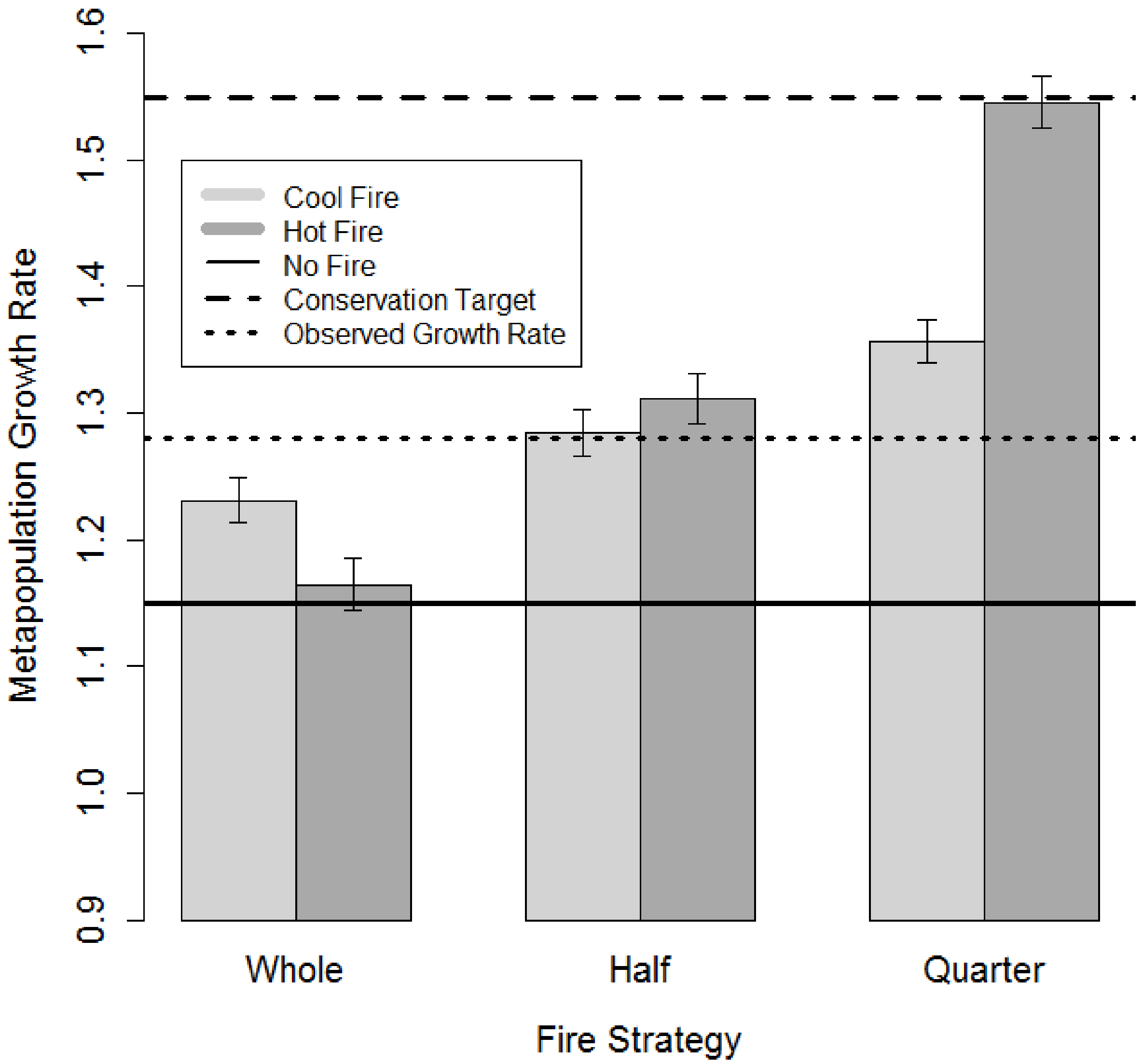


Figure 4.1.4-1 Metapopulation growth rate response to each fire strategy. No fire = solid line, conservation target = dashed line, observed growth rate = dotted line, hot fire = dark gray bars, cool fire = light gray bars

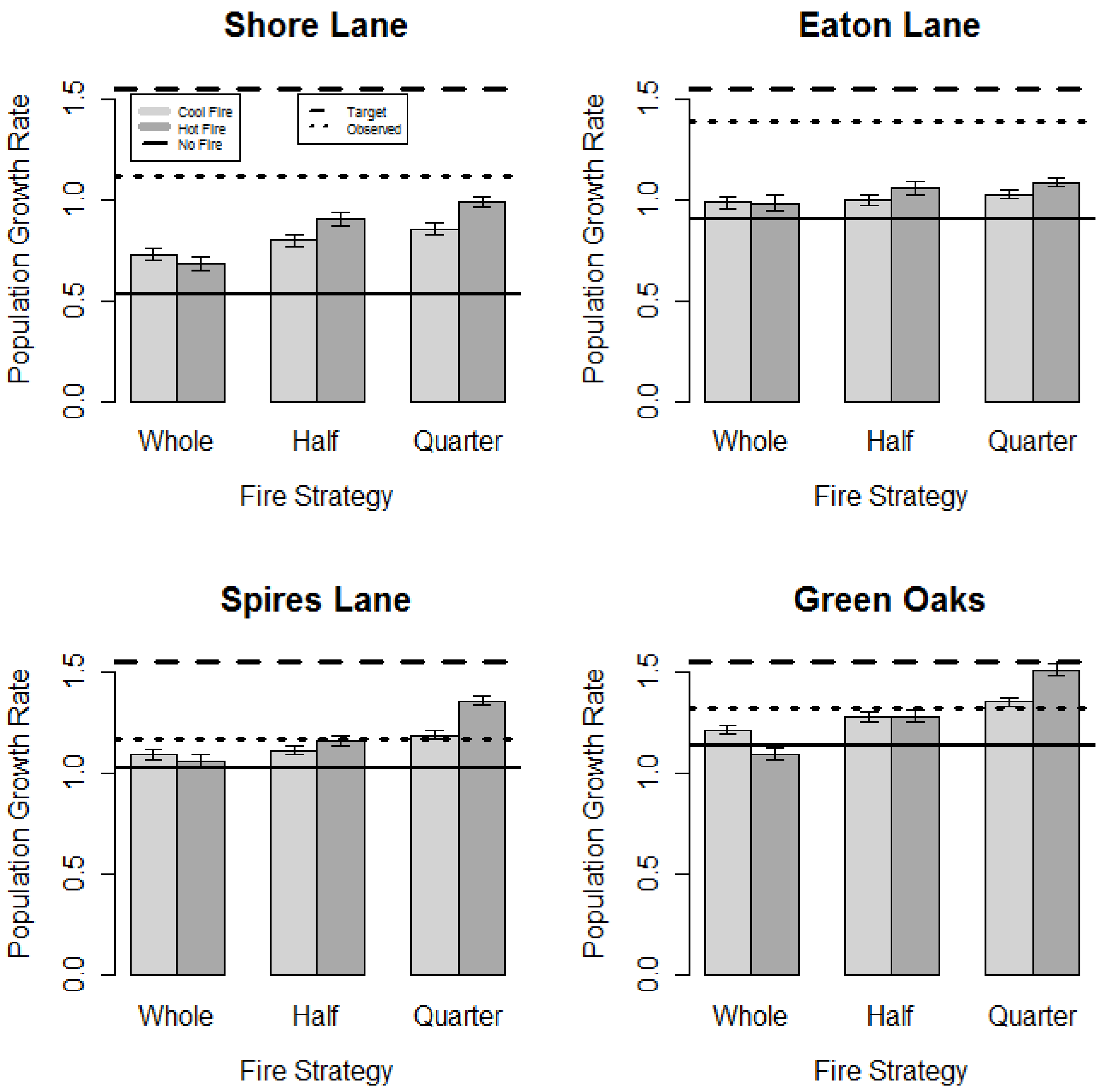


Figure 4.1.4-2. Site-level population growth rate response to each fire strategy. No fire = solid line, conservation target = dashed line, observed growth rate = dotted line, hot fire = dark gray bars, cool fire = light gray bars

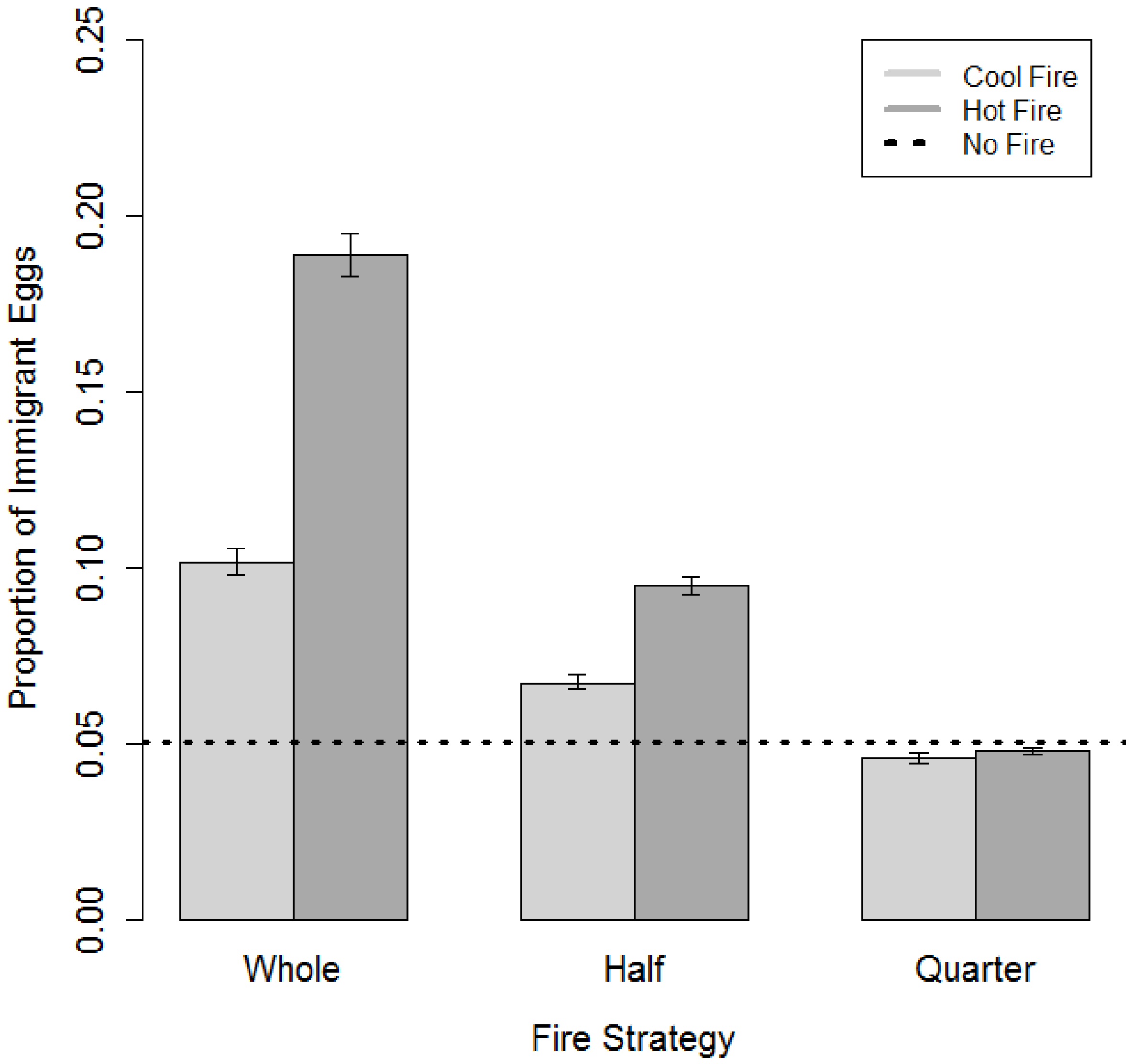


Figure 4.1.4-3. Proportion of immigrant eggs in the year after fire. No fire = dotted line, hot fire = dark gray bars, cool fire = light gray bars

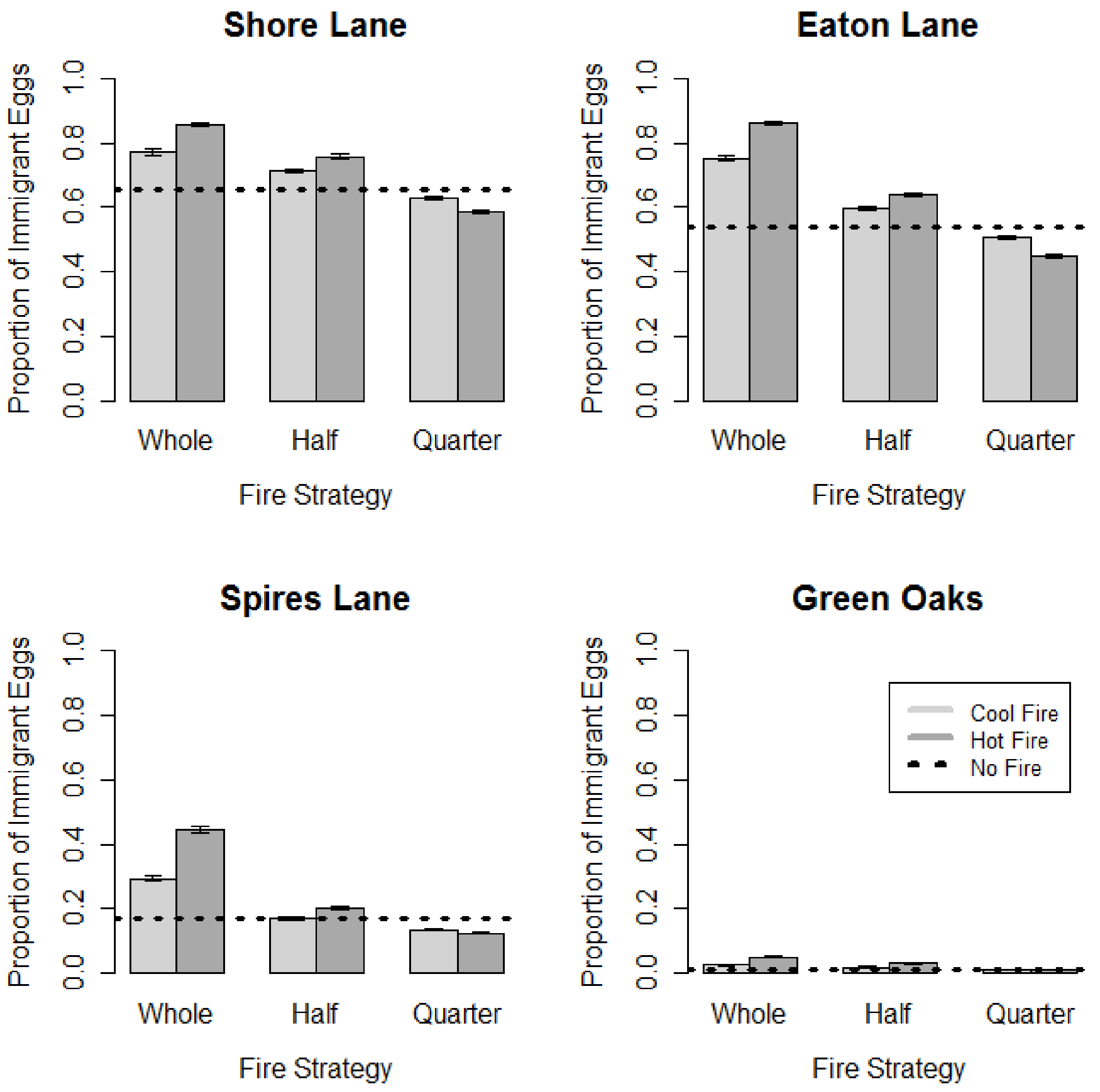


Figure 4.1.4-4. Site-level proportion of immigrant eggs in the year after fire. No fire = dotted line, hot fire = dark gray bars, cool fire = light gray bars

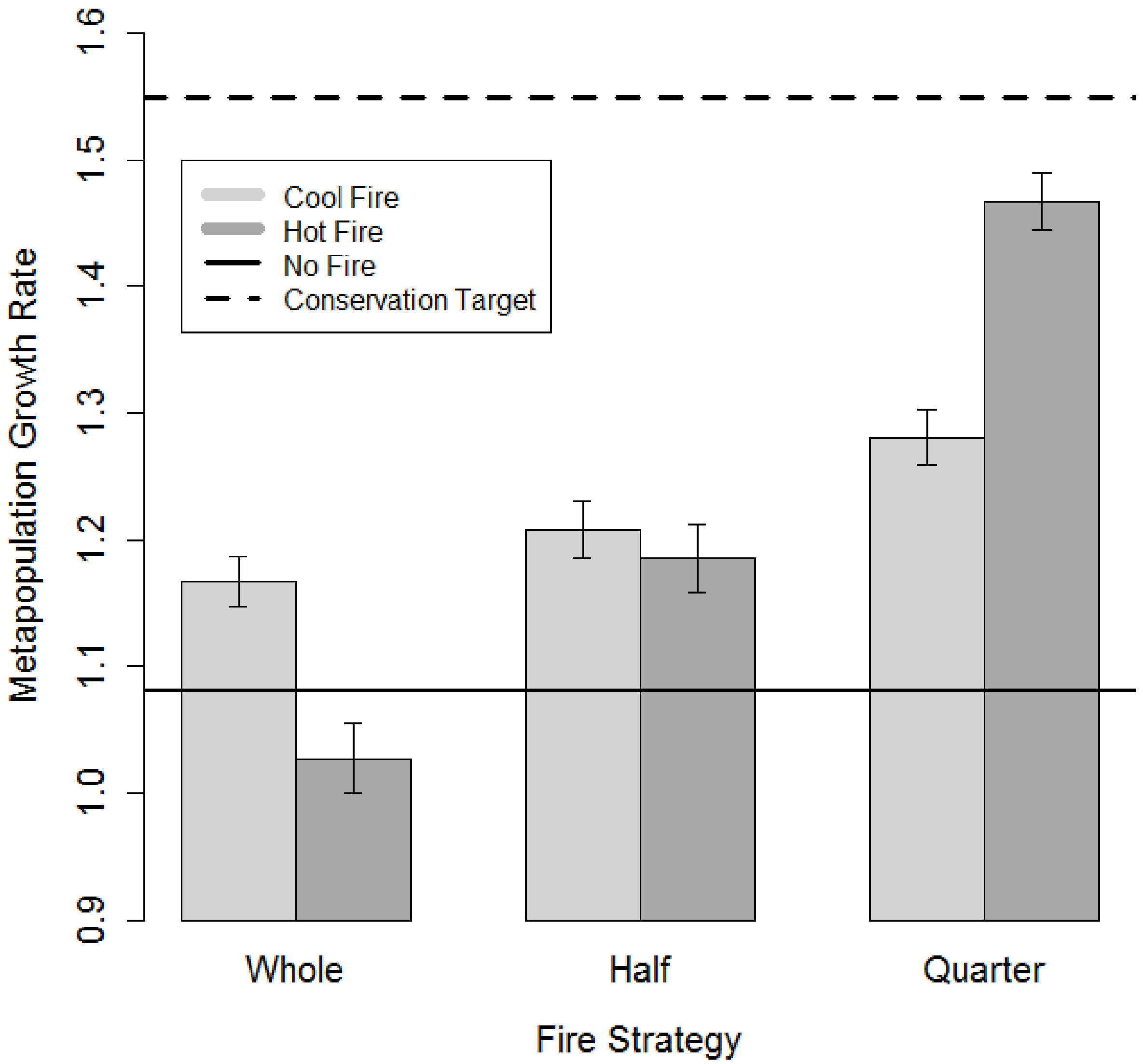


Figure 4.1.4-5. Metapopulation growth rate response to each fire strategy without immigrant eggs. No fire = solid line, conservation target = dashed line, hot fire = dark gray bars, cool fire = light gray bars

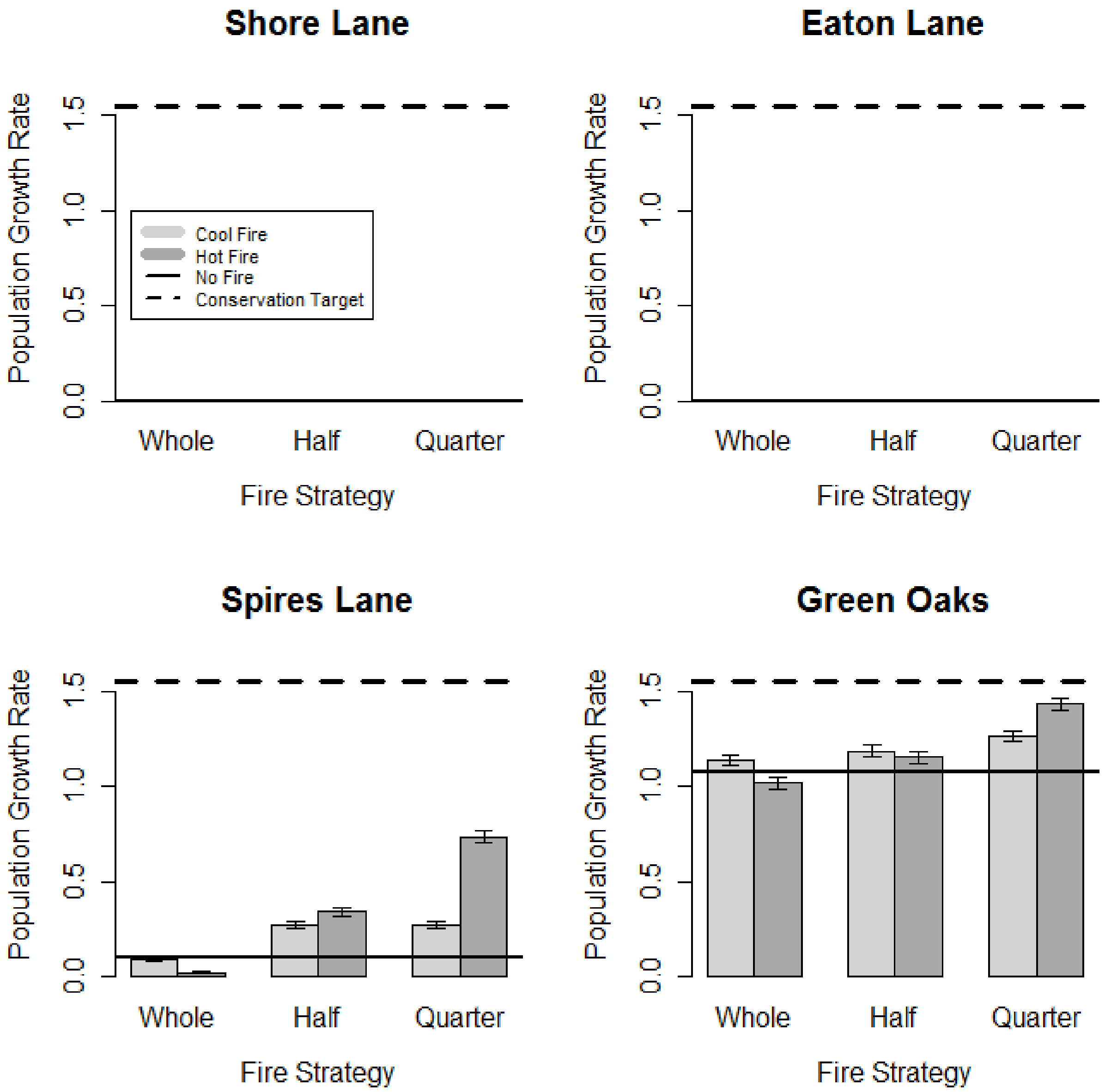


Figure 4.1.4-6. Site-level population growth rate response to each fire strategy without immigrant eggs. No fire = solid line, conservation target = dashed line, hot fire = dark gray bars, cool fire = light gray bars

4.2 St Francis' Satyr/ Appalachian brown

4.2.1 Demographic impacts of inundation and clearing

Despite the lack of strong direct effects, restoration treatments had strong predator-mediated indirect effects on the survival of *Appalachian brown* eggs and juveniles. When *Appalachian brown* eggs were exposed to predation, survival in the three types of restored plots was about one third of the survival in control plots (Fig. 4.2.1-1C). This suggests that our manipulation of tree cover and standing water substantially increased predation of butterfly eggs. Interestingly, we found that predation of eggs in plots with both tree removal and damming was less than would be expected if the effects of tree removal and damming were additive (Fig. 4.2.1-1B). While we do not know the mechanism behind this interaction, it reduces the strong negative indirect effect of both tree removal and damming on egg survival when applied alone. In contrast, when *Appalachian brown* juveniles were exposed to predation, survival rates differed among types of restoration. Survival of juveniles in dammed plots was two times higher than in control or tree removal and dammed plots, and five times higher than in tree removal plots (Fig. 4.2.1-1C). The differences in predation among restoration treatment types (Fig. 4.2.1-1B) are likely driven by changes in access to juveniles by ground predators. Dams increased the amount of standing water within our plots, and this likely reduced the ability of ground predators, such as ants and some spiders, to gain access to juveniles.

While the work presented here demonstrates the effects of restoration treatments on immature stages of *S. appalacia*, it does not assess these effects on the adult stage of *S. appalachia*. Positive responses of adult vital rates to restoration, such as increased recruitment due to higher oviposition rates where host plants are more abundant or higher adult survivorship due to lower adult predation, could ameliorate the strong negative effects we document in this study. Nevertheless, for species such as *S. appalachia* in which the annual population growth rate is simply the product of the separate vital rates, all demographic rates contribute equally to the population growth rate. This means improvements in adult vital rates would have to be proportionate to the reductions in immature survival that we document here for them to be fully compensatory. Future studies will integrate the complete suite of demographic responses to restoration in order to better inform long-term population growth predictions.

Technical Results

Restoration treatment (i.e., changing light and water availability) had mixed direct effects on the survival of eggs and juveniles. There was a significant negative effect of tree removal on eggs ($P = 0.05$) but not on juveniles ($P = 0.12$). The effect of damming was not significant for either eggs or juveniles ($P = 0.94$ and $P = 0.41$, respectively). The interaction between tree removal and damming was significantly positive for eggs ($P = 0.05$) but not juveniles ($P = 0.68$). When protected from predation, the survival of eggs differed significantly between flight periods for unknown reasons, and varied across the restoration treatments from 78% to 94% during the first flight period and from 47% to 58% during the second flight period. Juvenile survival in predator free enclosures ranged from 35% to 59% across the restoration treatments (Fig. 4.2.1-1A).

The restoration treatments differed in their effects on the intensity of predation. Across all restoration treatment combinations, predator exclusion had a significant positive effect on egg survival ($P < 0.001$). Although egg predation appeared to be more intense in plots with only tree removal or damming relative to controls (Fig. 4.2.1-1B), the tree removal × predator treatment and damming × predator treatment interactions were not significant ($P = 0.23$ and 0.92, respectively). However, the interaction of tree removal and damming significantly decreased the predation of eggs relative to what would be expected from the additive effects of tree removal and damming alone (Fig. 4.2.1-1B; tree removal × damming × predation treatment interaction: $P < 0.001$). Across all restoration treatments, predator exclusion had a significant, positive effect on juvenile survival ($P < 0.01$). Damming significantly decreased predation of juveniles (Fig. 4.2.1-1B, damming × predation treatment interaction, $P = 0.02$), but there was no significant effect of tree removal (tree removal × predation treatment interaction, $P = 0.26$).

The net effect of restoration is the combination of direct effects (i.e., bottom-up and abiotic environmental effects) and indirect effects (predation). When exposed to predation, egg survival in the different restoration treatments varied from 32% to 74% during the first flight period and from 12% to 56% in the second flight period (Fig. 4.2.1-1C). There was no significant effect of tree removal ($P = 0.36$), damming ($P = 0.68$), or their interaction ($P = 0.38$) on the survival of eggs exposed to predators. Survival of juveniles that were exposed to predation ranged from 7% to 37% (Fig. 4.2.1-1C). There was a significant negative effect of tree removal on juvenile survival ($P = 0.04$), but no significant effect of damming ($P = 0.25$) or the interaction between tree removal and damming ($P = 0.80$).

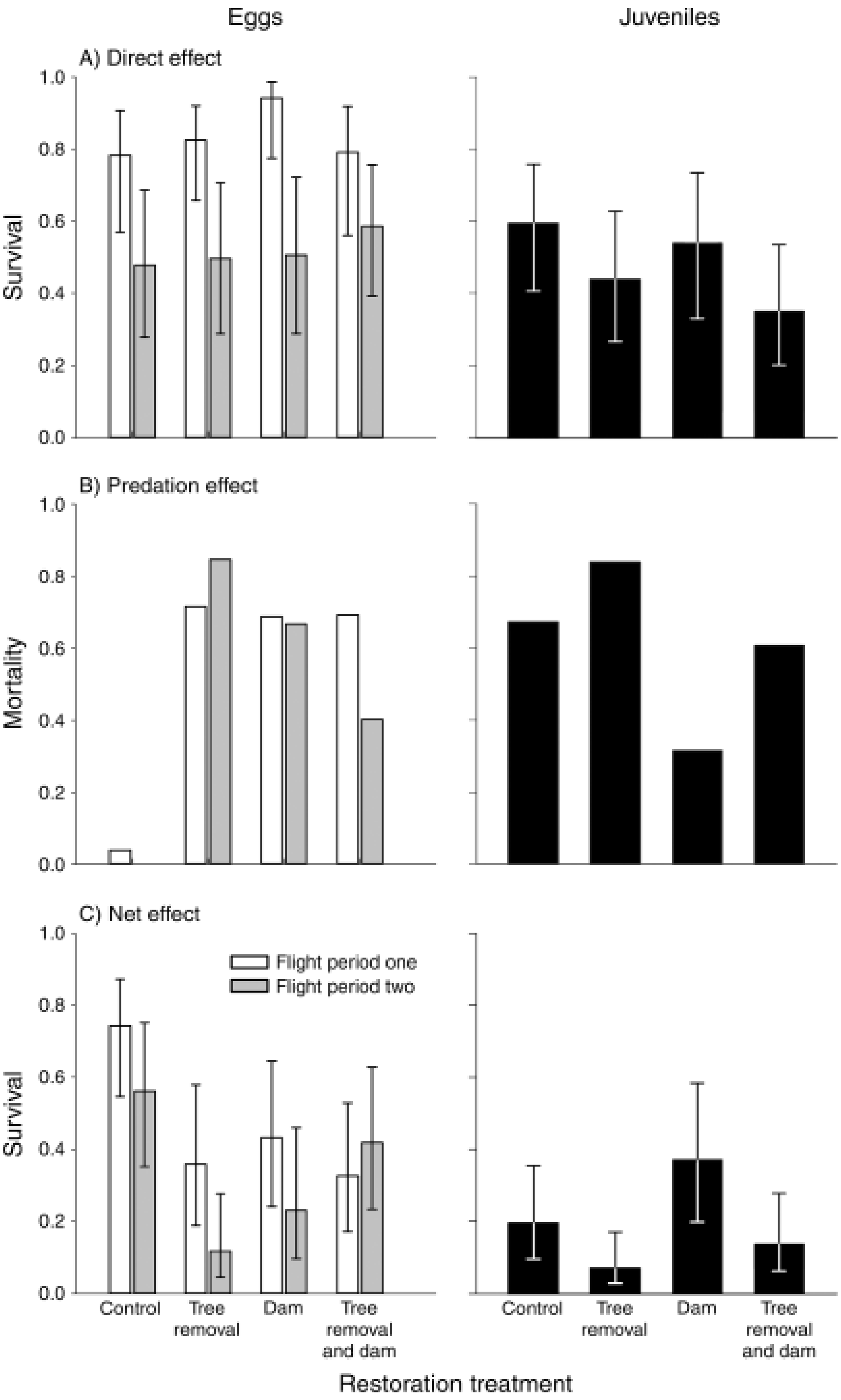


Figure 4.2.1-1. Proportional survival of *Satyrodes appalachia* eggs and juveniles (A) when protected from predation or (C) accessible to predators in different restoration treatment types. Open bars represent eggs from flight period one (15 May–15 June) and gray bars represent eggs from flight period two (7 July–7 August). (B) The response ratio of eggs and juveniles estimates mortality due to predation in different restoration treatments. Error bars show upper and lower 95% confidence limits.

4.2.2 Movement in response to inundation and clearing

We tracked 121 Appalachian Brown and 22 St. Francis' satyr butterflies for movement behavior over the two flight periods. There was no significant difference, for either species, of the distributions of move lengths, turn angles, or R_n^2/n in our four different restoration treatments. However, Appalachian Brown butterflies had significantly larger move lengths and R_n^2/n compared to our target species, St. Francis satyr (Figure 4.2.2-1).

Movement behavior under different restoration treatments was similar one year after restoration treatments. However, anecdotally, butterflies seemed more active in the sunnier sites that received the hardwood removal treatment. Cut sites were also the only restoration plots where St. Francis' satyr colonized naturally. Compared to the Kuefler et al. (2010) study of movement behavior in continuous riparian forest and wetland habitat, the move lengths and R_n^2/n were smaller in the 30m x 30m restoration plots, possibly due to the abrupt forest edges at the boundaries.

In the future, we will use demographic information to test whether our restored habitat serves as population sources or sinks for the larger meta-population of butterflies. One danger that must be tested is whether restoration creates an ecological trap, in which butterflies falsely sense that poor habitat is suitable. Combining our movement behavior study with demographic information will allow us to determine whether butterflies appropriately assess restored habitat quality. If they move more slowly in restored sites that have low resources or high predation risk, we would be concerned about restoration creating an ecological trap.

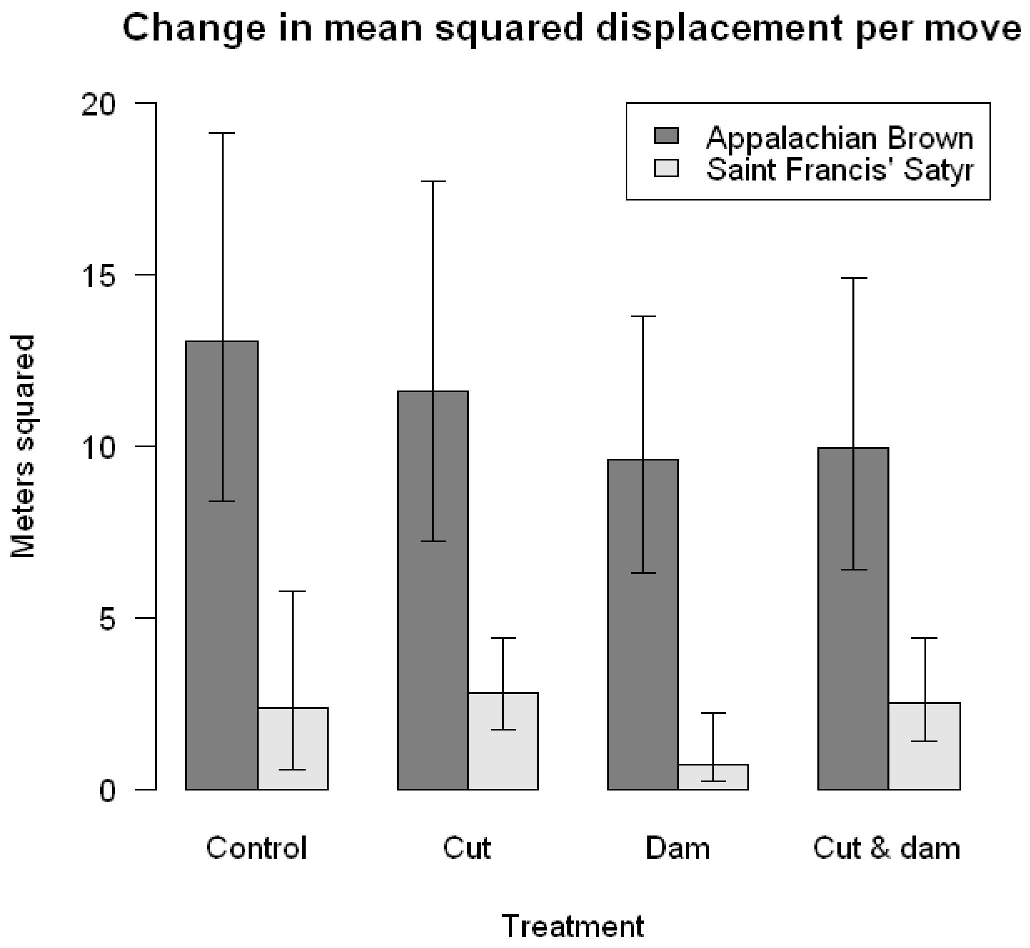


Figure 4.2.2-1 Differences in R_n^2/n (mean squared displacement per move) between restoration treatments for our target species, St. Francis' satyr, and our surrogate species, Appalachian Brown. The 95% confidence intervals are from a bootstrapped dataset.

4.2.3 Predator communities

We were able to positively identify four dragonfly species and two damselfly species. We observed a greater number of species in cut plots than uncut plots (Figure 4.2.3-1), although the difficulty in identifying individual species made determining species richness a challenge. In terms of abundance, we observed that cut plots (~6/plot/day) had significantly more dragonflies than uncut plots (~2/plot/day) (Figure 4.2.3-2). For damselflies, we noticed that cut and dam plots had approximately twice as many damselflies as other plot types (5 vs. 2.5). When all Odonates are combined, there is a significant direct effect of cutting and damming, with cut and dam plots averaging 11 individuals (SE=0.6), cut plots averaging 7 individuals (SE=1.0), dam plots averaging 5 individuals (SE=0.5) and control plots averaging 4 individuals (SE=0.5). In particular, Eastern Pondhawks (*Erythemis simplicicollis*), which we have directly observed preying on St. Francis' satyrs, were four times as abundant in cut sites than uncut sites (1.6/plot/day vs. 0.4/plot/day).

The number of ants observed in each sample ranged from 0-291, with an average of 29 ants per sample. We detected an average of 31 individuals (SE = 4.5) per sample in control plots, 25 individuals (SE=3.6) in cut plots, 37 individuals (SE=4.7) in cut and dam plots, and 23 individuals (SE=4.1) in dam plots (Figure 4.2.3-3).

Our clearest observation from conducting dragonfly surveys is that dragonfly abundance is much higher in cut plots than uncut plots. The open nature of the habitat most likely allows for dragonflies to fly more easily, and makes them better able to find and catch prey. Dragonflies are known to be predators of adult butterflies, and we have observed on multiple occasions Eastern Pondhawks catching a St. Francis' satyr in mid-flight. While this suggests that hardwood removal might increase predation on adult butterflies, it is unknown whether these predation levels are unsustainable or if they highly impact survival rates. We currently have no information on the proportion of adult mortalities caused specifically by predation.

We saw a much less significant effect in ant populations between treatment types. Ant abundance seems to be relatively similar across all plots, indicating that ants are not likely a major factor in driving differences in larval mortality between treatment types. Future work will determine the species identities of all individuals collected, and give a better idea of whether ant species richness varies among different plots. This may be crucial information, if certain species of ants are more likely to prey on larvae than others, particularly St. Francis' satyr larvae.

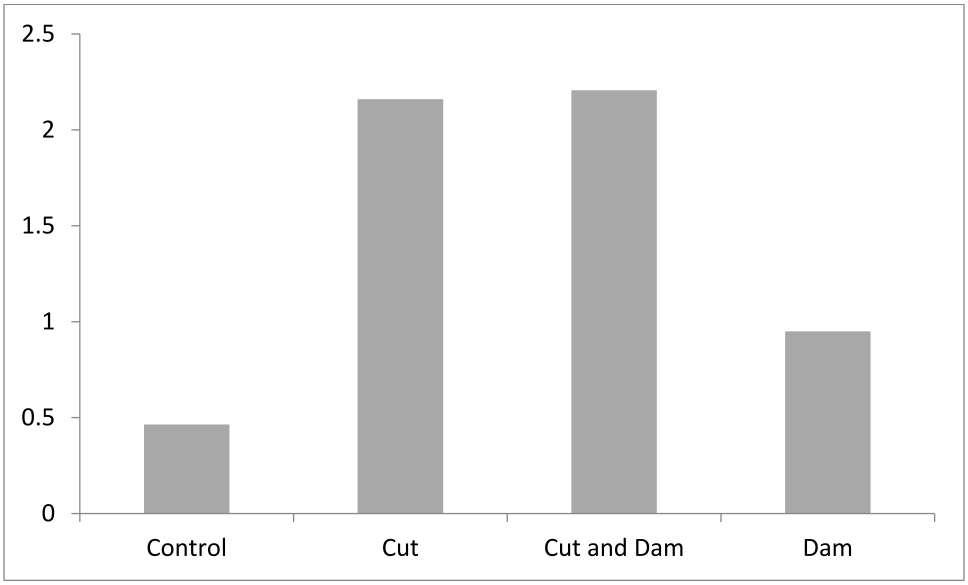


Figure 4.2.3-1. Average number of dragonfly species observed per day.

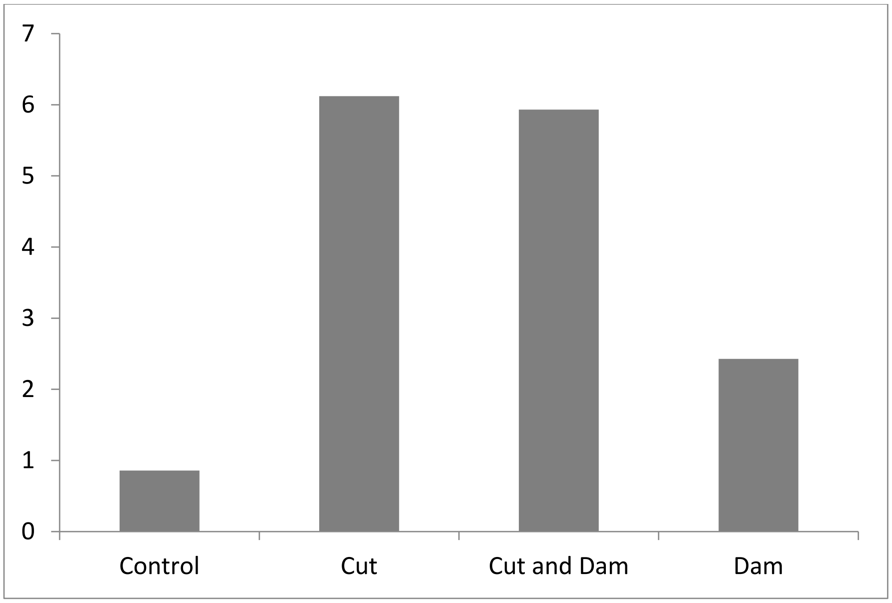


Figure 4.2.3-2. Average number of individual dragonflies observed per day.

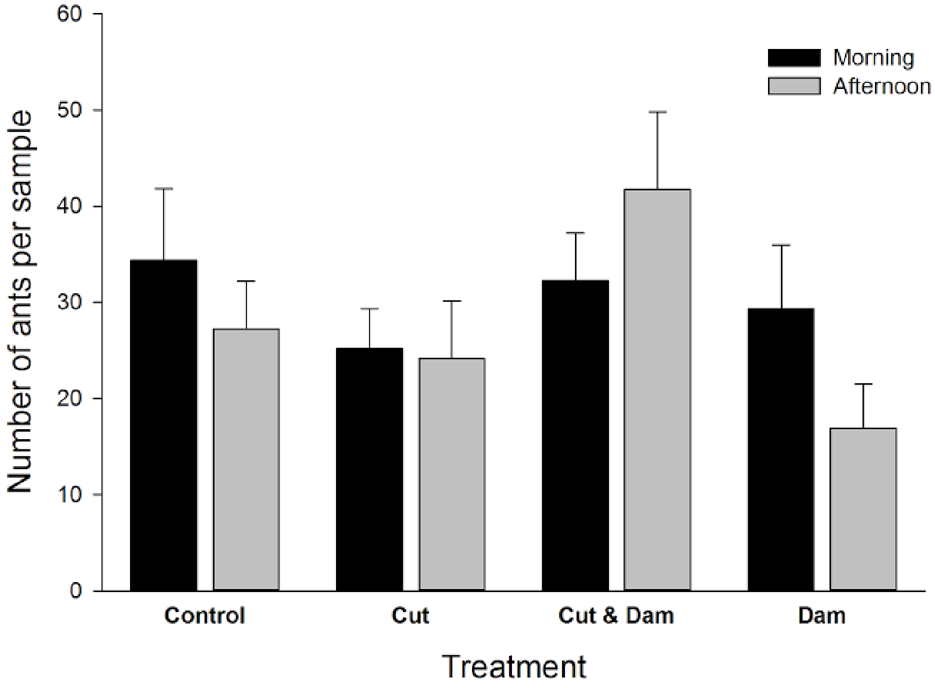


Figure 4.3.2-3. Average number of ants observed per sample.

4.2.4 SEIBMs: Scenario analysis on real landscapes

The results of our SEIBM source-sink simulations showed that in all three source scenarios (Eastern rapidly growing, Western slowly declining, and hypothetical Western slowly growing), the presence of sink habitat increased population growth rates (Fig. 4.2.4-1) and population abundance (Table 4.2.4-1). Similarly, increasing quality of sink habitat (from 5% to 10% sedge cover) also increased population growth rates and mean population abundance (Table 4.2.4-1). In all cases the effect sizes were small, but in the case of population growth in the Western population, the relative effect of the small increase was substantial, given that for the empirical slowly declining simulated population, the population growth rate increased enough when butterflies used the sink habitat to allow the population to grow rather than decline. The growth rate for the hypothetical slow growing Western population more than doubled when butterflies had access to low quality (5% sedge cover) habitat, and the rate quadrupled when butterflies used the sink habitat with 10% sedge cover.

Table 4.2.4-1. Results of the ANOVA analyses for population growth and mean abundance for each of the Source scenarios (Eastern, Western, and Hypothetical Western). The table shows the mean value for the parameter under the control scenario with no sink habitat present, and the effect sizes for the two sink scenarios. All differences among the three sink scenarios (control-no sink, 5% sedge sink, 10% sedge sink) were highly statistically significant.

				Effect Size	
Source Population	**Source Scenario**	**Parameter**	**Control Mean**	**5%**	**10%**
Eastern	rapid growth	Population Growth	0.8828	0.0052	0.0106
Western	slow decline	Population Growth	-0.0074	0.0157	0.0524
Hypothetical Western	slow growth	Population Growth	0.0150	0.0193	0.0457
Eastern	rapid growth	Mean Abundance	4,727	96	260
Western	slow decline	Mean Abundance	179	12	35
Hypothetical Western	slow growth	Mean Abundance	190	13	34

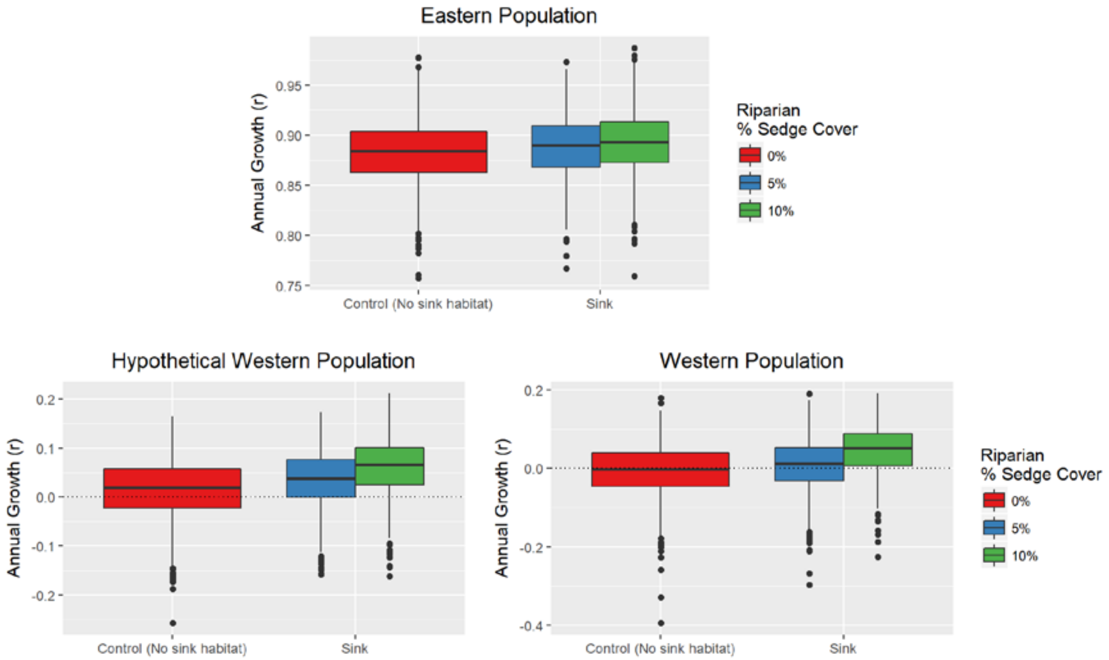


Fig. 4.2.4-1. Mean annual growth rate for each source population scenario (Eastern, Western, Hypothetical Western) and for the three sink scenarios: control simulations with no sink habitat present, and sink simulations in which riparian forest is sink habitat with 5% and 10% sedge cover. All differences between the control, sink 5%, and sink 10% are significantly different.

Mean maximum dispersal distance also increased when butterflies used sink habitat, but effect sizes were again small. For example, in the Eastern rapidly growing population, at a constant mean population size, maximum dispersal distance will increase by an estimated 16m (95%CI: 9.5-22.8m) when sink habitat is utilized (F=159.3, p-value<2.2e-16), but there was no significant difference between the two sink scenarios (p=0.064). In the two Western source scenarios, maximum dispersal increased between the control simulations and the sink simulations (Western: F=547.9, p-value<2.2e-16; Hypothetical Western: F=587.3, p-value<2.2e-16) and as sink habitat increased in quality (Fig. 4.2.4-2).

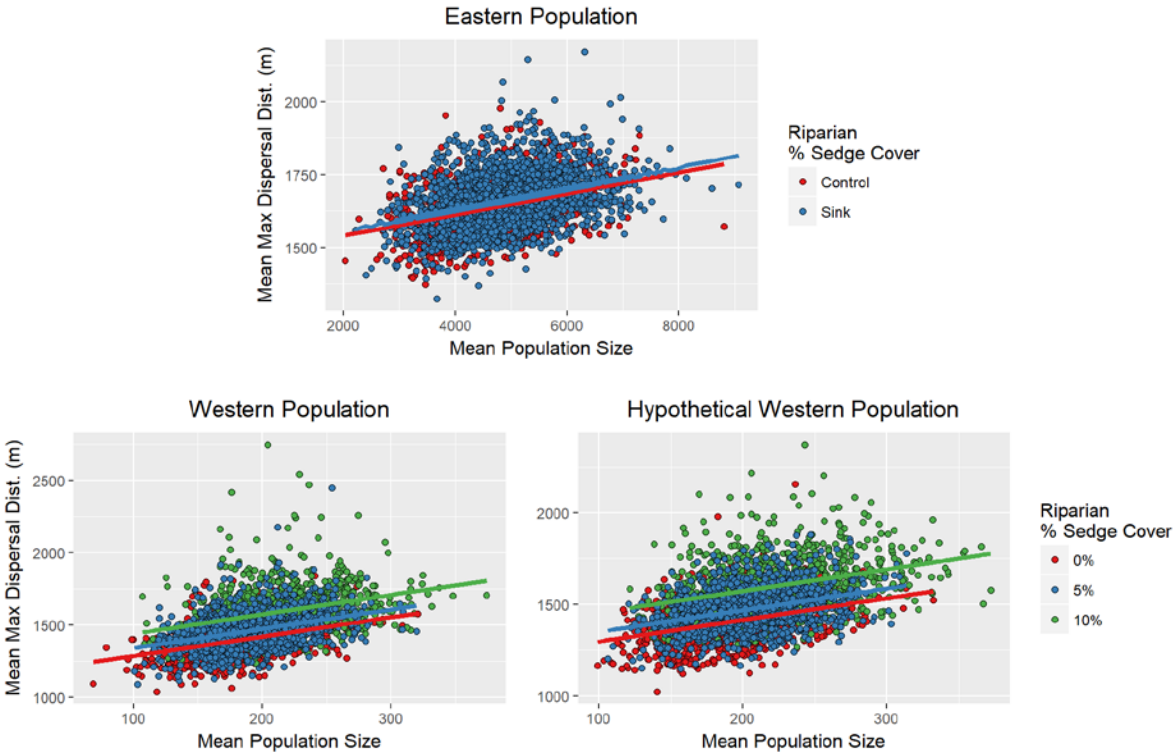


Fig. 4.2.4-2. Mean maximum dispersal distances in each of the source population scenarios (Eastern, Western, and Hypothetical Western) for control and sink simulations

Theoretical models have shown a wide variety of population responses to the presence of sink habitat from positive to negative depending on a wide range of factors. For one endangered butterfly species, our model demonstrates that sink habitat can provide small but significant benefits by increasing its growth rate and population size, and facilitating dispersal. While the impact of such sink habitat may be small, for small populations with negative or slow growth such as the Western St. Francis satyr population, these increases may make the difference between continued existence and extirpation. While more research will be necessary to understand if St. Francis satyrs are indeed using riparian forests as sink habitat, our models provide insight into the value of any type of sink habitat, whether it be riparian forest or degraded wetland, to the species. This may be particularly helpful for this species which relies on ephemeral sedge wetlands that degrade over time in the absence of disturbance. Degraded wetland habitat can itself be a sink if it fails to maintain stable or growing population (as illustrated by our Western St. Francis satyr population), but our study indicates that restoration of adjacent habitat may benefit the population more than restoring the existing degraded wetland since it could serve as sink habitat that contributes to the overall growth and health of the population. More broadly, our empirically based SEIBM model demonstrates how SEIBMs can be used to bridge the gap between theoretical models and empirical studies to better understand the ecological role of sink habitats for a given species.

4.2.5 Refine measurements of vital rates, trends and abundance

ABB and SFS caterpillar behavior and survival results

Caterpillar host use and survival

We released a total of 37 St. Francis' satyr caterpillars into field arenas, 10 of which successfully survived to become adult butterflies (21% survival). Based on our estimates of egg laying rates and egg survival from the greenhouse, we expect each St. Francis' satyr female to produce, on average, 60 eggs, 48 of which hatch, and to replace herself, we expect two caterpillars to survive to adult (4.2% survival), assuming a stable population. The overall survival we measured was considerably higher than this expectation.

Small, green caterpillars are difficult to find within arenas supporting dense growth of sedges. However we were able to find some caterpillars each day we checked arenas. In the four arenas that contained multiple sedges, 67 ± 27% of the St. Francis' satyr caterpillars we found were feeding on *C. atlantica*, until they were fourth instars, at which point 100% of our observations were on *C. mitchelliana*. The remaining 33% of the St. Francis' satyr caterpillars were found feeding on *C. mitchelliana* as early instars. We did not release Appalachian brown caterpillars into arenas as part of this project so we do not have data on their host preferences. However, we released Appalachian browns into arenas in 2012 and have conducted subsequent arena work with them as part of other experiments. In prior experiments in these same arenas (Aschehoug, et al. 2015), we have never observed Appalachian browns feeding on *C. atlantica*. Occasionally they will feed on grass species when grass is abundant within arenas, but *C. mitchelliana* is by far the preferred host of Appalachian browns.

Caterpillar survival did not differ between species (p=0.42) or treatments (p=0.58). The interaction term is marginally significant (p=0.10) and in the context of small sample sizes for St. Francis' satyr indicates a trend toward differential survival between Appalachian browns and St. Francis' satyrs across treatments (Figure 4.2.5-1).

Caterpillar behavior

Appalachian brown caterpillars forage at heights twice as great as St. Francis' satyrs (df=1, F=149.3, p<0.0001); Appalachian browns forage at 12.6 ± 5.2 cm off the soil and St. Francis' satyrs at 6.5 ± 3.7 cm. This difference is consistent across caterpillar development, the species*date interaction was not significant (df=8, F=0.25, p=0.98).

Caterpillar microhabitat

Appalachian brown and St. Francis' satyr caterpillars forage under different levels of canopy cover (χ^2=134.87, df=4, p-value<0.0001). Fifty-eight percent of Appalachian brown caterpillars are found with no sedge cover above them, only 4% and 1% are found under 3 and 4 sedge blades, respectively. Just over half of St. Francis' satyrs, were found under the shelter of 3 or 4 sedge blades, and only 10% forage in the open with no cover.

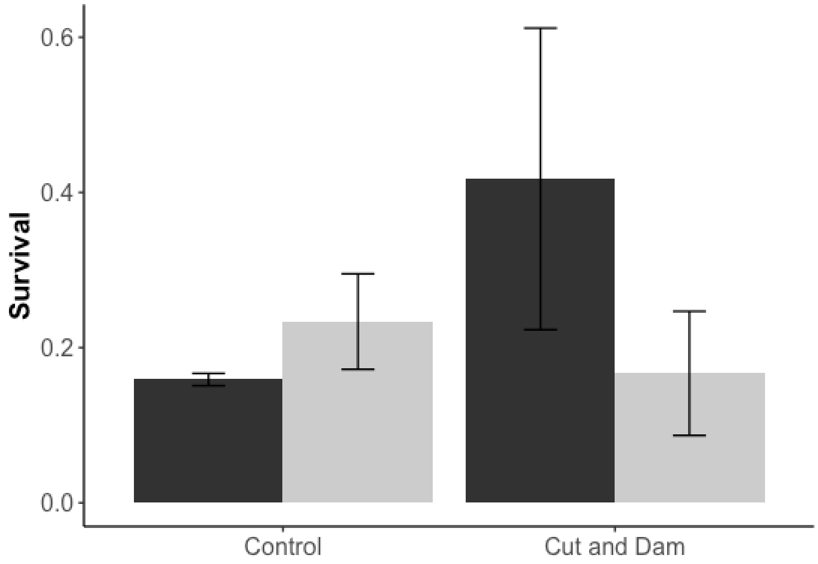


Figure 4.2.5-1. Means and standard error of St. Francis satyr (black bars) and Appalachian brown (grey bars) caterpillar survival.

Refining ABB egg survival and population growth rate

Of the 32 females we enclosed in arenas, 27 laid viable eggs. Females that did not lay viable eggs were excluded from analyses. Population growth rates were highest in un-cut (control and dam) treatments (Table 4.2.5-1). These results suggest that cut treatment leads to declining Appalachian brown butterfly populations.

Egg survival was higher in the first flight period than the second ($p<0.0001$), and damming had negative effect on survival ($p=0.016$). Cut treatment and Site did not significantly affect egg survival (Figure 4.2.5-2).

Table 4.2.5-1. Population growth rates for Appalachian browns in all treatment types. Population growth rate = (adults emerged/females with viable eggs)/2. Population growth rate >1 are emphasized in italics

	Females with viable eggs	Adults emerged	Population growth rate
D3S			
Control	*4*	*18*	*2.25*
Dam	*3*	*14*	*2.33*
Cut	4	2	0.25
Cut/Dam	3	4	0.67
M2			
Control	*2*	*10*	*2.50*
Dam	*3*	*9*	*1.50*
Cut	4	3	0.38
Cut/Dam	4	5	0.63

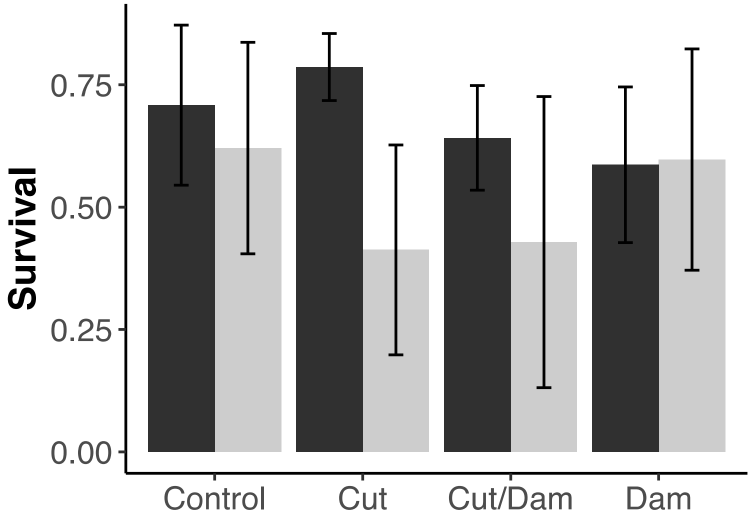


Figure 4.2.5-2. Egg survival by flight period, first flight period is in black, second in grey. Bars are means ± standard error.

4.3 Taylor's/ Baltimore Checkerspot

4.3.1 Effects of hostplants

Across life cycle stages, there were differences in the suitability of *C. glabra* versus *P. lanceolata* as inferred from demographic parameters: values for demographic parameters were higher on *C. glabra* for 2/6 of the parameters used to estimate host plant-specific λ, and higher on *P. lanceolata* for 3/6 of the parameters (Table 4.3.1-1).

<u>Demography: Larval survival</u>

Post-diapause larval survival was higher on *C. glabra* than *P. lanceolata* in 2012 and 2013 (χ^2=4.89, *df*=1, *p*<0.05) with an effect of year (χ^2=17.16, *df*=1, *p*<0.0001; Table 3.3.1.2-1; Figure 4.3.1-1A); a model with a random effect of enclosure did not fit the data better than a model without random effects (ΔAIC=2), indicating little difference in microsite between enclosures. Overwinter survival, on the other hand, was higher on *P. lanceolata* than on *C. glabra* (χ^2=3.25, *df*=2, *p*<0.10; Table 3.3.1.2-1; Figure 4.3.1-1B); a model with a random effect of enclosure was a better fit to the data than a model without the random effect (ΔAIC=344), indicating variation among microsites in estimates of overwinter survival beyond that attributed to host plant alone (among-site variance = 0.69).

Demography: Number of nests, nest size, and population-level oviposition preference

More nests were laid on *P. lanceolata* than *C. glabra* in both 2013 and 2014 (Table 3.3.1.2-1; Figure 4.3.1-2A), and *P. lanceolata* nests contained more larvae than *C. glabra* nests (Table 3.3.1.2-1; Figure 4.3.1-1C). In 2013, the proportion of nests in *P. lanceolata* versus *C. glabra* did not differ from the proportion of area covered by *P. lanceolata* and *C. glabra*, but in 2014 the proportion of nests on *P. lanceolata* was higher than its proportion of land cover (Figure 4.3.1-2B).

Demography: Female daily adult survival, population size, and individual mass

Daily survival of adult females did not differ based on their post-diapause host (*P. lanceolata* versus *C. glabra*; Table 3.3.1.2-1; Figure 4.3.1-3A). Females that were reared during the post-diapause period in enclosures with *C. glabra* were larger in mass than females reared in enclosures with *P. lanceolata* (χ^2=2.83, *df*=1, *p*<0.10; Table 3.3.1.2-1; Figure 4.3.1-3B). The population size of adult females increased from 2012 to 2014 (Figure 4.3.1-3C).

Demography: Host plant-specific population growth rates

Habitat-specific population growth rates, with and without adjusting for survival differences in fecundity, were higher on *P. lanceolata* than *C. glabra* (Figure 4.3.1-4). The survival-fecundity adjustment exaggerated this difference, but did not qualitatively affect our conclusions about host-plant specific population growth rates (Figure 4.3.1-4). Estimated annual population growth rates were high, but broadly consistent with observed increases in population size during the study period (Figure 4.3.1-3C). Replacing the value for overwinter survival on *C. glabra* with the value for overwinter survival on *P. lanceolata*, assuming all other parameter values were those of *C. glabra*, led to the greatest change in population growth rates relative the same replacement for other vital rates for *C. glabra*; all other means fell within the confidence limits of the original population growth rate estimates for *C. glabra* (Figure 4.3.1-5).

Table 4.3.1-1. Most suitable host plant inferred from parameter estimates, i.e., the host plant conferring higher values of the specified parameter; ϕ_1, ϕ_2, ϕ_3, m, and l were used to estimate λ on *C. glabra* and *P. lanceolata.*

Parameter	Host plant
Post-diapause (spring) larval survival, ϕ_1	*C. glabra*
Overwinter (fall to spring) larval survival, ϕ_2	*P. lanceolata*
Adult female survival, ϕ_3	Neither (slightly higher on *P. lanceolata*)
Adult female mass, m	*C. glabra*
Pre-diapause (fall) larvae per nest, l	*P. lanceolata*
Proportion of nests relative to area occupied	*P. lanceolata*
Habitat-specific population growth rates, $\lambda_{C.g.}$ or $\lambda_{P.l}$	*P. lanceolata*

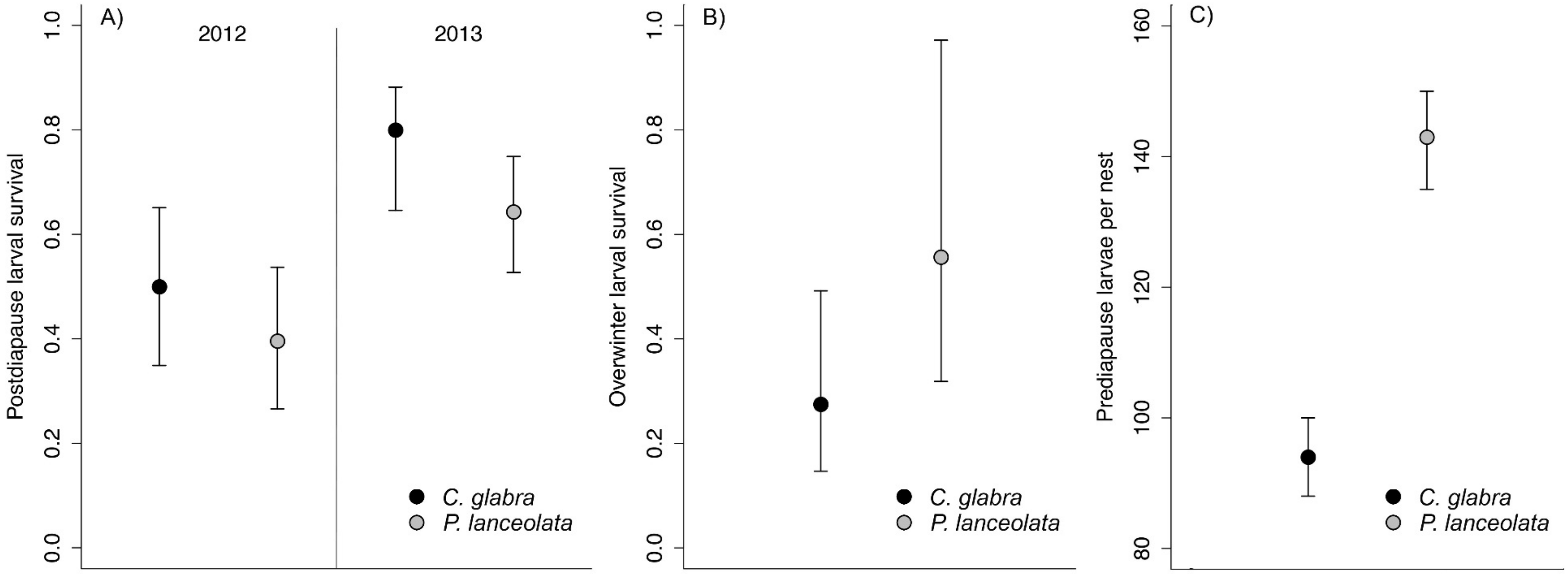


Figure 4.3.1-1. Larval survival rates and number of larvae per nest on *C. glabra* and *P. lanceolata*: a) post-diapause larval survival in 2012 and 2013, b) overwinter larval survival, c) mean number of larvae per nest. Error bars indicate 95% confidence intervals.

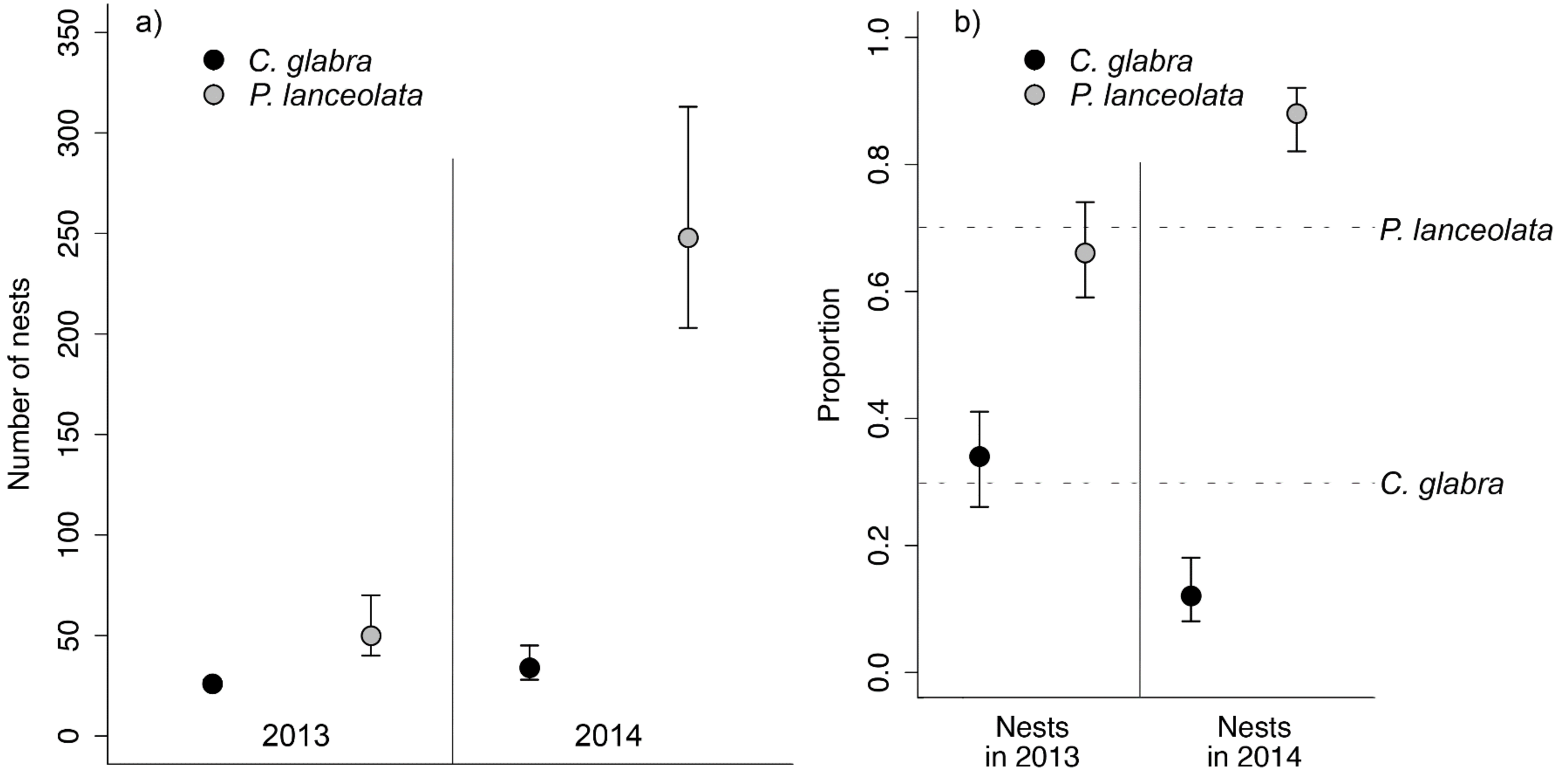


Figure 4.3.1-2. Nests in *C. glabra* and *P. lanceolata*: a) Total number of nests estimated in 2013 and 2014 on both host plants; b) Proportion of nests found on *C. glabra* and *P. lanceolata* in 2013 and 2014. Dashed lines indicate the proportion of the entire site covered by each host plant. Error bars indicate 95% confidence intervals.

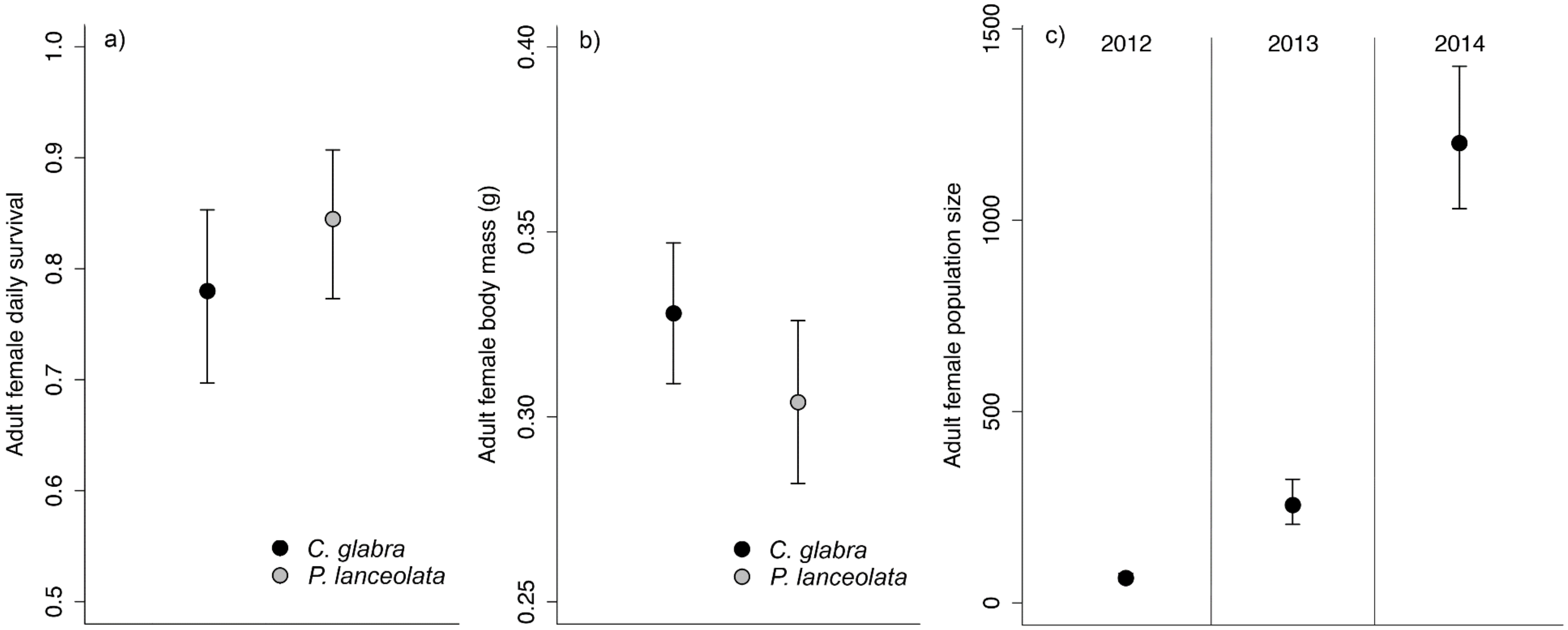


Figure 4.3.1-3. Female adult a) daily survival, and b) body mass on *C. glabra* and *P. lanceolata*, and c) total female adult population size from 2012-2014. Error bars indicate 95% confidence intervals.

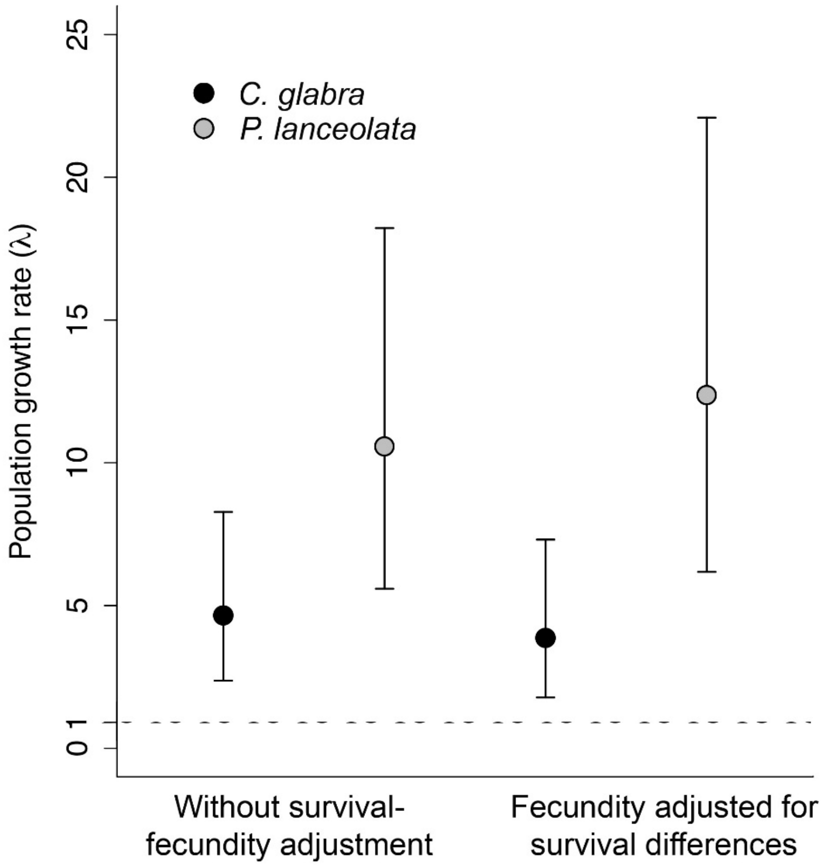


Fig. 4.3.1-4. Population growth rate on *C. glabra* and *P. lanceolata* estimated without and with adjusting for survival differences in fecundity of adult females. Error bars indicate 95% confidence intervals.

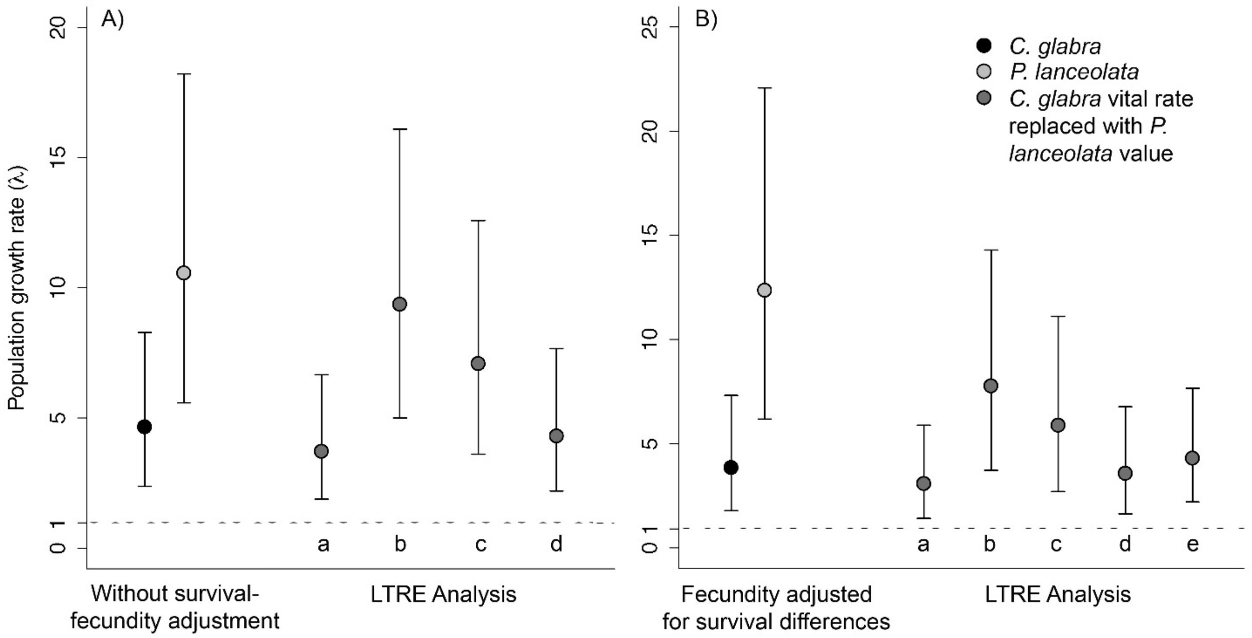


Fig 4.3.1-5. Population growth rates a) with and b) without adult survival correction, followed by LTRE analysis with growth rates for *C. glabra* where each vital rate was replaced in turn with the *P. lanceolata* value for a = post-diapause survival, b = overwinter survival, c = number of larvae per nest, d = female adult body mass, and e = female adult survival.

4.3.2 Effects of herbicide

Graminicide Experiment

Survivorship of *Euphydryas colon* to diapause was influenced by graminicide application (Figure 4.3.2-1a, χ^2 = 9.49, df = 4, P = 0.049). Sethoxydim reduced survivorship to diapause from 98% in control treatment to 78% in treated groups (P = 0.029). Effects of clethodim on survivorship to diapause, 85%, were not significantly different from the control group (P = 0.085). Neither fluazifop-p-butyl nor NuFilm influenced survival to diapause. Development time did not differ significantly among treatment groups (χ^2 = 0.62, df = 4, P = 0.960) nor did mass at diapause (F = 0.24, df = 4, P = 0.912).

Iridoid glycoside profiles differed among treatments. Iridoid glycosides were about a quarter of the dry weight of larvae in all treatment groups, including the control (Figure 4.3.2-1b). Total amount (in mg per larva) of iridoid glycosides did not vary among treatments (χ^2 = 6.69, df = 4, P = 0.153). However, graminicide treated larvae had substantially higher aucubin and lower catalpol than control larvae (χ^2 = 15.31, df = 4, P = 0.004). Percent dry weight of aucubin was almost double that of the controls in all three graminicide treatments while NuFilm treated larvae were not affected (Figure 4.3.2-1b). Fluazifop-p-butyl, sethoxydim and clethodim treated larvae all had significantly higher dry weight of aucubin relative to the control ($P< 0.05$ for all pairwise comparisons between graminicides and controls). In contrast, catalpol varied among groups (χ^2 = 10.19, df = 4, P = 0.037), but was only significantly lower than the control in clethodim-sprayed larvae (P = 0.018 for clethodim, $P>0.50$ for other comparisons).

Species x Hostplant Experiment

Herbicide treatment did not influence survival or development time of any of the *Euphydryas* species (Tables 4.3.2-1 and 4.3.2-2). Survival differed among *Euphydryas* and hostplant species (Table 2, Species, Host and Species x Host terms). Survival was >90% for all species and hostplant combinations except *E. colon* foraging on *Castilleja*. *Euphydryas editha* and *E. phaeton* took longer to reach diapause on the novel host (13.5 vs. 16.4 days by *E. editha*; 11.1 vs. 12.4 days by *E. phaeton*; Table 4.3.2-1).   Growth (i.e., change in mass during the experiment) was not consistently affected by treatment (Table 4.3.2-2, main effect of Treatment). However, there was a marginally significant (P = 0.057) of Treatment x Host interaction (Table 4.3.2-2). In general, herbicide consistently reduced growth on *P. lanceolata* but had no consistent effect on larvae reared on their native hosts (*C. glabra* or *C. hispida*).

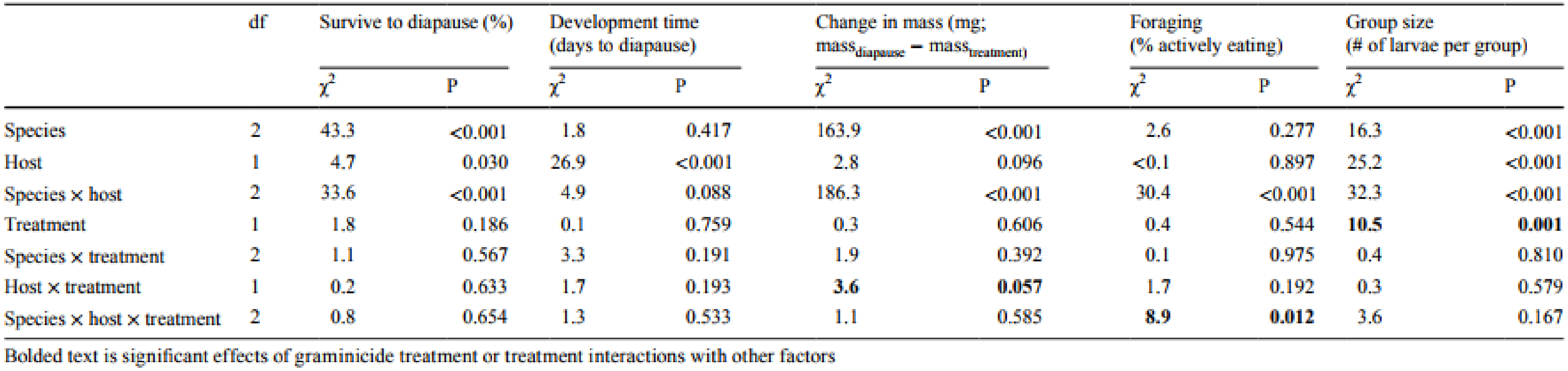
Graminicide only influenced the foraging frequency of one species on one hostplant (Table 4.3.2-2, 3-way interaction). *Euphydryas phaeton* was less likely to be observed foraging on treated than control *C. glabra* plants, but this effect was not present when foraging on *P. lanceolata* (Table 4.3.2-1). In general, the likelihood of observing active feeding was higher for *E. editha* and *E. phaeton* when feeding on *P. lanceolata* (Tables 4.3.2-1 and 4.3.2-2). Graminicide influenced group size in pre-diapause larva (Table 4.3.2-2, Treatment effect). Group sizes were smaller in graminicide cohorts for *E. colon* and *E. phaeton* (Figure 4.3.2-2). Group size also differed among *Euphydryas* and host plant species (Table 4.3.2-2, Species, Host, and Host x Species effects). Group sizes were larger in *E. colon* and *E. editha* cohorts on *P. Lanceolata* (relative to their native host *C. hispida),* and larger in *E. phaeton* on its native host, *C. glabra*.

Table 4.3.2-1 Results from Species × Hostplant experiment

	Survive to diapause (%)			Development time (days to diapause)			Final mass (mg at diapause)			Foraging (% actively eating)			Group size (# larvae in a group)		
	Mean	Lower CI	Upper CI	Mean	Lower CI	Upper CI	Mean	Lower CI	UpperCI	Mean	Lower CI	Upper CI	Mean	Lower CI	Upper CI
Euphyrdryas colon															
Castilleja host															
Graminicide	0.51	0.37	0.65	16.07	10.39	31.26	3.77	0.09	7.46	0.06	0.01	0.31	5.51	3.71	9.21
Control	0.55	0.41	0.69	17.01	10.75	33.76	4.33	0.66	8.01	0.09	0.01	0.43	6.22	4.05	10.66
Plantago host															
Graminicide	0.89	0.79	0.94	18.51	11.32	37.71	6.32	2.67	9.98	0.05	0.01	0.28	8.72	5.28	15.74
Control	0.92	0.83	0.96	16.56	10.58	32.50	6.80	3.15	10.46	0.04	0.01	0.25	11.66	6.72	21.76
Euphydryas editha															
Castilleja host															
Graminicide	0.88	0.79	0.93	13.14	10.04	19.40	8.84	6.23	11.45	0.07	0.02	0.25	3.48	2.78	4.80
Control	0.92	0.85	0.96	12.98	9.96	19.06	8.16	5.55	10.77	0.06	0.01	0.23	4.45	3.29	6.64
Plantago host															
Graminicide	0.87	0.77	0.92	15.87	11.40	24.88	9.36	6.75	11/98	0.02	0.01	0.10	5.44	3.92	8.17
Control	0.84	0.74	0.91	15.42	11.17	23.97	9.79	7.17	12.45	0.04	0.01	0.16	5.35	3.82	8.16
Euphydryas phaeton															
Chelone host															
Graminicide	0.95	0.89	0.98	12.67	10.40	16.45	12.38	10.49	14.27	0.03	0.01	0.10	12.06	8.74	17.04
Control	0.98	0.93	0.99	11.74	9.84	14.91	11.91	10.02	13.93	0.09	0.03	0.27	14.34	10.26	20.42
Plantago host															
Graminicide	0.91	0.84	0.96	10.92	9.34	13.56	8.05	6.16	11.97	0.32	0.12	0.62	11.16	8.13	15.67
Control	0.96	0.89	0.98	13.26	10.76	17.42	8.51	6.62	10.40	0.17	0.06	0.42	13.01	9.38	18.42

Data (mean, and upper and lower confidence intervals) are shown for survival to diapause, development time to diapause, mass at diapause, % of larvae actively feeding, and group size

Table 4.3.2- 2 Analysis of Species × Hostplant experiment



	df	Survive to diapause (%)		Development time (days to diapause)		Change in mass (mg; $\text{mass}_{\text{diapause}} - \text{mass}_{\text{treatment}}$)		Foraging (% actively eating)		Group size (# of larvae per group)	
		χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P
Species	2	43.3	<0.001	1.8	0.417	163.9	<0.001	2.6	0.277	16.3	<0.001
Host	1	4.7	0.030	26.9	<0.001	2.8	0.096	<0.1	0.897	25.2	<0.001
Species × host	2	33.6	<0.001	4.9	0.088	186.3	<0.001	30.4	<0.001	32.3	<0.001
Treatment	1	1.8	0.186	0.1	0.759	0.3	0.606	0.4	0.544	**10.5**	**0.001**
Species × treatment	2	1.1	0.567	3.3	0.191	1.9	0.392	0.1	0.975	0.4	0.810
Host × treatment	1	0.2	0.633	1.7	0.193	**3.6**	**0.057**	1.7	0.192	0.3	0.579
Species × host × treatment	2	0.8	0.654	1.3	0.533	1.1	0.585	**8.9**	**0.012**	3.6	0.167

Bolded text is significant effects of graminicide treatment or treatment interactions with other factors

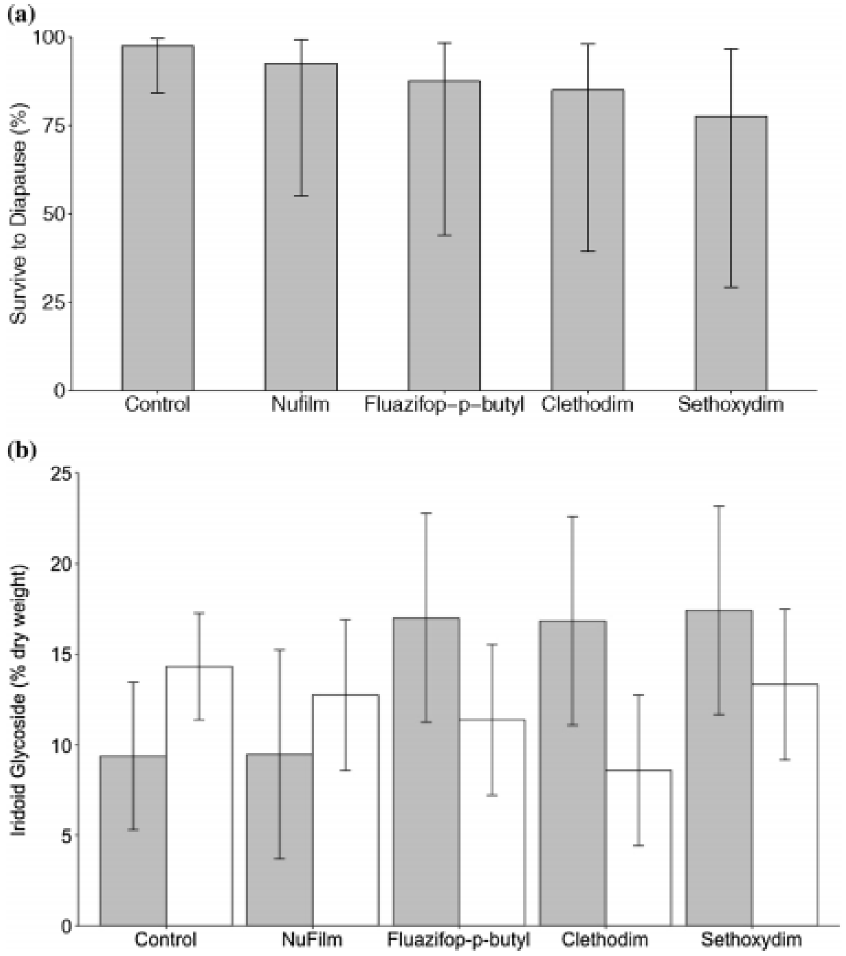


Figure 4.3.2-1 Results from Graminicide experiment. (a) Larvae surviving from treatment to diapause, (b) percent dry weight of iridoid glycosides (gray aucubin, white catalpol)

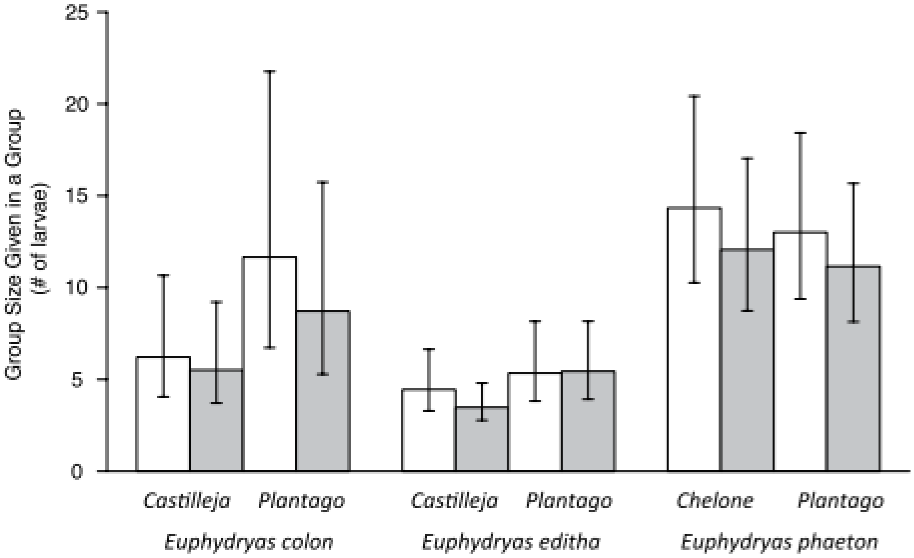


Fig. 4.3.2-2. Results from Species × Hostplant Experiment for gregariousness of larvae as measured by group size given that they were grouped. Within each species, the first set of bars reared on native plants (Castilleja for E. colon and E. editha; Chelone for E. phaeton), second set of bars reared on novel hostplant (Plantago lanceolata). Within each hostplant pair, white bars are control treatments and gray bars are graminicide treatments

4.3.3 Minimum patch size and connectivity

Minimum patch size

In our analytical (KSS) model, population growth rates increased rapidly with patch size in relatively small areas (<5 ha) and did not reach an asymptote until ~40 ha (Figure 4.3.3-1A-B). The minimum patch size (i.e., smallest patch at which $\lambda \geq 1$) was relatively small: ~1.5 ha (95% CI 0.6-7.5) based on raw fecundity values and ~0.7 ha (95% CI 0.4-2.5) with fecundity corrected for residence time.

In our habitat-nonhabitat only SEIBM, the estimated minimum patch size was ~0.7 Ha.

Dispersal distance

In our habitat-nonhabitat only SEIBM, the population-level mean distance moved was mean (SD)= 171.1 (9.2) m. The distance moved by any individual in a single year was mean (SD)= 169.3 (107.2) m, maximum=855.6 m.

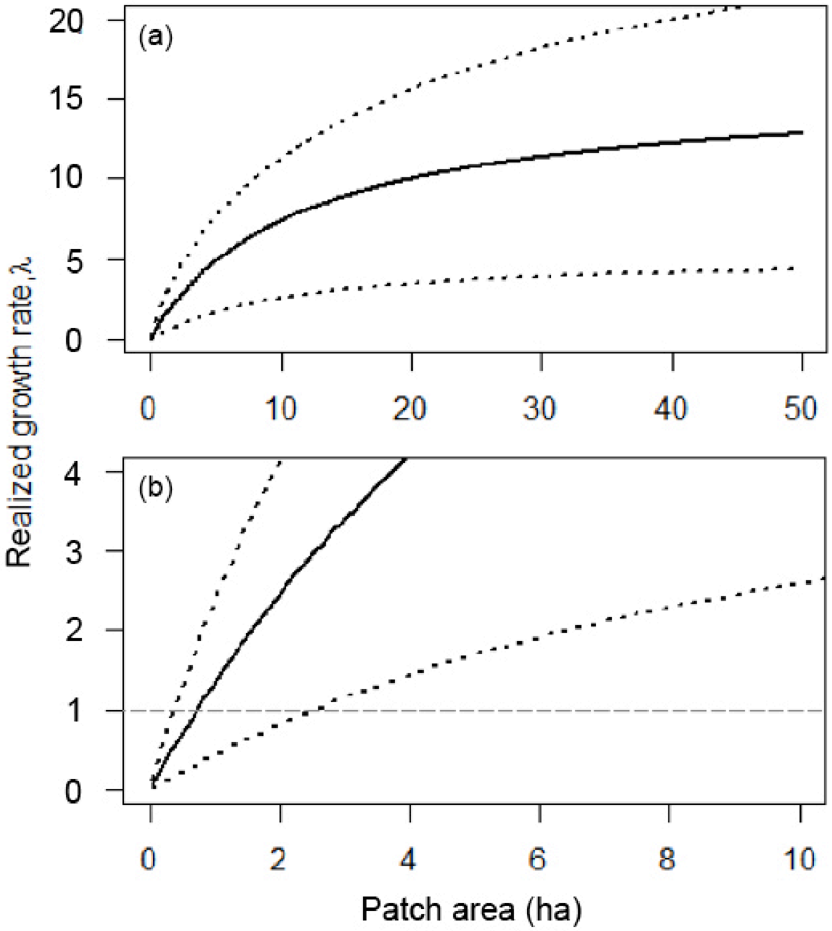


Figure 4.3.3-1. Baltimore checkerspot butterfly habitat patch size versus population growth rate and 95% CIs calculated by parametric bootstrapping over all flight and demographic parameters : (a) range of likely patch sizes in field conditions and (b) range of likely patch sizes in field conditions for 1-10 ha to show confidence limits of critical minimum patch size (horizontal dashed line).

4.3.4 SEIBMs: Scenario analysis on real landscapes

Population-Level Dynamics:

With a single restored host patch, populations under both the endogenous (with no stochasticity) and exogenous (with correlated high stochasticity) models exhibit boom-bust dynamics, as designed. Although both models produce high inter-annual variability in population size (CV=0.62 and 0.56, respectively), only under the endogenous model is extinction risk also high, with 62% of simulated populations going extinct before 30 years, compared to no extinction at the level of stochasticity we used in the exogenous model.

Regardless of the model used, dividing the habitat into an increasing number of patches (and thus decreasing the size of each patch) or moving the patches farther apart decreases the intrinsic growth rate, eventually leading to negative growth (Fig. 4.3.4-1). Despite this commonality between the models, the consequences of patchiness for boom-bust dynamics are very different under the two models.

Under the exogenous model, as the number of patches increases, boom-bust dynamics continue unabated at the whole population level (Fig. 4.3.4-2 A), with population variability increasing due to an increase in demographic stochasticity (Fig. 4.3.4-3 A) as mean population size decreases. Thus, under the exogenous model, splitting the habitat does not dampen boom-bust dynamics but rather leads to less population stability and a smaller population. Extinction risk remains low, however, for all scenarios with a positive intrinsic growth rate. In the endogenous model, splitting the restored area into multiple patches generally decreases population variability, with the amplitude of boom-bust fluctuations decreasing with an increasing number of patches (Fig. 4.3.4-2B & 4.3.4-3A). Under this model, extinction risk declines from 0.62 in the single patch scenario to 0 when the habitat is divided into 2 or more patches (at 20m spacing). Mean population size is generally larger in multiple patch scenarios with positive intrinsic growth rates relative to the single-patch scenario, and mean population size increases with an increasing number of patches (at 20m spacing).

Increasing patch spacing yields the same general pattern. Under the exogenous model, as distance between patches increases (and thus as intrinsic growth rate declines; Fig. 4.3.4-1), population variability increases (Fig. 4.3.4-2A & 4.3.4-3B) and mean population size decreases (Appendix S3: Table S1). Again, for all scenarios with a positive intrinsic growth rate, 30-year extinction risk remains at or near zero under the exogenous model. Under the endogenous model, for all multi-patch scenarios that yield a positive intrinsic growth rate (e.g., 2 patches at any spacing, 4 patches at 20 or 50m spacing, etc.), as patches get farther apart, population variability declines (Fig. 4.3.4-2B & 4.3.4-3B) and extinction risk remains at zero (Fig. 4.3.4-2B). Mean population size increases with increasing distance under the two-patch scenario up to 100m spacing, but decreases in all other scenarios. Regardless of the model, in scenarios in which the patches were too small and/or too far apart to maintain a positive intrinsic growth rate (see Fig. 4.3.4-1), extinction risk was high, or in a few cases, extinction risk was low but a slowly declining trajectory guaranteed extinction within a few years beyond the 30-year simulation window (e.g., see the 4-patch/100m scenario in Fig. 4.3.4-2B).

Patch-Level Dynamics:

Since movement parameters do not differ between models, as expected, all metrics related to dispersal and host patch residence time are the same in both models, exhibiting the following patterns. Time spent in host patches declines with decreasing patch size and increasing inter-patch distance. Similarly, dispersal among patches as measured by the proportion of time spent in non-natal patches declines with patch size and interpatch distance, with butterflies spending almost no time in non-natal patches when patches are spaced at 400m, regardless of patch size. As a result, patch recolonizations decrease with increasing distance and number of patches, and is near zero for patches at 400m spacing.

Individual patch populations generally mirror total population patterns under their respective models with correlated stochasticity. For example, under the exogenous model, patch population variability and patch extinctions generally increase with increasing number (and decreasing size) of patches and with increasing distance between patches. In the endogenous model, for scenarios in which the intrinsic growth rate is positive, as the patches get smaller and farther apart, individual patch population variability is dampened and patch extinctions decline.

Effects of Environmental Stochasticity Type and Level

Not surprisingly, when correlated environmental stochasticity is added to the endogenous model, in the single-patch scenario, population variability increases (Fig. 4.3.4-3A), and extinction occurs in all simulations for both levels of stochasticity. However, as the number of patches or inter-patch distance increases, boom-bust dynamics are dampened (Fig. 4.3.4-3A & B), and extinction risk declines up to the point at which the intrinsic growth rate drops below zero.

Relative to the correlated stochasticity versions, uncorrelated stochasticity results in dampened boom-bust dynamics in both models (cf. Fig. 4.3.4-3A, C & Fig. 4.3.4-3B, D) and lower extinction risk. In addition, under the exogenous model, multiple patches with uncorrelated stochasticity produce less variation in total population size relative to the single patch scenario (Fig. 4.3.4-3C) in contrast to the correlated case in which variability only increases with patch number (Fig. 4.3.4-3A). Increasing the distance between patches in the uncorrelated exogenous model, however, did not further dampen boom-bust dynamics (Fig. 4.3.4-3D). All other patterns associated with decreasing patch size and increasing inter-patch distance in the exogenous model are the same with uncorrelated as with correlated stochasticity (Fig. 4.3.4-3). Similarly, for the endogenous model with uncorrelated stochasticity, total population variability is lower relative to correlated stochasticity model output, but the general patterns resulting from decreasing patch size and increasing inter-patch distance are unchanged (Fig. 4.3.4-3C & 4.3.4-3D).

Patch extinctions decrease and recolonization increases under both models with uncorrelated stochasticity compared to correlated stochasticity. Temporal variability in patch populations (patch CV) is lower under uncorrelated stochasticity in both models but demonstrates the same overall patterns relative to correlated stochasticity (e.g., increasing with number of patches under the exogenous model).

Discussion

Our models illustrate that the mechanism driving fluctuations can dictate how boom-bust populations respond to patchy environments, and thus, how best to manage such populations. We found that when boom-bust dynamics are driven exclusively by exogenous factors such as climatic variability, patchy environments generally increase inter-annual variability and put populations at greater risk of extinction due to an increase in demographic stochasticity. Although our 30-year extinction risk metric did not indicate that a low to moderate number of patches spaced relatively closely would result in higher extinction risk under the exogenous model, these populations were slower growing, more variable, and smaller relative to the single-patch populations. Thus, we expect their longer-term extinction risk would be elevated (Inchausti and Halley 2003), and that intentionally creating resource patchiness offered only disadvantages relative to the single patch scenario. In contrast, when boom-bust dynamics are driven primarily by endogenous factors - such as overconsumption of food resources that produce strong, but delayed, density dependence - then a patchy distribution of resources can reduce population fluctuations, increase population size, and decrease extinction risk. This result holds even when environmental fluctuation (an exogenous factor) is added to the endogenous model.

Another key finding is that the primary mechanism by which patchiness induces stability in the face of endogenously generated fluctuations is a reduction in the intrinsic growth rate across all patches rather than via processes that require the dynamics of patches to differ. In theory, the total population could vary less across multiple patches than in a single large patch if the patch populations fluctuate independently of – or better yet, out of phase with – each other, a population-level portfolio effect (Schindler et al. 2010, Schindler et al. 2015). If this were occurring, as the sizes of the patch populations decrease when we divide the resources into more patches, we would expect the temporal variability of the patch populations to increase due to the increasing strength of demographic stochasticity, even as the total population might become more stable. We do see precisely this pattern in the exogenous model with uncorrelated stochasticity– population-level stability increases with an increased number of patches (Fig. 4.3.4-3C) while individual patch stability declines (patch CVs increase). In contrast, under the endogenous model, both the total population (Fig. 4.3.4-3A) and the individual patch populations (Fig. 4.3.4-4) become more stable and less extinction prone as patchiness increases (provided the growth rate remains positive), and this pattern holds for both correlated and uncorrelated environmental stochasticity.

This is not to say that classical metapopulation processes such as recolonization of extinct patch populations (Levins 1969) and rescue effects (Brown and Kodric-Brown 1977, Gotelli

1991) are not making some contribution to stabilizing the total population. We do see local extinction and recolonization occurring in both models, and as we would expect under classical metapopulation dynamics, recolonizations increase when stochasticity is uncorrelated among patches. Similarly, evidence for a rescue effect in both models is apparent in the decline in patch extinctions and patch variability when stochasticity is uncorrelated versus correlated. But classical metapopulation theory alone does not explain why extinction risk under the endogenous model is positively correlated with the intrinsic growth rate when the growth rate is positive. This positive correlation indicates that a lower growth rate leads to a reduction in the population's ability to overshoot the patch carrying capacity and thus a reduction in the resulting over-compensatory response (Bjorkstedt 2012). More generally, the endogenous model shows two features that do not follow classic metapopulation theory, namely, that larger patches do not have lower extinction risk, and higher growth rate does not decrease extinction risk (Hanski 1999, Maschinski and Quintana-Ascencio 2016 and empirical references therein). Instead, smaller patches and lower growth lead to lower extinction when fluctuations are endogenously driven.

While somewhat counterintuitive, and in contrast to traditional restoration and reserve design principles (Maschinski and Quintana-Ascencio 2016, Donaldson et al. 2017), the result that patchiness begets stability is consistent with other work both outside of and within the metapopulation literature. Root's (1973) "resource concentration hypothesis" suggests that large contiguous habitats can lead to irruptive population dynamics and that splitting habitat into smaller patches generally dampens boom-bust dynamics. This concept has been applied widely in the field of agro-ecology and pest management (e.g., Tonhasca and Byrne 1994, Banks and Gagic 2016), where the focus has been on eliminating the "boom" phase in pest species, but rarely, if ever, has it been considered in conjunction with species of conservation concern, where the “bust” phases are more problematic. Previous metapopulation theory has shown that dispersal among two or more populations exhibiting chaotic fluctuations (one form of boom-bust dynamics) can be stabilizing (Gonzalez-Andujar and Perry 1993, Hastings 1993, Doebeli 1995, Gyllenberg et al. 1996, Doebeli and Ruxton 1997). While not all dispersal-induced stability derives from the mechanism of dampened growth rates (Doebeli 1995, Abbott 2011), many of the theoretical models implicitly (e.g.,Gonzalez-Andujar and Perry 1993, Hastings 1993) or explicitly (e.g., Doebeli 1995) demonstrate this stability mechanism. Our endogenous model not only confirms the stabilizing effect of a dampened growth rate for boom-bust populations using empirically estimated demographic and movement parameters, but also demonstrates that these theoretical patterns can have important implications in the applied context of species management and habitat restoration. Below we discuss implications of our results for our understanding of the biology and management of checkerspots and other boom-bust populations.

Our results have several important implications for managing fluctuating populations including Taylor’s checkerspot specifically. First, when fluctuations are endogenously driven, it may in fact make sense to “manage the fluctuations”, rather than seeking to increase intrinsic growth, maximize population size, or enhance dispersal and connectivity, which are most often the focus in conservation and recovery efforts (Gerber and Hatch 2002, Donaldson et al. 2017). While a clear positive relationship has been established between population variability and extinction risk (Goodman 1987, Fagan et al. 2001, Inchausti and Halley 2003), management often focuses on mitigating for variability rather than managing it directly. For example, in classic metapopulations, local extinction or low sizes of local populations may not be considered problematic as long as dispersal among populations is sufficient to allow for recolonization or rescue of declining populations (Levins 1969, Brown and Kodric-Brown 1977, Gotelli 1991). In such cases, management or restoration priorities might focus primarily on maximizing intrinsic growth rates and local population sizes, and ensuring adequate connectivity among resource patches. However, given the results of our endogenous model, achieving a mean growth rate in the optimal range, by balancing immigration and local population growth rather than maximizing both, will result in dampened boom-bust dynamics, stabilization of the population, and reduction in extinction risk at both the patch and population levels. More generally, intentionally creating conditions (in this case, large resource patches) that support high intrinsic growth may only increase extinction risk. Instead, facilitating lower effective fecundity, for example, by the intentional creation of multi-patch metapopulations, may have the counterintuitive effect of producing more effective long-term recovery of threatened species, even at the “cost” of slower growth. Because population variability is greatly reduced under this strategy, however, it actually matches well with what we know about extinction risk drivers (Fagan et al. 2001).

The decision to “manage fluctuations” versus mitigating for fluctuations, however, may depend on available resources, including habitat. It may be that Taylor's checkerspots have intrinsically boom-bust dynamics and that these dynamics play an ecological role (e.g., preventing parasite populations from building to high levels; Stamp 1982, Van Nouhuys and Hanski 2004). As discussed above, the notion of metapopulation dynamics driven by local extinction and recolonization has a longstanding history in conservation biology (Hanski 1999). Nonetheless, we suspect that local land managers nearly always view local extinction as a signal that something has gone wrong. If it turns out that Taylor's checkerspots naturally have boom-bust dynamics, then a major challenge for managers is to decide whether to attempt to maintain persistent populations at a limited number of sites by facilitating lower growth rates via patchily distributed resources, or to plan proactively for a habitat network that is large enough to allow for independently fluctuating populations, local extinctions, and the potential for recolonization. Determining the size, proximity, and number of colonies that could persist indefinitely as a metapopulation at broader spatial scales despite boom-bust dynamics and frequent extinctions will take experimentation and/or additional simulation models, and may require better collection of species-specific movement and demographic data. Our present simulations suggest that no dispersal will occur between the Mima Mounds and Glacial Heritage reintroduction sites, so additional sites between these two would likely be necessary.

Because the optimal management of fluctuating populations may depend on the mechanism, managers may need to determine what mechanism is responsible in order to manage effectively. The first step in doing so, would be to determine of the focal species has the growth rate capacity to yield endogenously driven boom-bust dynamics. Over-compensatory density dependence in species with non-overlapping generations, as in the checkerspots and as simulated in our endogenous model, cannot occur without high intrinsic growth rate (May 1974, Bjorkstedt 2012). Determining if Taylor's checkerspot intrinsic growth rate is high enough for over-compensatory dynamics to operate would elucidate whether endogenous mechanisms are even a possibility. We suggest this should be a research priority for Taylor's checkerpots, and any species for which this question is relevant. While we recognize that studies – even observations – of threatened species may pose challenges and limitations, gathering data on growth rates, and if justified, on potential mechanisms that would generate endogenous feedback, such as correlational studies examining larval performance in relation to local host plant abundance or even host plant addition experiments, might have the advantage of allowing construction of an accurate population model and thus avoiding mismanagement. Similarly, determining the drivers of exogenous fluctuations, as we argued in the preceding paragraph, may improve management and reduce long-term population risk.

Finally, the type (correlated vs uncorrelated) and magnitude of environmental fluctuations can modulate the effect of resource division in damping endogenous fluctuations. For example, with a high degree of stochasticity uncorrelated between patches, extinction risk with 4 patches at 20m spacing remains low even at $\bar{r} \approx 0.3$, whereas the risk would be notably higher with 2 patches and 50m spacing even though they have the same intrinsic growth. With correlated and no environmental stochasticity, extinction risk depends only on the intrinsic growth rate, not the details of patch number and spacing, because the populations across all patches effectively acts as a single large population (Harrison 1991). Thus, understanding the spatial structure of stochastic environmental effects may also improve management of fluctuating populations.

We close with a caveat about model uncertainty. Simulation models such as those we developed here rely on a variety of assumptions and expert opinion in addition to empirical data, with the model output more or less dependent on each of these inputs and assumptions. We relied on surrogate species data to parameterize the demographic and movement portion of our model, which adds uncertainty to our results as they apply to Taylor’s checkerspot. Because of this uncertainty, we do not expect the precise patch sizes and distances between patches that yield stable and growing populations in the model to represent a prescription for Taylor’s checkerspot restoration strategies on the ground. Similarly, our estimated relationship between total area restored and extinction risk and growth rates may not be representative of the real relationship Taylor’s checkerspots have with restored habitat area. The general patterns present in the model output, however, are robust to this broad model uncertainty - namely that endogenously driven boom-bust populations can become stabilized by a reduction in growth rate that may be achieved through habitat fragmentation on a small scale, and that the mechanism driving high temporal variability has broad management implications that should be acknowledged and understood.

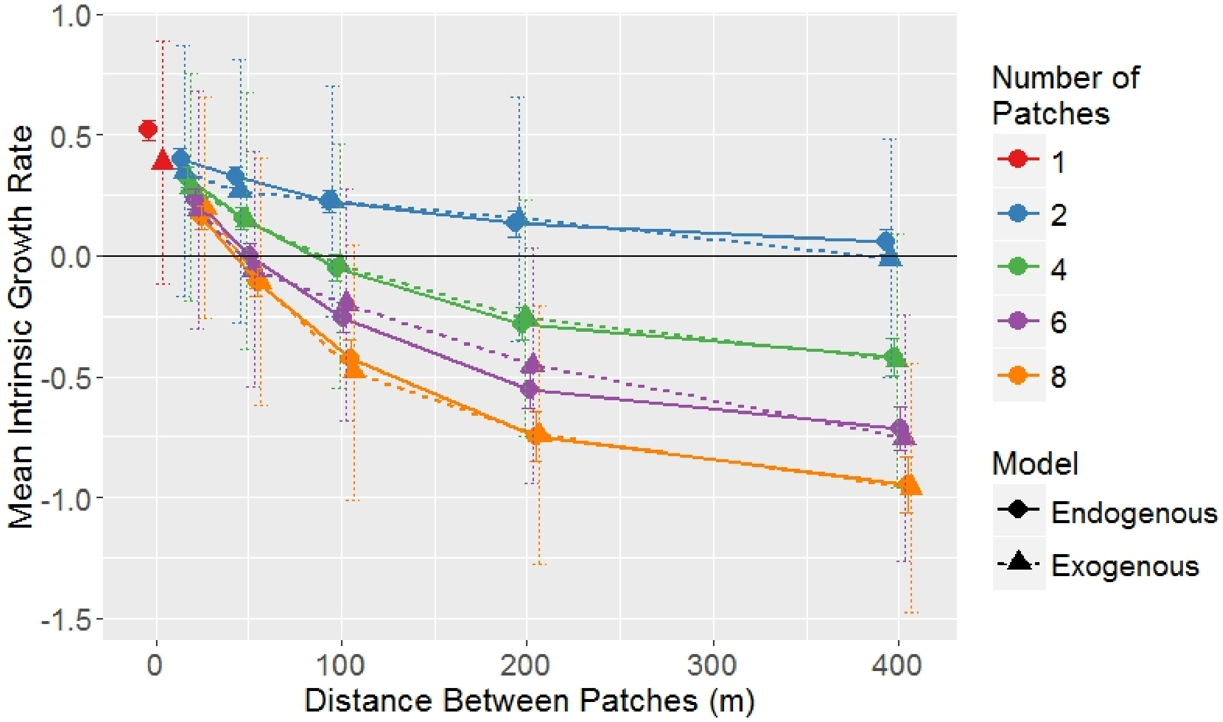


Figure 4.3.4-1 Mean intrinsic growth rate under the endogenous model with no environmental stochasticity (circles and solid line) and the exogenous model with high environmental stochasticity (triangles and dashed line), as a function of distance between patches and number of patches. Error bars represent the mean ± standard deviation

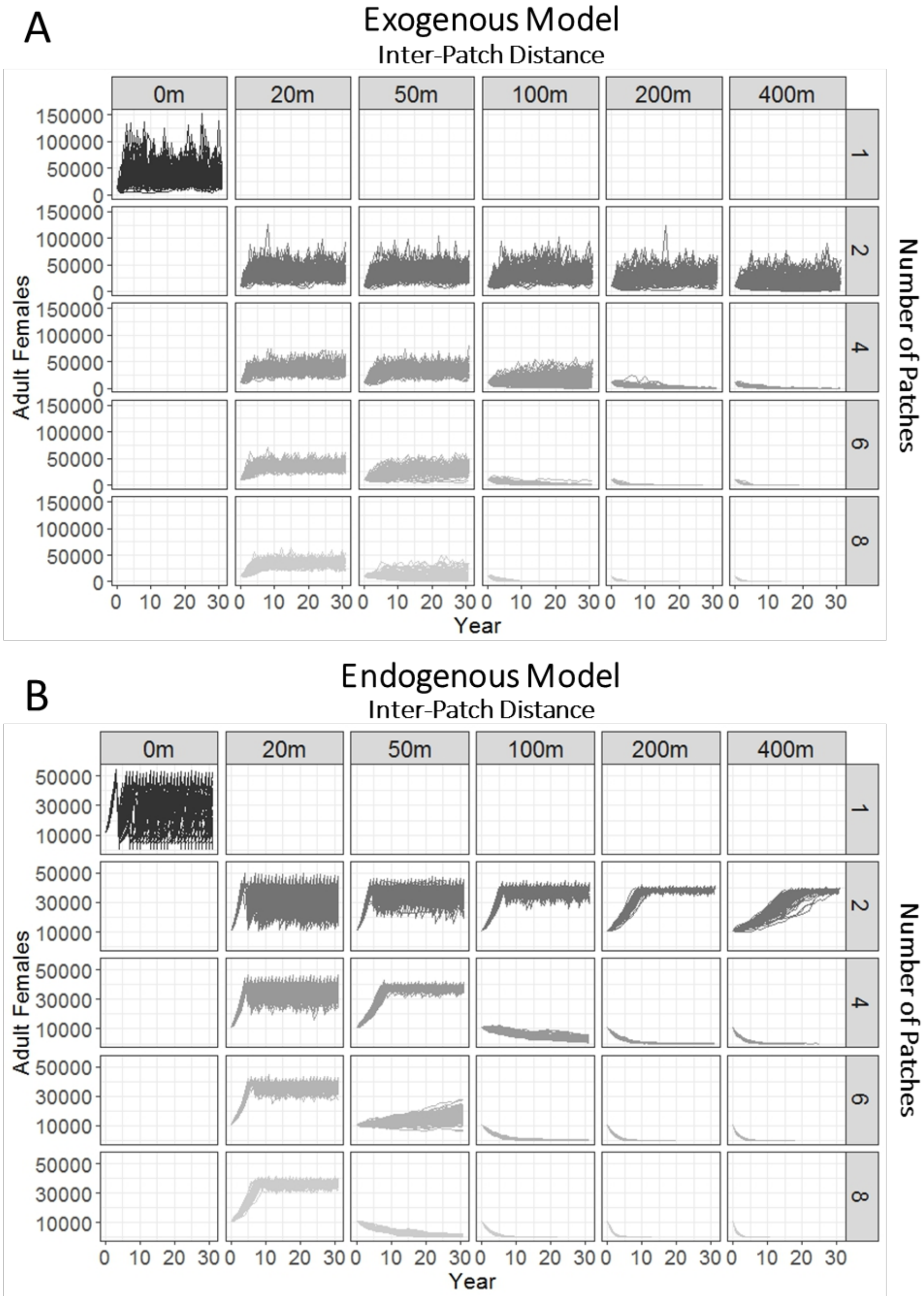


Figure 4.3.4-2 Population trajectories for all restoration scenarios from A) the exogenous model with high environmental stochasticity, and B) the endogenous model with no environmental stochasticity. Each line represents the population trajectory from one simulation. Each panel shows the trajectories for all 100 simulations for the given restoration scenario.

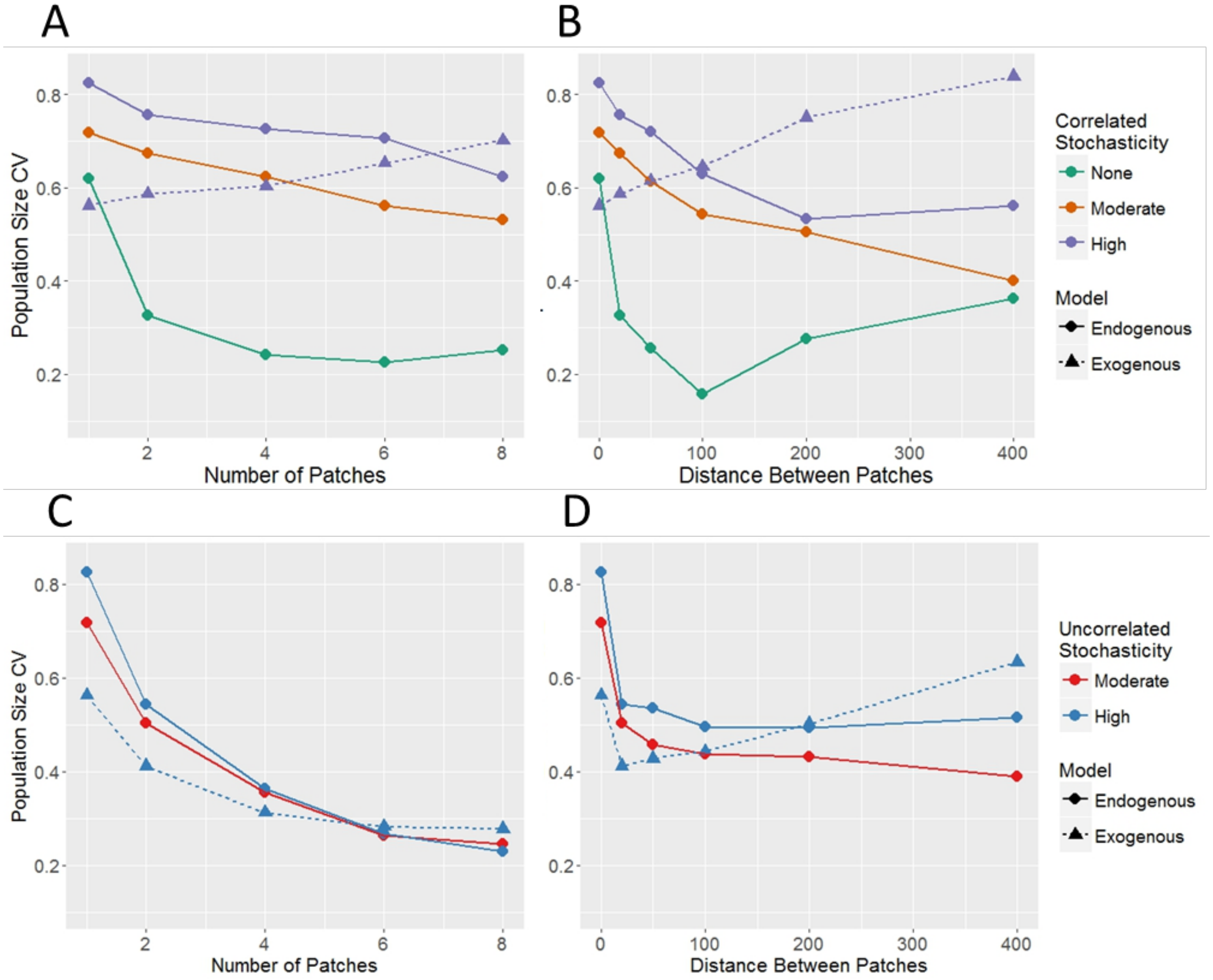


Figure 4.3.4-3 Coefficient of variation (CV) of total population size as a function of the number of patches (at an inter-patch distance of 20m for 2 or more patches; A, C), and distance between patches (for 1 patch at zero distance, and 2 patches at greater distances; B, D) under the exogenous and endogenous models with correlated or no environmental stochasticity (A, B), or uncorrelated stochasticity (C, D). (Note, the 1-patch scenario is included on the correlated and uncorrelated graphs for comparison, but stochasticity can be neither correlated nor uncorrelated when there is only a single patch.)

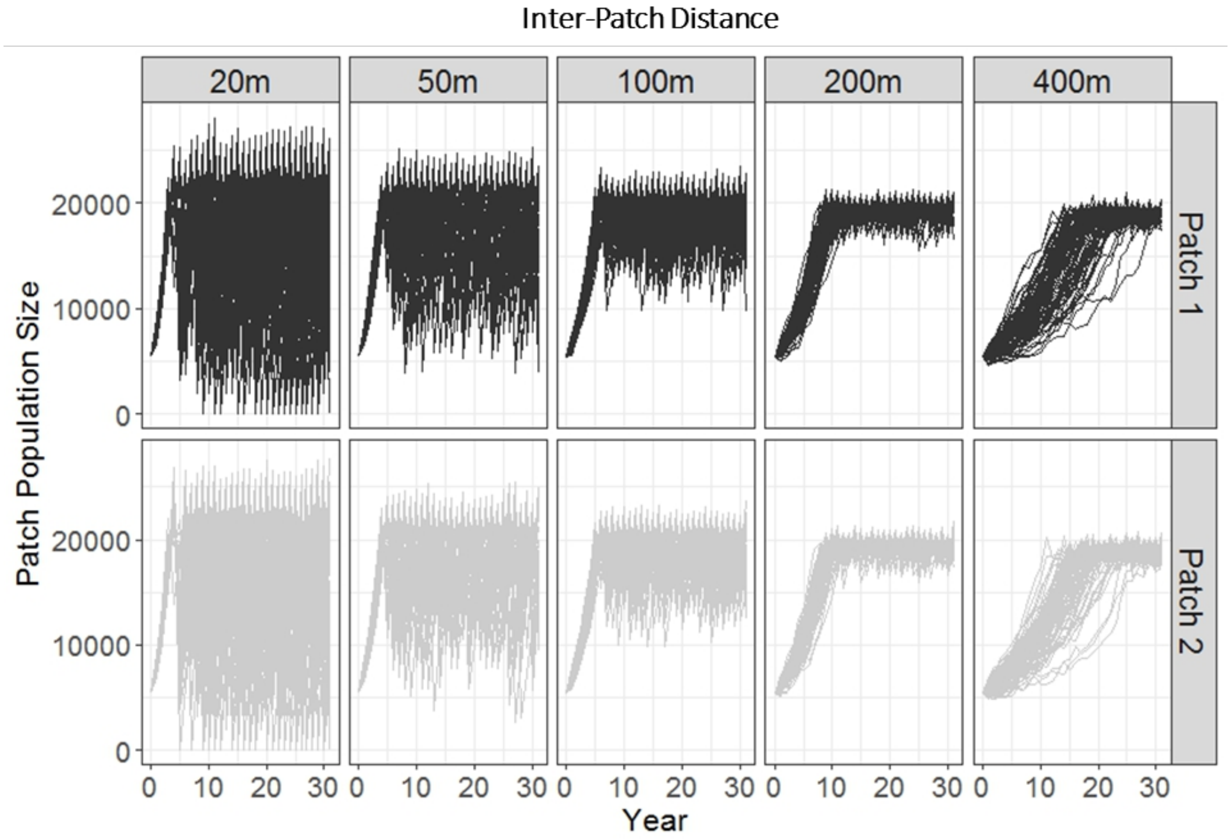


Figure 4.3.4-4. Individual patch population trajectories for the 2-patch scenario and all inter-patch distances under the endogenous model with no environmental stochasticity. Given the very low level of dispersal that occurs between patches when they are 400m apart, the patch dynamics are indicative of what would happen in an isolated patch of the same size (i.e., 0.72ha). Population variability increases as inter-patch spacing decreases.

4.4 Transition Activities

4.4.1 Review of management actions for TERS

We identified 27 managers at 26 installations (Table 4.4.1-1) who were responsible for restoring and managing habitat for TERS and willing to participate in the survey. Most habitat management conducted on participating installations involves restoring existing degraded habitat using prescribed burns, herbicides, and mechanical treatments (Figure 4.4.1-1a). Fewer installations attempt to create new habitat or acquire land to preserve habitat. Only a few attempt to create dispersal corridors. About a third of the installations reintroduce animals into habitat that has been created or restored.

When asked about management questions that need to be addressed, most managers indicated a need to know which habitat patches should be restored or managed to have the greatest impact on viability, and whether restoring all available habitat will improve viability (Figure 4.4.1-1b). Over half the managers also wanted to know where to locate new areas of habitat to ensure connectivity, whether restoration or creation of habitat would mitigate for the loss of suitable habitat, and whether viability is affected by the timing and frequency of disturbances used to manage habitat. Although only 7% of managers create corridors on their installations, 44% wanted to know if adding corridors would improve population viability. About a third of the managers wanted to know where animals should be reintroduced. Only 37% of managers indicated they were in a position where they needed to choose between alternative restoration strategies to meet management objectives. In addition, 3 managers who are trying to deter wildlife from entering airfields or firing ranges, asked if SEIBMs could predict whether restoring or creating habitat would draw animals away from areas of military use. One manager also wanted to know whether animals would use new habitat after it had been created.

Managers provided information on 25 monitoring data sets for wildlife species whose habitats were being restored or managed on 23 installations (Fort Bragg and Vandenberg AFB each provided information for 2 species, Table 4.4.1-2). Of these data sets, 12 were birds, 6 were insects, 5 were reptiles, and 2 were mammals. Nearly all installations (96%) collected data on population size, and 88% had habitat data in a GIS database (Figure 4.4.1-2a). Over half also collected demographic and movement data, and 48% had behavioral information on individual movement paths. Of the 12 bird data sets, 7 were red-cockaded woodpecker (*Picoides borealis*), a species whose recovery efforts have been guided by SEIBMs since the late 1990s (USFWS 2003). Therefore, installations managing red-cockaded woodpeckers likely already collect the types of data necessary to parameterize an SEIBM. Likewise, since our research group is building SEIBMs for Fender's blue butterfly (*Icaricia icarioides fenderi*) and St. Francis' satyr (*Neonympha mitchellii francisci*), data sets for these species are also adequate for building SEIBMs. If we omit the red-cockaded woodpecker, Fender's blue butterfly, and St. Francis' satyr data sets to better reflect the typical amount of data a DoD manager is likely to possess, a slightly smaller proportion of the remaining 16 data sets on 15 installations possess the necessary data to parameterize an SEIBM (Figure 4.4.1-2a), and the amount of population size data shifts downward, with the percentage of data sets with greater than 10 years of data decreasing from 52% to 25% (Figure 4.4.1-2b). However, most installations (81%) still had GIS databases of environmental variables that could be used to construct habitat maps (Figure 4.4.1-2a), and most data sets (69%) had more than 5 years of population size data. Approximately half of the installations collected multiple years of data on survival and reproductive success, and 44% possessed radio telemetry or satellite tag data that could be used to estimate movement parameters.

Only 6 (22%) of the 27 managers surveyed had previous experience with SEIBMs and only one (Eglin AFB) was currently using an SEIBM to manage species on the installation (Figure 4.4.1-3). Nevertheless, 89% were open to the idea of using an SEIBM, with 33% responding that they definitely thought using an SEIBM would enhance their ability to manage habitat and 56% undecided. (Figure 4.4.1-3). The main factors that managers felt would prevent them from using SEIBMs (Figure 4.4.1-4) were lack of modeling experience (74%), lack of data (52%), and lack of resources to collect necessary data (52%). 30% of managers had doubts about the reliability of predictions, and 26% felt that the simpler decision-making methods they currently use were adequate. In these cases, methods were generally habitat-based and decisions depended more on practicality or needs of the military that were not related to viability of the species being managed. Only 7% of managers felt the types of questions that SEIBMs address were not relevant to management on DoD installations.

After reviewing the questionnaires, we believe SEIBMs have potential for general application on military installations. Most questions typically addressed by SEIBMs are the same questions that the surveyed DoD managers take into consideration when making habitat management decisions; in particular, what is the impact of restoring habitat on population viability, and which patches have the greatest impact on viability? In addition, SEIBMs are capable of addressing two other questions brought up by military managers: whether animals will actually use habitat that has been newly created, and whether habitat can be created or restored in such a way to draw animals away from an area of military use. In fact, SEIBMs have previously been applied to similar questions. Kanagaraj et al. (2013) used an SEIBM to predict whether tigers will find and use corridors connecting habitat patches in India and Nepal, based on landscape context and individual movement behavior. In Japan, an SEIBM has been used to design a strategy of establishing “alternate feeding areas” to alleviate damage to wheat crops by white-fronted geese (Amano et al. 2007). Therefore, the types of questions that SEIBMs address have great applicability to management of TERS habitat on military installations. Only 7% of surveyed managers felt the types of questions that SEIBMs address were not relevant to management on their installations. Ironically, one of the reasons given was that SEIBMs are unnecessary because red-cockaded woodpeckers have been increasing under the current management practice of placing recruitment clusters in suitable habitat next to existing clusters. In fact, this practice was developed using insights from an SEIBM (Letcher et al. 1998, Crowder et al. 1998, Walters et al. 2002, USFWS 2003).

In general, the DoD managers surveyed were open to using SEIBMs, but their main limitations were insufficient data and lack of modeling experience. Although most installations collect habitat and population size data, only about half collect the demographic or movement data required to build an SEIBM. The DoD-managed species for which SEIBMs have already been built (red-cockaded woodpecker, Fender's blue butterfly, St. Francis' satyr) have been the subjects of detailed research and data collection for decades. However, not all SEIBMs start off being built with such extensive data sets. If only one or two parameters are unknown, a method called "pattern-oriented modeling" can be used to estimate parameter values whose simulated population dynamics most closely match observed data (Rushton et al. 1997, Stephens et al. 2002). Parameters may also be derived from literature or surrogate species. Predictions from initial models built with short-term or incomplete data sets should be used with caution to guide management decisions. However, even preliminary models built with sparse data can generate insights and testable hypotheses, and are useful for pinpointing what data need to be collected to improve future predictions.

Besides the installations that manage for red-cockaded woodpecker, St. Francis' satyr, and Fender's blue butterfly, four installations (Camp Shelby, U.S. Air Force Academy, Camp Grayling, and Fort Riley) currently seem to have sufficient data to consider building an SEIBM. Because military training at Camp Shelby occurs in the DeSoto National Forest, management of the gopher tortoise is shared by the Mississippi Army National Guard, U.S. Fish and Wildlife Service, U.S. Forest Service, and the Nature Conservancy. To manage gopher tortoise (*Gopherus Polyphemus*), Camp Shelby surrounds each tortoise colony with a 200' buffer zone, and has established a 2200-acre refuge that is managed to achieve optimal habitat conditions using prescribed burns (MSARNG 2014). A major objective is to keep tortoises off the artillery firing ranges, where exposure to vehicle activity poses a significant mortality risk. As described above, an SEIBM might be able to predict whether providing desirable habitat elsewhere is likely to result in the desired redistribution of tortoises away from the firing ranges. The U.S. Air Force Academy currently protects riparian habitat on its base along Monument Creek for the Preble's meadow jumping mouse (*Zapus hudsonius preblei*). As a result, the base contains one of the largest PMJM populations documented within the range of the subspecies (Grunau et al. 1999). However, species viability is still threatened by habitat fragmentation and degradation that has isolated sub-populations along the tributaries from the main stem sub-population, and the Monument Creek population from other populations outside the base. An SEIBM could be used to evaluate connectivity among habitat patches and determine where habitat might be restored or corridors created to facilitate movement among sub-populations. Camp Grayling has used clear cuts and fire to open tree canopy and create habitat for massasauga rattlesnakes (*Sistrurus catenatus*). An SEIBM could answer questions about whether snakes can access and benefit from these new habitat patches. Fort Riley uses prescribed burns and herbicides to restore tallgrass prairie habitat for the greater prairie chicken (*Tympanuchus cupido*). An SEIBM could inform managers about when, where, and how often to burn in order to achieve goals of species persistence.

The other major limitation preventing managers from using SEIBMs is lack of modeling experience. SEIBMs have the potential to capture the dynamics of complex systems, but coding that complexity into a model is beyond the abilities of the typical manager. However, limited modeling experience can be overcome by reaching out to researchers who specialize in ecological modeling. Some modelers are consultants who contract their services (*e.g.*, www.langrailsback.com, https://www.fws.gov/rcwrecovery/rcw_model.html). Others are academics who may have access to funding and graduate students who are looking for applied projects on which to develop their skills. Thus, collaboration with academic institutions may enable managers to collect data and build SEIBMs with fewer resources than might be imagined. The most successful collaborations require close communication between manager and modeler, so the modeler has the appropriate biological information and understanding of the system, and the manager understands how to interpret model outputs.

Based on our informal survey, most DoD managers viewed SEIBMs as potentially useful for addressing many of the questions they face when managing wildlife habitat. The main factors limiting their use are lack of data and modeling experience. Only a few of the installations are capable of building an SEIBM with the data on hand, and the majority of managers have no experience with modeling. However, if DoD managers were to collaborate with civilians specializing in ecological modeling, these obstacles are not insurmountable. Because of their complexity and high data requirements, SEIBMs are not practical for single decisions that need to be made immediately, or decisions that are dictated primarily by logistical feasibility or military needs. However, when integrated into the long term management of a TERS, SEIBMs provide insights into complex population dynamics and offer a science-based method for guiding habitat management that is accepted and used by regulatory agencies like the U.S. Fish and Wildlife Service and U.S. Forest Service.

Table 4.4.1-1. List of the 26 participating installations, and the species for which managers provided information on monitoring data

Installation	State	Branch	Species
Camp Bowie	TX	ARMY	Black-capped vireo
Camp Grayling	MI	ARMY	Massasauga
Camp LeJeune	NC	USMC	Red-cockaded woodpecker
Camp McCain	MS	ARMY	Northern long-eared bat
Camp Shelby	MS	ARMY	Gopher tortoise
Camp Swift	TX	ARMY	Comanche harvester ant
Eglin Air Force Base	FL	USAF	Red-cockaded woodpecker
Fort Bragg	NC	ARMY	Saint Francis' satyr, Red-cockaded woodpecker
Fort Custer	MI	ARMY	Eastern box turtle
Fort Gordon	GA	ARMY	Red-cockaded woodpecker
Fort Jackson	SC	ARMY	Red-cockaded woodpecker
Fort Pickett	VA	ARMY	Michaux's sumac
Fort Polk	LA	ARMY	Red-cockaded woodpecker
Fort Riley	KS	ARMY	Greater prairie chicken
Fort Stewart	GA	ARMY	Red-cockaded woodpecker
Joint Base Lewis-McChord	WA	ARMY	Taylor's checkerspot butterfly
Naval Facilities Engineering Command, Hawaii (Joint Base Pearl Harbor-Hickam)	HI	NAVY	Hawaiian stilt
Kansas Army National Guard	KS	ARMY	
McConnell Air Force Base	KS	USAF	
Naval Air Station Patuxent River	MD	NAVY	Northern diamondback terrapin
Naval Base Guam	GU	NAVY	Green sea turtle
Naval Support Activity Monterey	CA	NAVY	Smith's blue butterfly
Pueblo Chemical Depot	CO	ARMY	Mountain plover
USACE Willamette Valley Project (Fern Ridge Reservoir)	OR	ARMY	Fender's blue butterfly
US Air Force Academy	CO	USAF	Preble's meadow jumping mouse
Vandenberg Air Force Base	CA	USAF	El Segundo blue butterfly, Western snowy plover

Table 4.4.1-2. Types of monitoring data collected on DoD installations (n=25). Installations in bold likely contain enough data to build a SEIBM

Installation	Species	Taxon	GIS habitat data	# yrs pop. size data	Survival data	Fecundity data	Move data (any type)	Ind. move paths
Camp Bowie	Black-capped vireo	Bird	x	6-10		x		
Camp Grayling	Massasauga	Reptile	x	6-10	x	x	x	x
Camp Lejeune	**Red-cockaded woodpecker**	**Bird**	**x**	**>10**	**x**	**x**	**x**	
Camp McCain	Northern long-eared bat	Mammal		1			x	x
Camp Shelby	**Gopher tortoise**	**Reptile**	**x**	**>10**	**x**	**x**	**x**	**x**
Camp Swift	Comanche harvester ant	Insect	x	6-10				
Eglin AFB	**Red-cockaded woodpecker**	**Bird**	**x**	**>10**	**x**	**x**	**x**	
Fern Ridge Reservoir	**Fender’s blue butterfly**	**Insect**	**x**	**>10**	**x**	**x**	**x**	**x**
Fort Bragg	Red-cockaded woodpecker	Bird	x	>10		x	x	
Fort Bragg	**St. Francis’ Satyr**	**Insect**	**x**	**>10**	**x**	**x**	**x**	**x**
Fort Custer	Eastern box turtle	Reptile	x	2-5	x	x	x	x
Fort Gordon	Red-cockaded woodpecker	Bird	x	>10		x	x	x
Fort Jackson	Red-cockaded woodpecker	Bird	x	>10	x	x		
Fort Polk	**Red-cockaded woodpecker**	**Bird**	**x**	**>10**	**x**	**x**	**x**	**x**
Fort Riley	Greater prairie chicken	Bird	x	6-10	x	x	x	x
Fort Stewart	**Red-cockaded woodpecker**	**Bird**	**x**	**>10**	**x**	**x**	**x**	**x**
Joint Base Lewis-McChord	Taylor’s checkerspot butterfly	Insect	x	6-10				
Joint Base Pearl Harbor-Hickam	Hawaiian stilt	Bird		0			x	x
NAS Patuxent River	Northern diamondback terrapin	Reptile	x	2-5	x	x		

Naval Base Guam	Green sea turtle	Reptile	x	6-10		x	x	x
Naval Support Activity Monterey	Smith’s blue butterfly	Insect		2-5				
Pueblo Chemical Depot	Mountain plover	Bird	x	>10				
USAF Academy	**Preble’s meadow jumping mouse**	**Mammal**	**x**	**>10**	**x**	**x**	**x**	**x**
Vandenberg AFB	El Segundo blue butterfly	Insect	x	6-10				
Vandenberg AFB	Western snowy plover	Bird	x	>10	x	x		

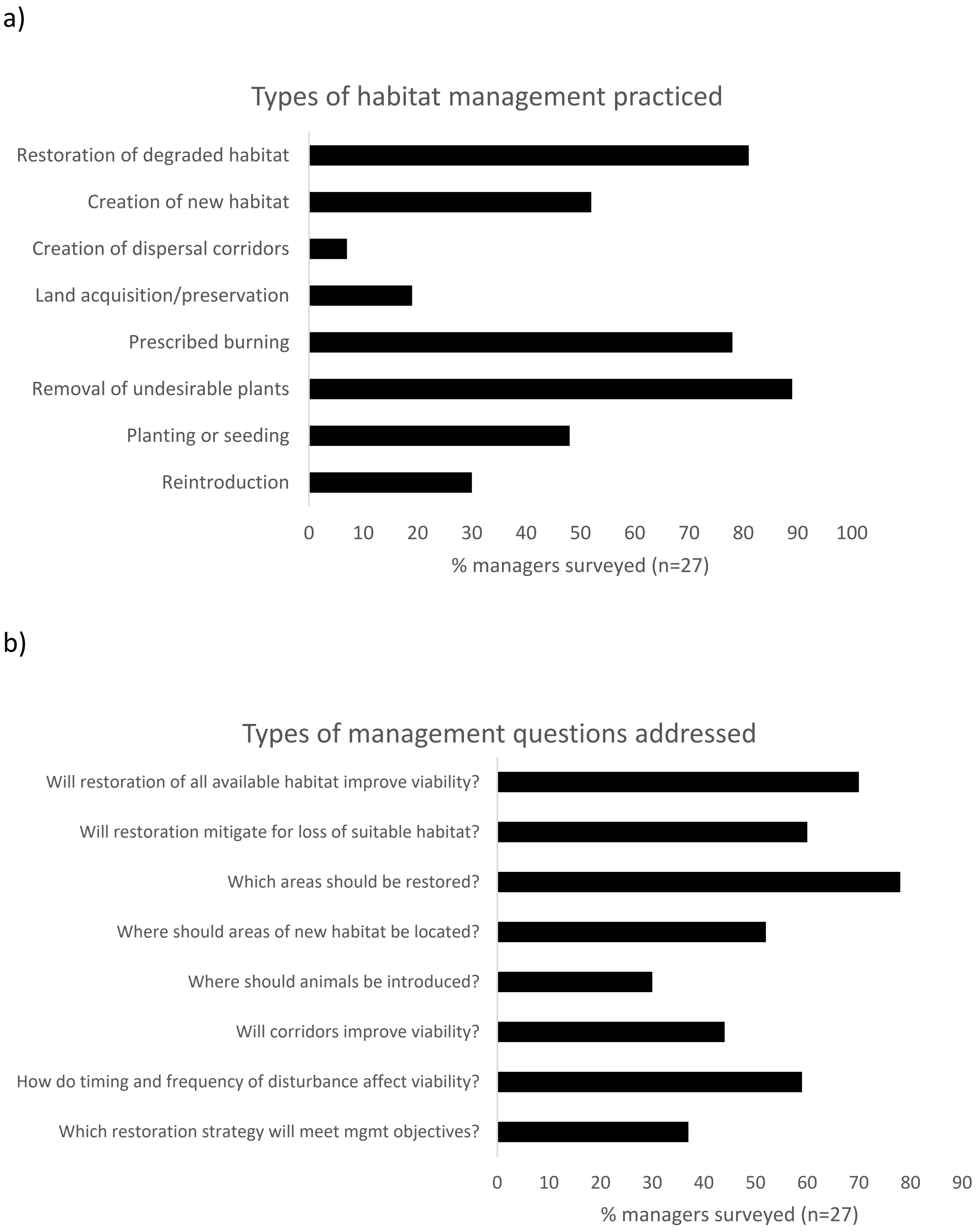


Figure 4.4.1-1. (a) Types of habitat management conducted by the 27 managers surveyed, and (b) the types of management questions they need to address

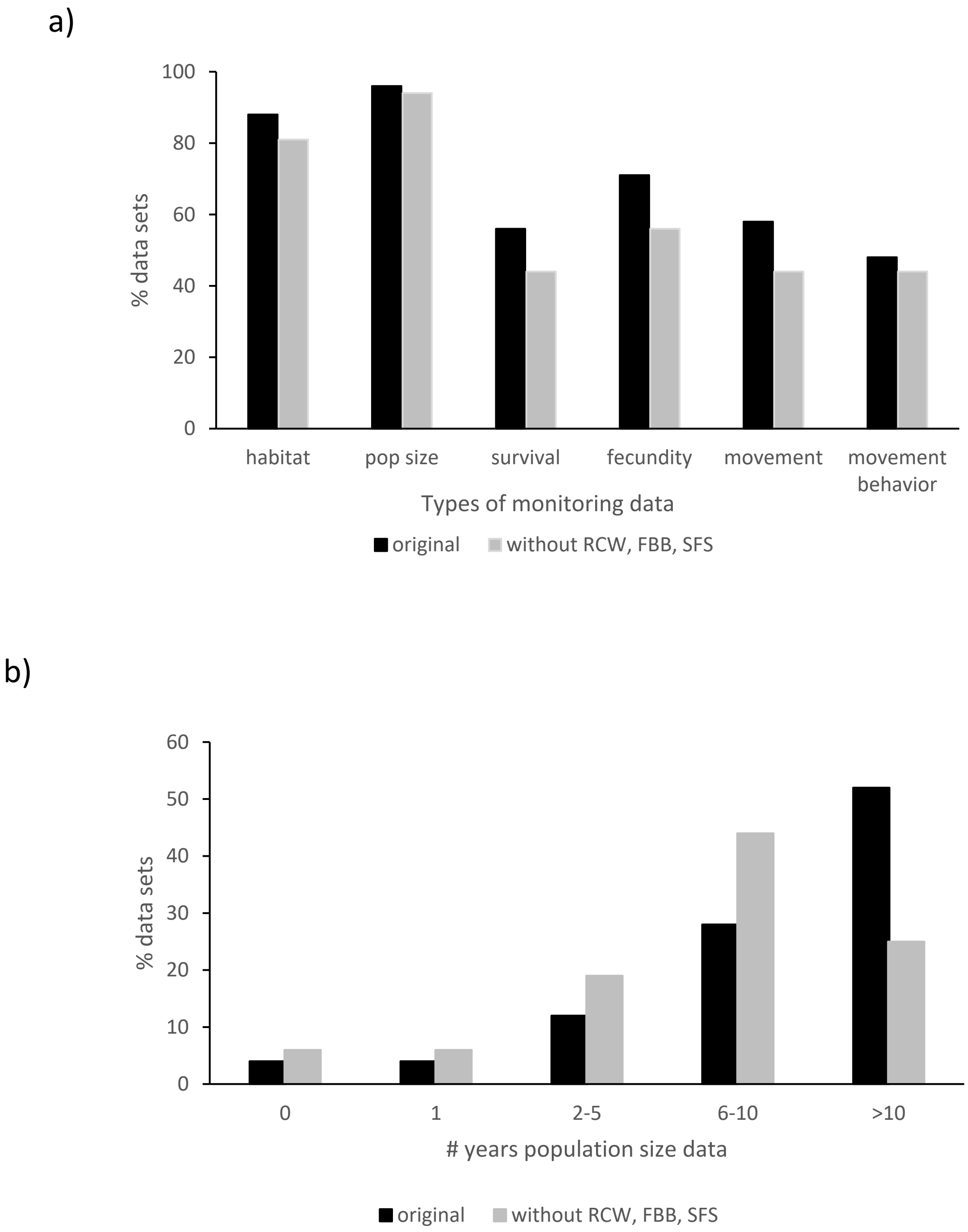


Figure 4.4.1-2. Types and amounts of monitoring data collected on DoD-managed species. Figure (a) shows the % of monitoring data sets that include habitat, population size, survival, fecundity, movement (any type), and individual movement path data. Figure (b) shows the % of data sets for which 0, 1, 2-5, 6-10, and >10 years of population size data are collected. Black bars indicate the original collection of data sets with red-cockaded woodpeckers included (n=25). Red bars indicate the data sets remaining after the red-cockaded woodpecker, Fender’s blue butterfly, and St. Francis’ Satyr data sets are removed (n=16).

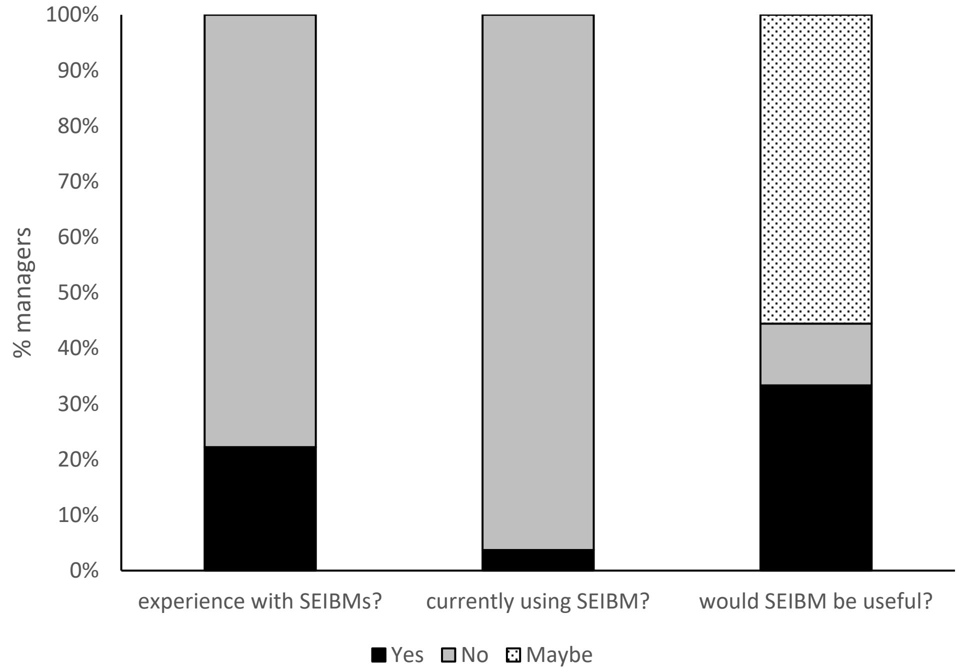


Figure 4.4.1-3. DoD managers' experience and perception of SEIBMs. n=27 manager responses.

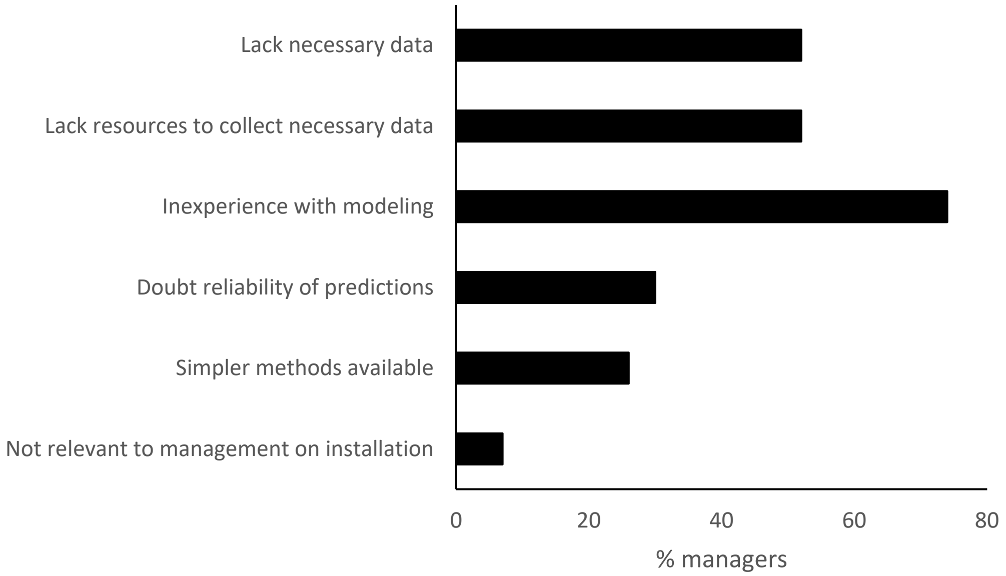


Figure 4.4.1-4. Factors that would prevent managers from considering using SEIBMs. n = 27 manager responses.

4.4.2 User guide to SEIBMs

Our review of the literature found that SEIBMs are best suited for addressing questions for species with complex life histories in which dynamics may be driven by individual variation, and viability depends on the synergy between demography, behavior, dispersal ability, and landscape structure. Under these conditions, SEIBMs have outperformed simpler methods for addressing habitat management questions. Thus, they have been well suited for modeling small populations that are disproportionately affected by variation in individual behavior or demography, and social species whose population dynamics are driven by dispersal or carrying capacity rather than solely by vital rates. Although SEIBMs are generally not reliable enough to predict the exact outcomes of management (*i.e.*, the population will reach *x* individuals if plan A is implemented), they have proven robust enough for comparative analysis (*i.e.*, the population is more likely to reach *x* individuals if plan A is implemented vs. no restoration). This makes SEIBMs a scientifically defensible method for ranking proposed management alternatives.

Of the 9 working SEIBMs we reviewed, all had data on variables such as vegetation, stand age, canopy cover, topography, soils, or hydrology to produce GIS maps of the study area that explicitly describe spatial distribution of habitat (Table 4.4.2-1). Five had at least 10 years of population count data that could be used to either validate models or estimate unknown parameters. Six were parameterized with empirical survival data from the species of interest, mostly obtained from capture-recapture studies or monitoring of marked or radio-tagged individuals (Table 4.4.2-2). All of these survival data sets were age- or stage-specific, and 2 were habitat-specific. The amount of survival data varied widely, with sample sizes ranging from 87 to over 5000 individuals, and number of years of data ranging from 1 to 24 years. Of the 3 remaining SEIBMs, 2 (Bachman’s sparrow, St. Francis’ satyr) estimated survival using other methods (see Table 4.4.2-2). For the third SEIBM (wood stork), mortality was imposed not by a predetermined survival rate but by whether an indvidual's energy reserves fell below a minimum threshold. Thus, this model did not require survival data *per se*. All SEIBMs were parameterized with empirical fecundity data, mostly gathered from observing nests or monitoring reproductive activities of marked individuals (Table 4.4.2-3). Only 2 fecundity data sets were age- or stage-specific, and only 2 were habitat-specific. Studies ranged from 1 to 24 years, and sample sizes ranged from 24 nests to 11,450 individuals.

Seven of the 9 SEIBMs based their movement simulations on at least some field-collected data from the species of interest (Table 4.4.2-4). Four movement data sets (Cape Sable seaside sparrow, gray wolf, northern spotted owl, red-cockaded woodpecker) were obtained by tracking radio-marked individuals or recording locations of marked individuals. These types of studies ranged from less than 1 year with 31 individuals to 15 years and over 1000 individuals, and provided information on dispersal distances and probability of dispersal. Only one of these 4 studies (northern spotted owl) collected data on dispersal direction. Movement data for the 2 butterfly SEIBMs were collected by recording movement paths of individuals released in different habitats. These single year studies had samples of 42-606 individuals, and yielded fine scale data on habitat-specific move lengths and turn angles. For the Saint Francis' satyr model, probabilities of crossing habitat boundaries were parameterized with habitat-specific data from the Saint Francis' satyr and a surrogate species, the Appalachian brown butterfly. Resting times and habitat-specific move lengths and turn angles were estimated solely from individual flight paths of the surrogate species. Only 2 SEIBMs included field-collected estimates of dispersal mortality.

Of the 25 data sets collected by managers on DoD installations (see section 3.4.1), 10 contained data equivalent to those used to parameterize working SEIBMs (section 4.4.1. Table 4.4.1-2). In other words, the DoD data sets contained GIS habitat data; survival, fecundity, and movement data; and at least 10 years of population size estimates. Six of these data sets were for species (red-cockaded woodpecker, Fender's blue butterfly, St. Francis' satyr) whose habitats are already being managed with input from SEIBMs. However, there appear to be sufficient data to construct SEIBMs for four additional species: gopher tortoise (*Gopherus polyphemus*), Preble's meadow jumping mouse (*Zapus hudsonius preblei*), massasauga (*Sistrurus catenatus*), and greater prairie chicken (*Tympanuchus cupido*).

Although only 10 installations appeared to have data equivalent to those used in working SEIBMs, more installations likely have sufficient data to consider building an SEIBM. Most of the data sets had sufficient habitat data to build maps. Although half of the data sets lacked data to empirically estimate survival and fecundity, most had at least 5 years of population size data to estimate these parameters using a process called "pattern-oriented modeling", which looks for the set of parameter values that are most likely to produce the observed trends in population size. The greatest data limitation would be the paucity of information on how animals move across the landscape. Although most of the working SEIBMs were parameterized with some empirical movement data, less than half the managers surveyed collected this type of data, probably due to differences in monitoring goals. Some analyses have suggested that uncertainty in dispersal parameters, especially dispersal mortality, may translate to large errors in SEIBM predictions (Wennergren et al. 1995, Ruckelshaus et al. 1997, but see Mooij and DeAngelis 1999, South 1999). Thus, managers wishing to build SEIBMs might focus more resources towards obtaining accurate estimates of dispersal capability and movement characteristics.

Obviously, the most reliable model predictions will come from models that are based on copious amounts of species-specific empirical data. However, managers who are interested in building SEIBMs need not necessarily wait for complete data sets to consult with a modeler about building models with the data they have. Data gaps can be filled using estimates from the literature, surrogate species, or pattern-oriented modeling. Validation and sensitivity analyses should be applied to evaluate reliability of model predictions and parameter estimates, and identify studies that can be undertaken to reduce parameter uncertainty and improve model performance. Initial predictions may not be accurate or robust enough to make credible conservation decisions. However, each iteration of data collection, updating, and validating the model yields new insights about the system and refines model predictions. Thus, when treated as a component of a long term adaptive management program, SEIBMs can improve the understanding of complex systems and be a useful tool in guiding habitat management decisions.

The user guide has been submitted to the DoD as part of this project. It will also be disseminated to all of the DoD managers who participated in the survey described in section 3.4.1.

Table 4.4.2-1. Availability of habitat and population size data for the species of interest for 9 SEIBMs developed to guide habitat management. NR = not reported. Because some data were obtained from multiple studies, number of years of population size data are approximate. This table is only intended to give a general idea of the amount of data used to parameterize SEIBMs.

		Habitat		
Species	**Reference(s)**	**GIS data?**	**Data layers**	**Yrs pop size data**
Bachman's sparrow	Liu et al. (1995); Dunning et al. (2000)	Y	age, type, size, and boundaries of forest stands	4
Cape Sable seaside sparrow	Elderd and Nott (2008)	Y	topography, hydrology, vegetation	5
Fender's blue butterfly	Smokey et al. (in prep)	Y	vegetation/land cover	23
Gray wolf	Carroll et al. (2003, 2006)	Y	road density, human population, tasseled cap greenness, slope, vegetation	NR
Northern spotted owl	Forsman et al. (2011); USFWS (2011)	Y	owl distribution, nest sites, vegetation, tree basal area, tree density, canopy cover, stand height, stand age, snags, coarse woody debris	17-24
Red-cockaded woodpecker	Schiegg et al. (2005); Zeigler and Walters (2014)	Y	cavity tree clusters, vegetation/land cover	12-13
Red squirrel	Rushton et al. (1997); Lurz et al. (2003)	Y	age, species, and location of forest stands	16
Saint Francis' Satyr	Himes Boor et al. (in prep)	Y	vegetation/land cover	4-14
Wood Stork	DeAngelis et al. (1998)	Y	vegetation, surface elevation, soil type, road locations	NR

Table 4.4.2-2. Survival data available for the species of interest for 9 SEIBMs developed to guide habitat management. Available data may either have been collected specifically for the SEIBM or obtained from literature. NR = not reported. Because some data were obtained from multiple studies, years and sample sizes are approximate. This table is only intended to give a general idea of the amount and types of data used to parameterize SEIBMs.

Species	Reference(s)	Survival data avail?	Method	Stage specific	Habitat specific	n	# yrs
Bachman's sparrow	Pulliam et al. (1992); Liu et al. (1995)	N	No data; Pattern-oriented modeling	N/A	N/A	N/A	0
Cape Sable seaside sparrow	Nott et al. (1998); Elderd and Nott (2008);	Y	Survival rates based on literature for Cape Sable seaside sparrow and surrogate species. Data collection methods unknown.	Y	N	16-112 indiv.	1-10
Fender's blue butterfly	Smokey et al. (in prep)	Y	Estimate larval survival by counting eggs, plants w/ larval damage, and adults in plots and analyzing with general linear mixed model. Estimate avg. adult life span to be 15 days	Y	Y	934 total plots	3
Gray wolf	Ballard et al. (1987); Carroll et al. (2003, 2006)	Y	Radio telemetry	Y	N	151 indiv.	7
Northern spotted owl	Forsman et al. (2011); USFWS (2011); Schumaker et al. (2014)	Y	Capture/resight studies of marked individuals	Y	Y	5224 total indiv.	17-24
Red-cockaded woodpecker	Letcher et al. (1998); Schiegg et al. (2005); Zeigler and Walters (2014)	Y	Monitor marked individuals	Y	N	>5000 indiv.	15
Red squirrel	Lurz et al. (2003)	Y	Survival rates based on literature for red squirrel. Data collection methods unknown	Y	N	NR	NR
Saint Francis' Satyr	Aschehoug et al. (2015); Sivakoff et al. (2016); Himes Boor et al. (in prep)	N	Surrogate data from Appalachian brown butterfly. Habitat-specific larval survival from 1 yr mesocosm study (n=480). Habitat-specific adult survival from 1 yr mark recapture study (n=87)	N/A	N/A	N/A	0
Wood stork	Wolff (1994)	N	Mortality in model is based on energetic threshold and does not require survival data	N/A	N/A	N/A	0

Table 4.4.2-3. Fecundity data available for the species of interest for 9 SEIBMs developed to guide habitat management. Available data may either have been collected specifically for the SEIBM or obtained from literature. NR = not reported. Because some data were obtained from multiple studies, years and sample sizes are approximate. This table is only intended to give a general idea of the amount and types of data used to parameterize SEIBMs.

Species	Reference(s)	Data avail	Method	Stage specific	Habitat specific	n	# yrs
Bachman's sparrow	Haggerty (1988); Pulliam et al. (1992); Liu et al. (1995)	Y	Observe marked nests	N	N	66 nests	3
Cape Sable seaside sparrow	Lockwood et al. (1997); Elderd and Nott (2008);	Y	Observe marked nests	N	N	24 nests	2
Fender's blue butterfly	Smokey et al. (in prep)	Y	Count eggs in plots. Use general linear mixed models to estimate fecundity based on observed growth rates	N	Y	934 total plots	3
Gray wolf	Ballard et al. (1987); Carroll et al. (2003)	Y	Count placental scars and observe packs	N	N	16 scars, 28 packs	7
Northern spotted owl	Forsman et al. (2011); USFWS (2011); Schumaker et al. (2014)	Y	Monitor marked individuals	Y	Y	11450 indiv.	17-24
Red-cockaded woodpecker	Letcher et al. (1998); Schiegg et al. (2005); Zeigler and Walters (2014)	Y	Monitor marked individuals	Y	N	>5000 indiv.	15
Red squirrel	Rushton et al. (1997); Lurz et al. (2003)	Y	Litter size and % females breeding based on literature for red squirrel. Data collection methods unknown.	N	N	NR	NR
Saint Francis' Satyr	Himes Boor et al. (in prep)	Y	Some data from counting eggs from captive butterflies. Also used pattern-oriented modeling	N	N	81 indiv.	1
Wood stork	Kahl (1964); Wolff (1994)	Y	Observation of nesting pairs threshold and does not require survival data	N	N	>16000 nesting pairs	7

Table 4.4.2-4. Movement data available for the species of interest for 9 SEIBMs used for habitat management. NR = not reported. Because some data were obtained from multiple studies, years and sample sizes are approximate. This table is only intended to give a general idea of the amount and types of data used to parameterize SEIBMs.

Species	Reference(s)	Method	Habitat specific	Probability of dispersal	Dispersal distance	Dispersal direction	Individual movement paths	Dispersal mortality	n	# yrs
Bachman's sparrow	Liu et al. (1995)	No data; use best estimates	N/A	N	N	N	N	N	N/A	0
Cape Sable seaside sparrow	Elderd and Nott (2008)	Radio telemetry	N	N	Y	N	N	N	31	7 mos.
Fender's Blue Butterfly	Schultz and Crone (2001); Schultz et al. (2012)	Follow flight paths of individuals released in different habitats	Y	Y	Y	Y	Y	N	98-606 indiv.	1-2
Gray wolf	Ballard et al. (1987); Carroll et al. (2003)	Radio telemetry	N	Y	Y	N	N	Y	151 indiv.	7
Northern spotted owl	USFWS (2011); Forsman et al. (2002); Schumaker et al. (2014)	Track radio-marked and banded individuals.	N	Y	Y	Y	Y	Y	324 radio-marked, 1151 banded indiv.	11
Red-cockaded woodpecker	Letcher et al. (1998); Walters et al. (2002)	Record locations of marked individuals	N	Y	Y	N	N	N	>1000 records	15
Red squirrel	Rushton et al. (1997); Lurz et al. (2003)	No data	N/A	N	N	N	N	N	N/A	0
Saint Francis' satyr	Himes Boor et al. (In prep)	Probability of moving between habitats measured by following individuals of St Francis' satyr and Appalachian brown butterfly. Also used individual flight paths from ABB to quantify habitat-specific move length and turn angles.	Y	Y	N	N	N	N	42 SFS indiv.	1
Wood stork	Kahl (1964); Wolff (1994)	Followed individuals in plane	N	N	Y	N	N	N	NR	NR

4.4.3 Apply tools to additional case studies

4.4.3.1 Diffusion and Density

We observed a total of 2287 butterflies from 42 species, and recorded 1868 movement paths in 19 sites. After excluding observations at a distance of 10 m from field margins, we obtained a dataset of 1260 movement paths from 40 species. Diffusion rates were calculated for the 25 species among these 40 that had at least 4 complete moves (i.e., included 5 move lengths, 5 move durations, and 4 turn angles) in at least one of the four land cover classes (Fig. 4.4.3.1-1). Sufficient observations to calculate land cover class-specific diffusion rates were available for 22 species in semi-natural areas, 19 species in field margins, 14 species in olive groves and 7 species in wheat fields.

As predicted by general theory, diffusion was associated with density: butterfly densities were higher in land cover types through which they moved more slowly (Table 4.4.3.1-1, Fig. 4.4.3.1-2). Neither body size nor the interaction of body size and diffusion were significant predictors of density (fixed effects of wingspan and fixed effects of wingspan × diffusion, Table 4.4.3.1-1). When including land cover class in models, diffusion, wingspan and land cover class were strong predictors of density (Table 4.4.3.1-2), and densities differed significantly among land cover classes (Table 4.4.3.1-2, Fig. 4.4.3.1-2). Smaller butterfly species (≤ 30 mm, *Apharitis acamas, Freyeria trochylus, Pseudophilotes vicrama, Satyrium spini, Thymelicus hyrax, Thymelicus sylvestris* and *Ypthima asterope*) tended to occur with higher frequency (i.e. high enough frequency to be included in our movement dataset, Fig. 4.4.3.1-1, Table 4.4.3.1-3) only in field margins and semi-natural areas and most of the observed species × land cover class combinations for these species had diffusion rates of < 3 m^2/sec. Based on models including diffusion, wingspan, and land cover class as predictors, expected densities were highest in the field margins (median = 24.2 butterflies/ha, CI = 14.5 – 38.8), intermediate in semi-natural areas (median = 10.3 butterflies/ha, CI = 6.5 – 16.3), and lowest in agricultural areas (wheat: median = 2.8 butterflies/ha, CI = 0.9 – 7.5; olive groves: median = 1.7 butterflies/ha, CI = 0.7 – 3.2).

Move length, turning angle and expected net squared displacement were not significant predictors of density (Table 4.4.3.1-1). Move time, however, was a significant predictor of density with more time per step in areas with higher density (Table 4.4.3.1-1). Wingspan and the interaction of wingspan with length, time, turning angle and expected net squared displacement were all non-significant predictors of density ($P > 0.10$, Table 4.4.3.1-1). When land cover class was included as a fixed effect, move time was not a predictor of density, most likely because land cover class accounted for differences in move time and move times were shortest (least time per step) in olive groves and longest in wheat fields.

Analysis of diffusion among species as a function of wingspan indicated that diffusion was strongly associated with wingspan and that larger butterflies had higher diffusion rates ($F = 21.23$, $P = 0.001$). Analysis of density among species as a function of wingspan indicated that wingspan is not strongly associated with density ($F = 0.028$, $P = 0.869$).

Table 4.4.3.1-1. Models testing relationship of diffusion or component parameters (move length, turning angle or move time) with density. Wingspan is a fixed effect in models and models are fit using best model for structure of random effects (Table S2). Shown are $\chi^2$from type II χ^2tests from analysis of deviance.

	Model	χ^2	df	$P(\chi^2)$
Diffusion	**Diffusion**	**6.84**	**1**	**0.0089**
	Wingspan	2.74	1	0.0976
	Diffusion × Wingspan	3.05	1	0.0809
Move Length	Move Length	1.29	1	0.2556
	Wingspan	0.03	1	0.8716
	Length × Wingspan	0.47	1	0.4913
Turning Angle	Cos (Turn Angle)	3.63	1	0.0566
	Wingspan	0.30	1	0.5812
	Cos (Turn Angle) × Wingspan	1.21	1	0.2726
Move Time	**Move Time**	**5.76**	**1**	**0.0164**
	Wingspan	0.27	1	0.6011
	Move Time × Wingspan	0.02	1	0.8966
$E(R^2)$	$E(R^2)$	**1.57**	**1**	0.2201
	Wingspan	0.17	1	0.6803
	$E(R^2)$× Wingspan	2.15	1	0.1430

Table 4.4.3.1-2. Models testing relationship of diffusion or component parameters (length, turning angle or time) with density. Wingspan and land cover class are fixed effects and models are fit using best model for structure of random effects Models are fit using same factors for random effects as in Table S2. Models were fit using backwards procedure with non-significant interaction terms (P > 0.10) sequentially removed and final model presented below. Shown are $\chi^2$from type II χ^2tests from analysis of deviance.

	Model	χ^2	df	P(χ^2)
Diffusion	**Land cover class**	**84.75**	**3**	**< 0.0001**
	Diffusion	**6.57**	**1**	**0.0104**
	Wingspan	**9.20**	**1**	**0.0024**
	Diffusion × Land cover class	**4.39**	**3**	**0.0361**
	Diffusion × Wingspan	**8.41**	**1**	**0.0383**
Move Length	**Land cover class**	**69.57**	**3**	**<0.0001**
	Move Length	0.91	1	0.3398
	Wingspan	**4.56**	**1**	**0.0328**
Turning Angle	**Land cover class**	**70.17**	**3**	**<0.0001**
	Cos (Turn Angle)	1.56	1	0.2108
	Wingspan	2.93	1	0.0871
Move Time	**Land cover class**	**87.29**	**3**	**<0.0001**
	Move Time	3.35	1	0.0672
	Wingspan	**3.97**	**1**	**0.0464**
E(R^2)	**Land cover class**	**65.87**	**3**	**<0.0001**
	E(R^2)	<0.01	1	0.9251
	Wingspan	2.50	1	0.1135

Table 4.4.3.1-3: Table of diffusion rates by species [median and Confidence Intervals (CIs)]; semi-natural = grassland or shrubland – depends on region of Israel; wingspan. Many species have a range of sizes, including size differences between males and females. Therefore we estimated size to the nearest 0.5 cm as a coarse estimate of size, with the recognition that this coarsely classifies butterfly species and therefore is not a systematic measure of precise size

Species	Wing-span	Semi-natural Areas	CIs for semi-natural	Field Margins	CIs	Olive Groves	CIs	Wheat Fields	CIs
HESPERIIDAE									
Carcharodus orientalis, oriental marbled skipper	30	1.00	(0.29, 4.36)	---		---		---	
Spialia orbifer hilarus, Hungarian skipper	30	0.95	(0.26, 4.06)	4.59	(0.01, 30.54)	---		---	
Thymelicus hyrax hyrax, Levantine skipper	30	1.07	(0.48, 2.20)	0.44	(0.18, 0.92)	---		---	
Thymelicus sylvestris syriaca, small skipper	30	---		1.72	(0.23, 5.29)	---		---	
LYCAENIDAE									
Apharitis acamas, leopard butterfly	30	1.91	(1.91. 5.72)	6.94	(0.01, 48.22)	---		---	
Chilades trochylus, grass jewel	15	0.20	(0.20, 0.46)	1.12	(0.28, 2.74)	---		---	
Lampides boeticus, long-tailed blue	35	---	---	---		15.12	(3.36, 110.92)	---	
Polyommatus icarus, common blue	35	2.71	(0.60, 7.39)	1.11		---		---	
Pseudophilotes vicrama astabene, Eastern baton blue	25	2.24	(1.08. 4.27)	1.11	(0.68, 1.71)	---		---	
Satyrium spini melantho, blue-spot hairstreak	30	2.57	(1.09, 5.81)	2.54	(1.24, 5.82)	---		---	

NYMPHALIDAE									
Maniola telmessia telmessia, Turkish meadow brown	50	6.62	(2.6, 16.65)	12.53	(3.0, 79.4)	2.77	(1.41, 5.50)	---	
Melanargia titea titania, Levantine marbled white,	60	2.64	(2.17, 3.30)	7.67	(3.39, 16.66)	5.86	(2.70, 11.15)	24.61	(9.43, 56.10)
Melitaea deserticola macromaculata, desert fritillary	40	8.19	(4.75, 13.82)	48.34	(25.64, 88.33)	---		---	
Melitaea phoebe, knapweed fritillary	45	1.53	(0.68, 2.81)	6.71	(2.50, 19.90)	12.95	(3.46, 33.97)	---	
Melitaea trivia syriaca, lesser spotted fritillary	35	14.33	(6.69, 37.79)	9.16	(4.00, 22.31)	---		---	
Vanessa cardui cardui, painted lady	55	16.31	(4.60, 48.13)	---		703.5	(161.90, 1000.00*)	76.3	(27.77, 415.93)
Ypthima asterope, African ringlet	30	8.37	(3.74, 20.13)	---		---		---	
PAPILIONIDAE									
Papilio machaon syriacus, old world swallowtail,	75	18.98	(9.91, 34.82)	15.47	(7.71, 30.71)	6.40	(0.90, 17.53)	12.43	(5.07, 24.08)
PIERIDAE									
Anthocharis cardamines phoenissa, orange tip	45	3.34	(0.69, 9.44)	2.43	(0.93, 4.44)	110.57	(17.01, 261.88)	----	
Colias croceus, clouded yellow	50	17.68	(9.56, 33.19)	9.18	(6.74, 13.01)	8.05	(2.86, 19.11)	5.37	(2.80, 10.21)
Euchloe belemia belemia, green striped white	35	11.97	(5.16, 24.99)	15.49	(6.69, 30.29)	15.06	(5.92, 49.18)	----	
Gonepteryx cleopatra taurica, Cleopatra butterfly	55	----		----		50.56	(8.25, 200)	----	
Pieris brassicae, large cabbage white	60	25.71	(12.47, 45.68)	10.49	(5.75, 19l88)	11.59	(7.51, 16.79)	192.09	(18.36, 536.40)
Pieris rapae leucosoma, small cabbage white	50	12.85	(9.18, 18.23)	9.05	(6.98, 11.84)	6.74	(4.72, 9.52)	15.01	(10.51, 21.00)
Pontia daplidice daplidice, bath white	45	26.92	(10.58, 74.25)	16.11	(6.16, 33.27)	3.82	(1.09. 102.8)	7.15	(0.17, 200)

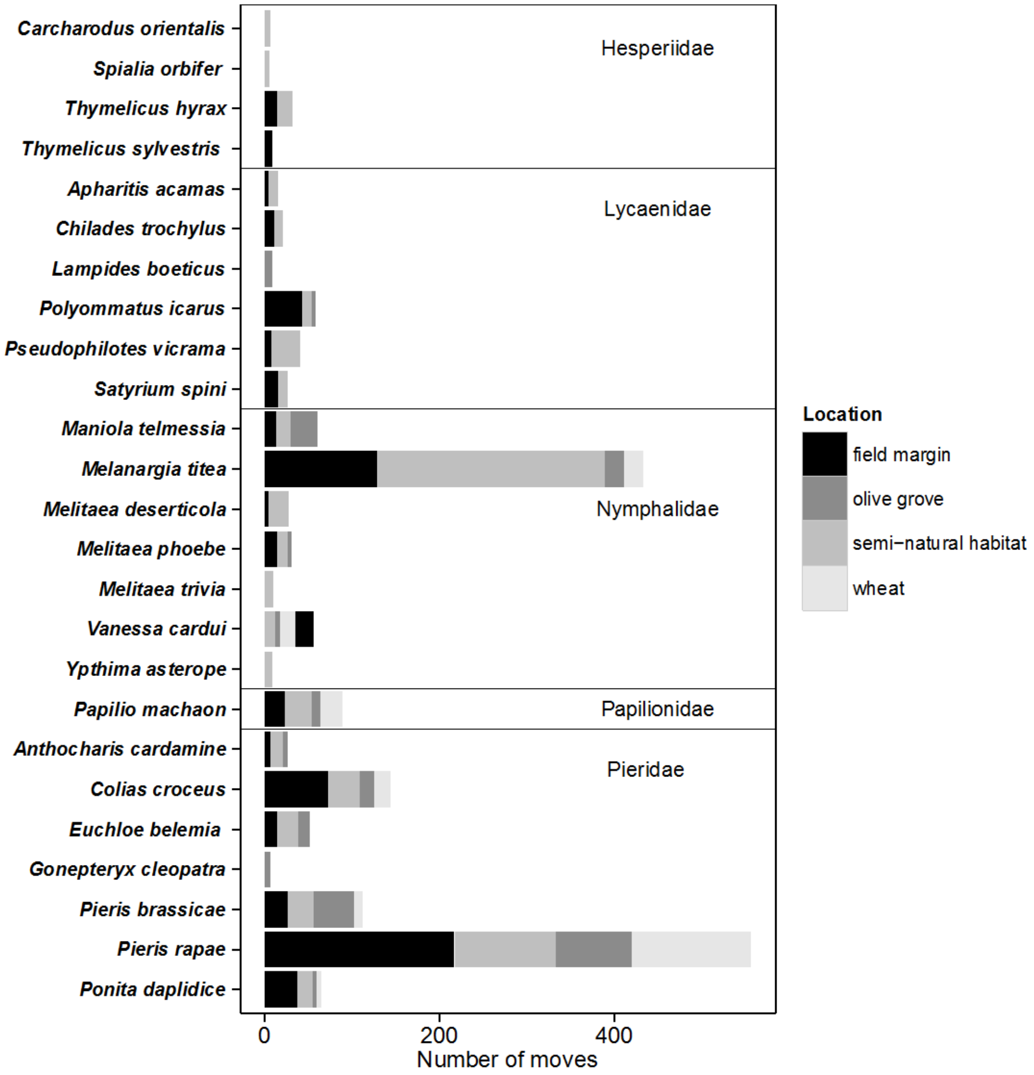


Figure 4.4.3.1-1. Sample sizes of 25 species included in analyses. Included are those species × land cover class combinations with at least four complete moves (4 turning angles, 5 move lengths and 5 move times).

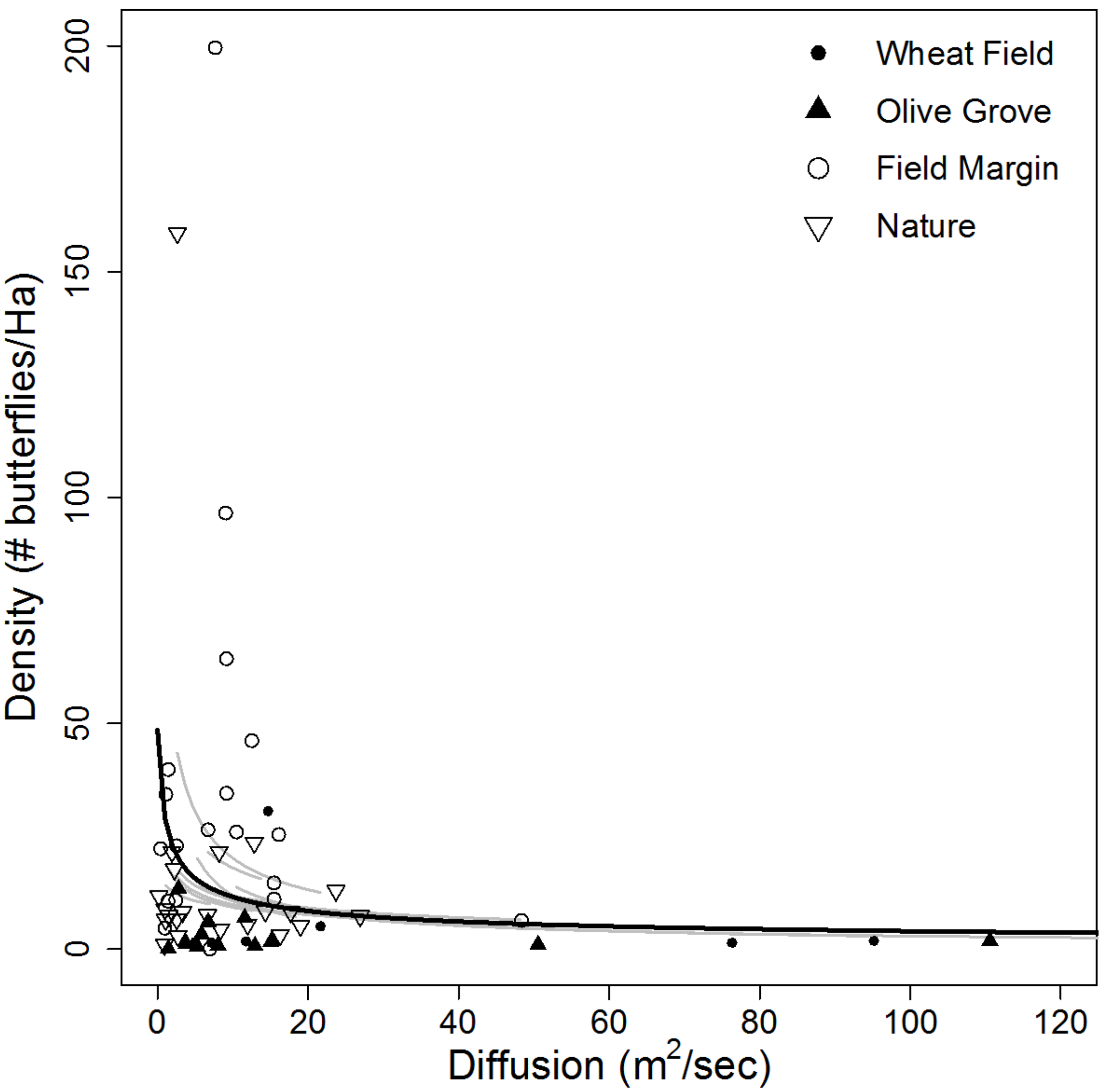
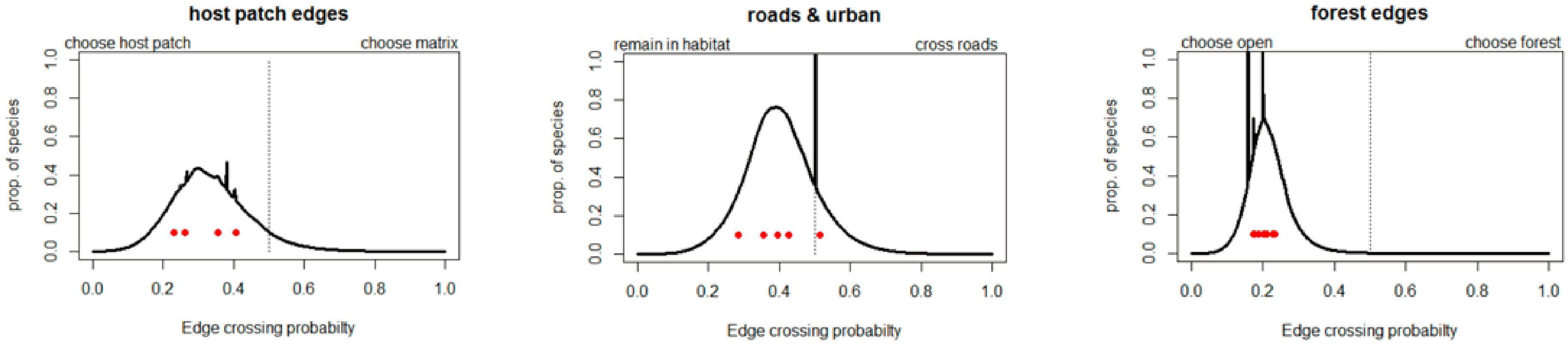


Figure 4.4.3.1-2. Relationship between diffusion and butterfly density. Each point represents one species × land cover class combination for which there were at least four moves. Black curve based on model fit to whole dataset. Gray curves are output of predicted model fit to species-specific wingspans and model coefficients.

4.4.3.2 Edge behavior mini meta analysis

Overall, butterflies preferred habitat over matrix at patch edges. Edge preference differed among edge types (c2 = 28.6, df = 2, P < 0.001, n = 18 species x edge type combinations). Therefore, we analyzed preference separately for each edge type (Figure 4.4.3.2-1). In general, butterflies had the strongest preference at structural open/forest patch edges (probability of choosing matrix = 0.201, 95% CI 0.152, 0.264; logit-scale among species SD =0.239, 95% CI: 0.000 – 0.677; z = -8.7, P < 0.001). Butterflies showed weaker preference at host plant patch edges (probability of choosing matrix = 0.307, 95% CI 0.187, 0.483; among species SD =0.426, 95% CI: 0.000 – 1.309 ; z = -2.9, P = 0.003). Butterflies showed the weakest preference at boundaries of roads or other developed habitat types (probability of choosing matrix = 0.390, 95% CI 0.263, 0.519; among species SD =0.410, 95% CI: 0.099– 1.063 ; z = -1.9, P = 0.056).

Figure 4.4.3.2-1 Edge crossing behavior at vegetation edges



4.4.3.3 Movement in high quality vs low quality meta analysis

Basic taxonomic information & structure

We found studies comparing movement in high- and low-quality habitat types for 78 species from 8 Phyla. Studies were heavily biased toward arthropods and vertebrates, especially in the lepidoptera (butterflies and moths) and coleopteran (beetles) insect orders, and in the aves (birds) and mammalia (mammals) vertebrate classes (Figure 4.4.3.3-1A-C). Four families, all in the class Insecta, were represented by more than two studies; three lepidopteran families (Nymphalidae (8), Pieridae (6) and Papilionidae (3) and one coleopteran family (Chrysomelidae). Four species were represented by two studies (Brachionus calyciflorus, Euphydryas anicia, Plebejus icarioides fenderii, Protaphorura armata, Tetranychus urticae). Only one genus (the Nymphalid butterfly *Euphydryas*) was represented by more than three studies, and, in addition to the two-study species above, four genera (Calopteryx, Morus, Phyllotreta, Selasphorus) were represented in two studies. Because of their limited replication within units, Genus and Species were not included as taxonomic levels in GLMMs.

Nonetheless, there was no apparent effect of this taxonomic structure on the proportion of studies with faster movement in low-quality habitat (Table 4.4.3.3-1). GLMMs with random effects of Phylum, Class, Order and/or Family never significantly improved model AIC's relative to a simple GLM with no taxonomic structure. Furthermore, estimates of variance among Phyla and Classes were 0. In the GLMM with all four taxonomic levels included, the variance estimates for Phylum, Class, and Family were 0, and the model was identical to the Order-only model. Therefore, we base inference about general patterns on unstructured logistic models.

Relative movement in high- vs. low-quality habitat

Of studies with a clear directional response, 83.8% showed faster net movement (diffusion or related metrics) in lower-quality habitat (binomial family, logit link GLM; 95% CI: 73.9-91.3%, test for difference from 50%: Z = 5.00, P < 0.001). Polynomial logistic regression including studies with no clear directional response indicated that 73.1% of all studies showed faster movement in lower quality habitat (95% CI: 62.1-82.1%), compared to 14.1% with faster movement in higher-quality habitat (95% CI: 7.7-28.1%) (Figures 4.4.3.3-2 A&B).

Table 4.4.3.3-1. Statistical summary of GLMMs with taxonomic random effects

Random effect	df	Variance	AIC
Phylum	2	0.00	64.2
Class	2	0.00	64.2
Order	2	0.34	64.0
Family	2	0.35	64.2
none	1	NA	62.2
All	5	NA	70.0

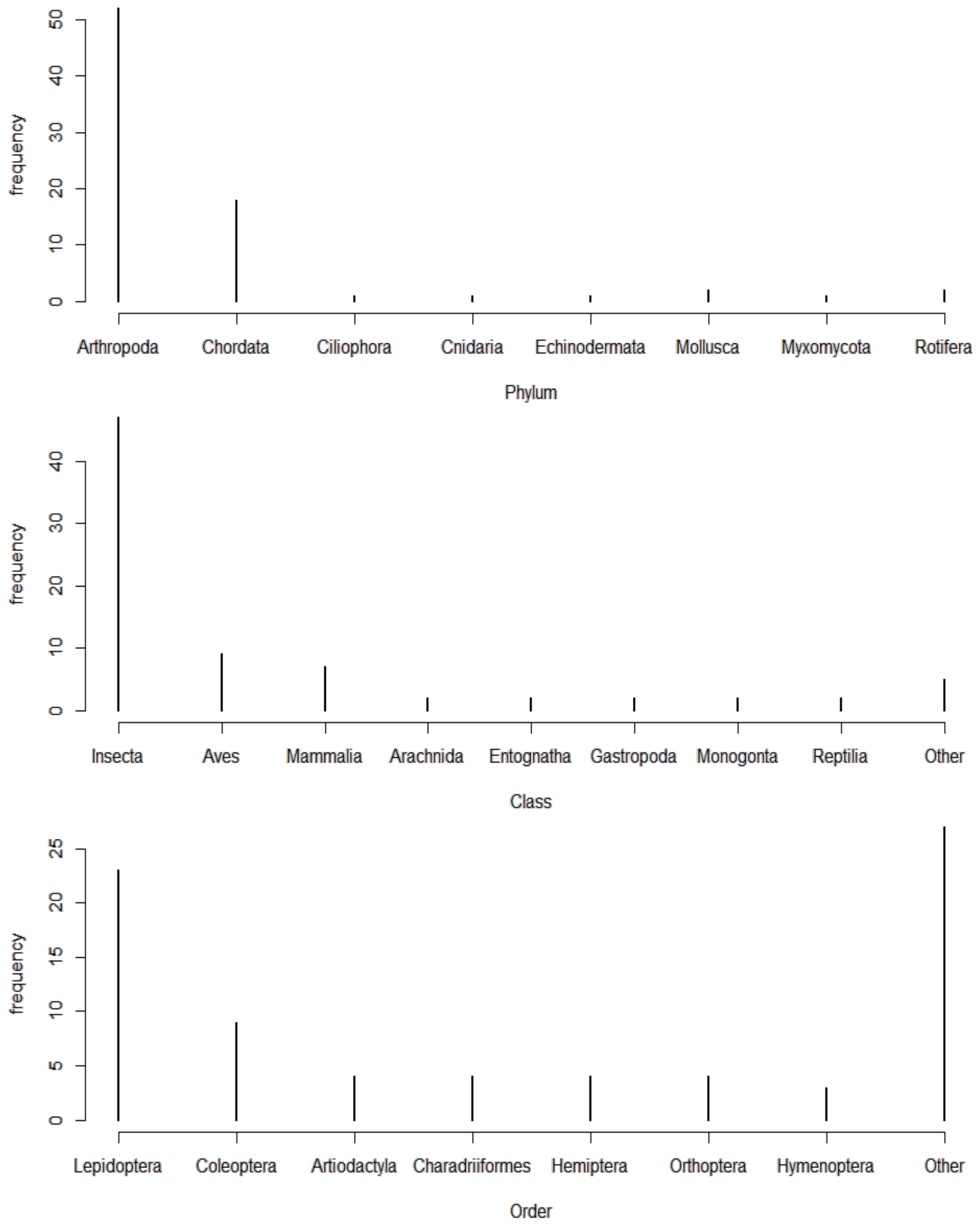


Figure 4.4.3.3-1. Taxonomic distribution of (A) Phyla, (B) Classes, and (C) Orders across species-study combinations used in our analysis.

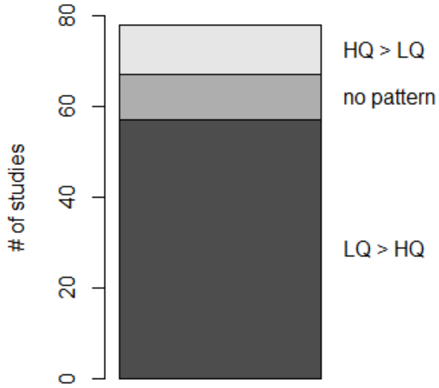


Figure 4.4.3.3-2. Number of studies showing faster movement in lower quality habitat (LQ > HQ), higher quality habitat (HQ > LQ), or no pattern.

4.4.3.4 Applications of source sink dynamics to bumblebees

Dispersal Kernels

The mean dispersal distance of *Bombus flavifrons* queens (based on data from Bowers 1985) was 216 meters, while the mean dispersal distance of *Bombus pascuorum* queens (based on data from Lepais *et al.* 1985) was 1871 meters. We used Weibull distributions to describe the distances that bumble bee queens disperse from their natal nest before initiating new colonies.

When these dispersal kernels were applied to heterogeneous landscapes, queens were more likely to nest within the same habitat in which they were produced when habitat was more aggregated. Habitat aggregation also had stronger effects on δ_{nat} and δ_{agr} (i.e., probability of remaining in their natal habitat) for bees with limited dispersal abilities (k_{short}) than on bees capable of dispersing long distances (k_{long}).

Asymptotic Dynamics – Long-Term Population Growth Rate (λ)

Population dynamics in heterogeneous landscapes followed the general expectations of any density-independent matrix model. After the stable stage structure was attained, the entire source-sink population, including sub-populations within each habitat type, grew or declined at the same constant rate, λ. In other words, populations could not persist indefinitely in one habitat while going extinct in another if dispersal was maintained between habitat types.

Loss of natural habitat (η) strongly reduced the long-term growth rate (λ) of the source-sink population (Fig. 4.4.3.4-1; conditions resulting in positive population growth are shaded in blue). However, the effect of habitat loss depended on the dispersal ability of bees (k_{short} *vs.* k_{long}) and the degree of habitat aggregation (α). Increased aggregation of habitat patches increased λ when queens were only capable of short-distance dispersal from their natal colonies (k_{short}), but had modest effects when queens were capable of dispersing long distances (k_{long}). Consequently, when landscapes were highly aggregated, more natural habitat was required to sustain long-distance dispersers than short-distance dispersers. When landscapes were highly fragmented, a similar and large amount of natural habitat (35-40% of the landscape) was required to sustain both short- and long-distance dispersers.

Asymptotic Dynamics – Long-Term Population Distribution

In our habitat-structured population models, the long-term stable population structure can be represented as either relative abundance of colonies in each habitat type (as in conventional stage-structured population models), or as relative density, calculated by dividing the relative abundances in each habitat by the relative area of each habitat type. Here, we present the stable population structure as relative densities, as this is likely to be the quantity measured in field settings.

The long-term relative density of colonies in each habitat type depended on landscape structure and dispersal ability of queens (Figure 4.4.3.4-2). The relative density of colonies in natural habitat increased when landscapes contained more natural habitat. More aggregated landscapes also led to higher relative densities of colonies in natural habitat, although the effect of habitat aggregation was weak for long-distance dispersers (cf. Fig. 4.4.3.4-2 a&b).

The landscape conditions that led to long-term population stability ($\lambda = 1$; depicted by solid white lines in Figure 4.4.3.4-2) differed from the conditions that caused relative densities to be equal in each habitat (depicted by dotted white lines in Figure 4.4.3.4-2). At the threshold where landscape conditions produced population stability, nest densities were higher in natural habitat than agricultural habitat. However, under conditions that led to long-term population declines (below the solid white line in Figure 4.4.3.4-2), natural habitats could either contain higher or lower nest densities than agricultural habitats, demonstrating that habitat-specific density monitoring can be a misleading indicator of habitat quality in source-sink systems.

Transient Dynamics – Rapid Loss of Natural Habitat

Transient dynamics were generated when a proportion of completely natural landscape was abruptly converted to agricultural habitat, leading to 20% annual decline in abundance ($\lambda = 0.8$). These simulations assumed that land conversion initially destroyed bumble bee colonies (see *Methods*), leading to an unstable (i.e., non-equilibrium) initial population structure. Depending on bee dispersal ability and level of habitat aggregation, conversion of 82.5% to 92.5% of a natural landscape to agriculture was required to achieve $\lambda = 0.8$.

In all of these cases, the density of the total population initially increased (Fig. 4.4.3.4-3, black lines) as population growth and dispersal from highly productive natural habitats caused populations in agricultural habitats to initially increase (Fig. 4.4.3.4-3, orange dashed lines).

These transient dynamics dissipated quickly and populations converged on λ = 0.8 within 4-7 years (Fig. 4.4.3.4-3, black dots). Convergence on λ took longest for short-distance dispersers in highly aggregated landscapes. However, transient dynamics experienced in the first several years caused populations to remain larger in the long-term than if they had immediately and steadily declined at λ = 0.8 from the beginning (Fig. 4.4.3.4-3, gray lines), and total population density even remained above the initial density (i.e., immediately after the landscape change) for up to 4 years. Scenarios in which landscape change did not initially remove bees in converted patches produced dynamics that more closely matched asymptotic dynamics because the population structure was closer to the long-term stable distribution, though some transient dynamics remained (D. Iles, unpubl. models).

Transient Dynamics – Rapid Restoration of Natural Habitat

Transient dynamics were also generated when a proportion of completely agricultural landscape was abruptly restored to natural habitat, leading to 20% long-term annual increase in abundance (λ = 1.2). These simulations also assumed that restoration removed bees from restoration sites, so that the population started at a non-equilibrium spatial structure with no colonies in the restored sites. To achieve λ = 1.2, conversion of 45-50% of an agricultural landscape to natural habitat was required (Fig. 4.4.3.4-4).

In these cases, the density of the total population initially decreased, driven by rapid population declines in agricultural habitats that occurred until a sufficient number of queens dispersed into natural habitats to facilitate population growth (Fig. 4.4.3.4-4). These transient dynamics also dissipated quickly and populations converged on λ = 1.2 within 4-6 years (Fig. 4.4.3.4-3, black dots). As with the simulations of rapid loss of natural habitat, convergence on λ took longest for short-distance dispersers in highly aggregated landscapes. Yet, the transient dynamics experienced in the first several years caused populations to remain much smaller in the long-term than if they had immediately and steadily increased at λ = 1.2 from the beginning (Fig. 4.4.3.4-4, compare black and gray lines). Consequently, up to 8 years elapsed before population density returned to the initial abundance at the time of the restoration.

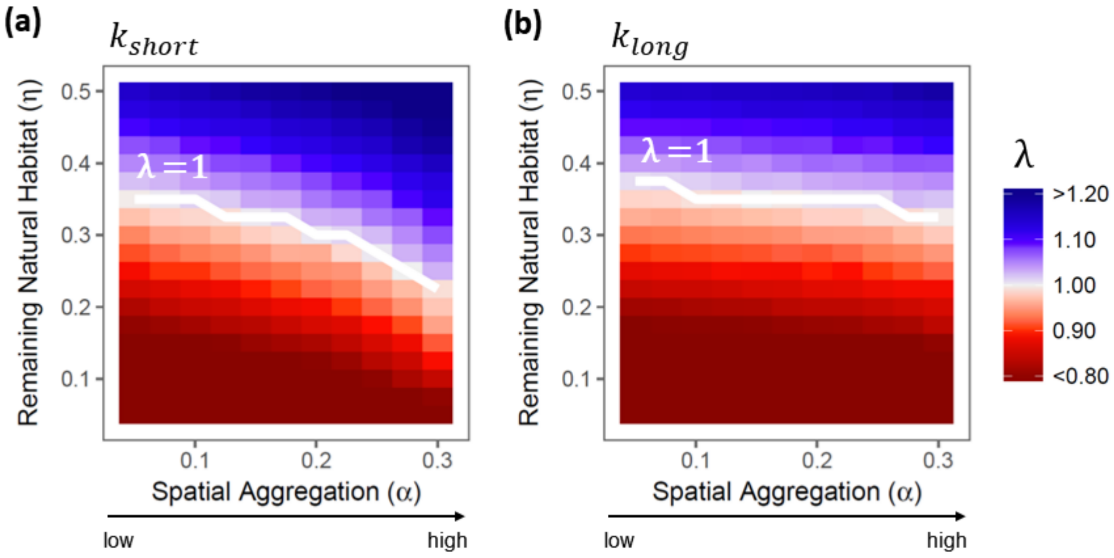


Fig. 4.4.3.4-1. Long-term population growth rate (λ) of bumble bees under different proportions of natural landscape (η) and levels of habitat aggregation (α). Results are shown for bumble bees with short (k_{short}) and long distance k_{long} dispersal (panels a & b, respectively). White line depicts boundary where λ = 1.

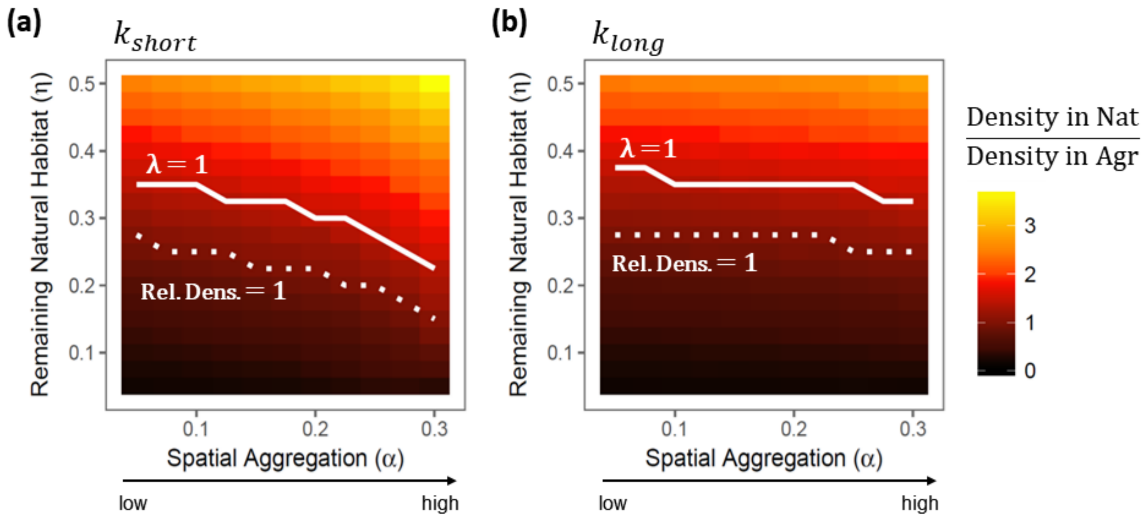


Fig. 4.4.3.4-2. Relative population density of bumble bees in natural and agricultural habitats under different proportions of natural landscape (η) and levels of habitat aggregation (α). Results are shown for bumble bees with short (k_{short}) and long distance k_{long} dispersal (panels a & b, respectively). Solid white line depicts boundary where λ = 1 (as in Fig. 2). Dotted white line depicts boundary where population densities in natural and agricultural habitats are equivalent.

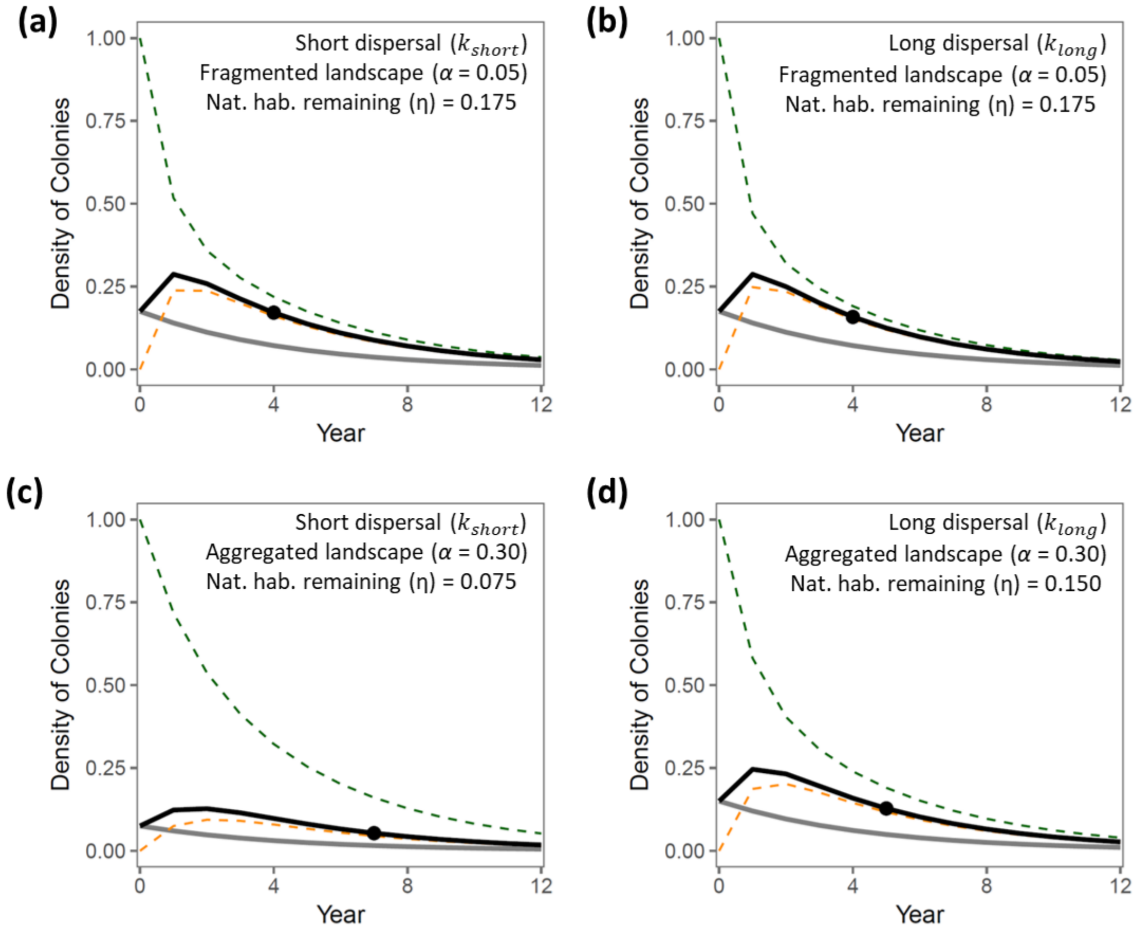


Fig. 4.4.3.4-3. Transient dynamics following immediate conversion natural habitat to agriculture resulting in $\lambda = 0.8$, assuming landscape was initially completely natural. Lines depict total population density across the landscape (black solid lines), density in remaining natural habitat (green dashed lines), and density in newly created agricultural habitat (orange dashed lines). Gray line depicts population dynamics at equilibrium, in the absence of transient dynamics equilibrium (i.e., for a population steadily multiplying at $\lambda = 0.8$). Solid circles indicate the year in which annual population growth rate converges on λ (with an accuracy of 0.01). Panels a-d show dynamics resulting from different combinations of dispersal ability, landscape aggregation, and amount of natural habitat remaining after landscape change.

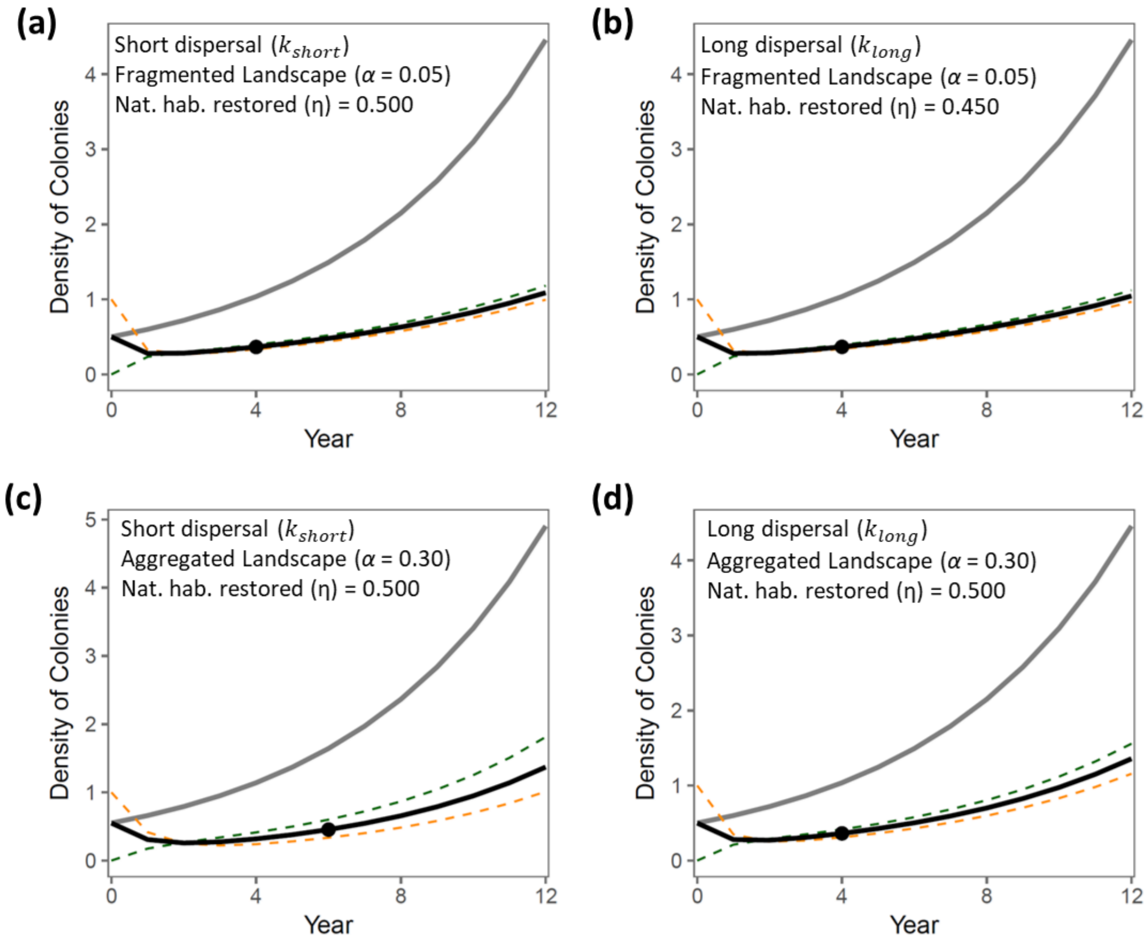


Fig. 4.4.3.4-4. Transient dynamics following immediate conversion agricultural habitat to natural habitat resulting in λ = 1.2, assuming landscape was initially completely agricultural. Lines and symbols are in interpreted as in Fig. 4.3

4.4.3.5 Karner blue & frosted elfin

At the site where we were working, we estimated a population of 70 (95% CI: 39-159) frosted elfins in 2015 and 24 frosted elfins (95% CI 5-115) in 2016. In 2017, we surveyed the property 10 times, and observed only 2 individuals. These data are not consistent with the expected pattern of a temporary drop in abundance, followed by recovery. With only three years of data, we cannot determine whether the demographic costs of this particular fire outweighed the long-term benefits, or whether the population will recover, but at a longer time scale that we observed for the Fender's blue in Oregon.

Karner blue dispersal kernels varied widely among years (Table 4.4.3.5-1). In most years, there was a high probability of movement between sites separated by 100 m, and a modest probability of movement between sites separated by 500 m. Resistance estimates also differed widely among years (Table 4.4.3.5-2), but were generally higher for roads and other paved surfaces (including the airport runway) than for forest (Table 4.4.3.5-2).

Table 4.4.3.5-1. Estimated Karner blue dispersal parameters (logit-scale slope and intercept of dispersal vs. distance in meters, with SE = standard errors)

Year	Intercept	Slope	SE Intercept	SE Slope	Probability of movement between sites separated by…	
					100 m	500m
2007	0.5129	-0.0126	0.3069	0.0012	0.321	0.003
2008	1.9192	-0.0185	0.3665	0.0017	0.517	0.001
2009	-4.1209	-0.0007	0.1666	0.0003	0.015	0.011
2010	-0.8884	-0.0020	0.2904	0.0004	0.252	0.131
2011	-2.8683	-0.0033	0.6140	0.0013	0.039	0.011
2012	-6.8651	-0.0012	0.7240	0.0012	0.001	0.001
2013	-1.7849	-0.0057	0.3091	0.0008	0.087	0.010
2014	-0.3025	-0.0070	0.3255	0.0007	0.268	0.022
2015	-2.3140	-0.0039	0.2542	0.0005	0.063	0.014

Table 4.4.3.5-2. Un-normalized coefficients and standard errors (SE) of multi-state mark-recapture model for Karner Blue movement across a heterogeneous landscape. A separate slope for transition probability was estimated for each land cover type: open habitat, road matrix, and forest matrix. When comparing the relative resistance between two land cover types, the higher slope value means a higher probability of movement through that class. All values are on a logit scale. Resistance was calculated as the ratio of the slope in road and forest to the slope in open, for each year.

	coefficients				**Standard errors (SE)**				**Resistance**	
Year	**Intercept**	**Open**	**Road**	**Forest**	**Intercept**	**Open**	**Road**	**Forest**	**Road**	**Forest**
2007	-0.0580	-0.0194	-0.2348	-0.0081	0.3259	0.0030	15.3921	0.0014	12.1	0.4
2008	1.3709	-0.0208	-0.1140	-0.0144	0.3635	0.0020	6.3701	0.0018	5.5	0.7
2009	-3.9452	-0.0001	-0.0022	-0.0019	0.1737	0.0004	0.0011	-0.0005	22.0	19.0
2010	-0.8824	-0.0014	-0.0039	-0.0023	0.2896	0.0006	0.0018	0.0006	2.8	1.6
2011	-2.6795	-0.0023	-0.0058	-0.0048	0.7060	0.0019	0.0083	0.0023	2.5	2.1
2012	-6.5876	0.0013	-0.0094	-0.0047	0.7600	0.0016	0.0070	0.0023	*	*
2013	-1.7462	-0.0054	-0.0056	-0.0061	0.3187	0.0011	0.0040	0.0011	1.0	1.1
2014	-0.5137	-0.0036	-0.0183	-0.0080	0.2991	0.0009	0.0057	0.0008	5.1	2.2
2015	-2.2744	-0.0049	-0.0012	-0.0038	0.2643	-0.0007	0.0020	0.0007	0.2	0.8

* Resistance estimates only make sense for years when the sign of the distance-dispersal relationship is negative for all three categories

4.4.4 End User Work Shop

The workshop was attended by DoD Natural Resource specialists and agency biologists working with focal species (Table 4.4.4-1). The workshop included a morning of presentations followed by an afternoon of hands-on demonstrations to provide familiarity with the project approach, and concluded with a Round Table discussion. The morning presentations focused on data needs to parameterize SEIBMs – demographic response of at-risk species across time and space to restoration-based disturbance which influences source/sink status of the habitat and movement of focal species across landscapes in response to these habitat and disturbance states.

The afternoon demonstrations included an introduction to SEIMBs, focal efforts with Fender's blue and Taylor's checkerspot, and a hands-one session with the St. Francis Satyr model. The afternoon concluded with a round table discussion including the following questions and discussions:

- Are the predictions of SEIBMs reliable?
- What are examples of models being used by managers that are acceptable to USFWS ?
- If you are still hesitant about these models, what can we address?
- How would they like to use models such as these SEIBMs?
- What would they like to know *about* the models?
- What would they like to know from these models/from our output? (We are NOT expecting at the end of the day- that attendees be able to make one of these models from scratch; rather to have a broad familiarity to think about when such an approach may be valuable
- What data collection methods are feasible for at-risk species that each works with? What are the alternatives?
- What is the value/use of SEIBMs vs either spatial models with less biology or stylized models without the maps
- How else might SEIBMs be used? That is, under what other restoration or management situations might SEIBMs be valuable?
- What is about this approach is surprising and/or counter-intuitive responses?

Finally, because the timing of the workshop co-occurred with the flight season of Fender's blue in Oregon and Taylor's checkerspot in Washington. The workshop included site visits to Washington sites that are part of JBLM's ACUB program (Army Compatible Buffer

Use program - Scatter Creek Wildlife Area and Glacial Heritage preserve) and to DoD sites in Oregon – US Army Corps of Engineers Fern Ridge Reservoir. Workshop participants left with a broad knowledge of a novel approach to managing habitat to endangered species as well as benefiting from the collaborative process of a small workshop designed to educate project participants and to learn from their experiences about how to develop tools to enhance the efficiency and effectiveness of managing DoD land for Threatened, Endangered and At-risk species.

Table 4.4.4-1 Attendees at End-user workshop

First	**Last**	**organization**	
Elizabeth	Crone	Tufts University	Research Team
Rebecca	Fuda	Tufts University	Research Team
Norah	Warchola	Tufts University	Research Team
Leone	Brown	Tufts University/University	Research Team
Joey	Smokey	Washington State Universit	Research Team
Cheryl	Schultz	Washington State Universit	Research Team
Bill	Morris	Duke University	Research Team
Nick	Haddad	North Carolina State Unive	Research Team
Gina	Himes Boor	Duke University/Montana	Research Team
Erica	Henry	North Carolina State Unive	Research Team
Brian	Hudgens	Institute for Wildlife Studie	Research Team
Chris	Damiani	Institute for Wildlife Studie	Research Team
Brian	Ball	Fort Bragg	SFS Biologist/Manager
Peter	Dunwiddie	Center for Natural Lands Management (CNLM)	TCB Biologist/Manager
Sarah	Hanman	Center for Natural Lands Management (CNLM)	TCB Biologist/Manager
Susan	Waters	Center for Natural Lands Management (CNLM)	TCB Biologist/Manager
Ted	Thomas	USFWS	TCB/USFWS
Rich	Szlemp	USFWS	TCB/USFWS
Mary	Linders	WDFW	TCB Biologist/Manager
Dan	Grosboll	Joint Base Lewis-McChord (	TCB Biologist/Manager
Jeff	Foster	Joint Base Lewis-McChord (	TCB Biologist/Manager
Ann	Potter	WDFW	TCB Biologist/Manager
Wes	Messinger	US Army Corps of Engineer	FBB Biologist/Manager
Mikki	Collins	USFWS	FBB/USFWS
Kevin	O'Hara	USFWS	FBB/USFWS
Jaret	Daniels	McGuire Center for Lepidoptera and Biodiversity	Butterfly conservation and captive rearing expert

5. General lessons and tools:

5.1 Modeling approaches & statistical tools:

Our set of case studies led to innovations in three categories of statistical and modeling tools:

5.1.1 *GLMMs and parameter estimation*: We adapted generalized linear mixed models (GLMMs) for use in estimating demographic and movement parameters for all our case studies. The general technique (GLMMs) is not new to our work; however, until now, ecologists and statisticians have tended to perceive GLMMs simply as a way to account properly for structured data and obtain correct p-values. The innovation of our work is interpretation of the variance terms as ecologically-important variation among individual animals, among species, among sites and/or among years.

5.1.2. *Analytically tractable source-sink models*: One key aim of our project was to evaluate the level of information needed to understand and predict source-sink status of habitat patches. In the process of evaluating spatially explicit models (section 5.1.3, below), we also developed two simpler methods of modeling spatial population dynamics. These are especially useful in providing rules of thumb for management, in cases where the exact landscape context is unknown, or may change through time.

5.1.2.1. Spatial matrix population models for source-sink environments: We adapted the technique of spatial mega-matrix population models to describe source-sink dynamics in spatially heterogeneous environments. These models provide a general first step to understanding source-sink dynamics when exact landscape configurations are unknown. They also allow users to evaluate spatial heterogeneity using familiar tools from nonspatial population ecology.

5.1.2.2. Integrodifference equations for isolated patches and heterogeneous landscapes: Source sink status of a habitat patch depends both on its size and on its quality. We developed a general framework for estimating the critical minimum size at which a patch switches from source to sink based on the balance between emigration and local reproduction. This simple model is an example of an integrodifference equation, in that the continuous-time processes associated with the mobile phase of the adult butterfly life cycle – movement, adult survival, and oviposition – are separated from larval growth and hibernation, which are approximately spatially fixed and occur over several months. We are continuing to develop this approach for application to additional ecological situations.

5.1.3. Spatially explicit individual-based models (SEIBMS): We developed spatially explicit-individual based models as tools to guide each management scenario. The basis of these models is movement described by a correlated random walk with preference at patch boundaries, combined with habitat-specific demographic parameters (stage-specific survival and fecundity). These approaches differ from many existing frameworks (e.g., the HexSim platform) in that they are more naturally related to the way in which movement is incorporated into analyticial reaction-diffusion and integrodifference models, so the assumptions and outputs are more similar. They are also more naturally suited to some species, including the insect taxa we have studied here.

5.2 Cross-species patterns

At the most fundamental level, the general lesson that managers took from our work was the importance of knowing vital rates – including movement – throughout species' life cycles, in order to assess the impacts of management. Though this may seem obvious in hindsight, there were situations for each species in which different vital rates showed qualitatively different responses to management (i.e., one vital rate would increase while the other decreased) emphasizing the importance of measuring vital rates throughout the life cycle, in order to determine the net effects of management actions.

In addition, our cross-species analyses confirmed assumptions of our underlying model. Specifically, for animal species like butterflies, movement can be modeled as a correlated random walk within habitat patches, with preference at patch boundaries. "Like butterflies" refers specifically to not having a central foraging place or den, and not during strongly directed migration. Furthermore, for animals in general, movement is faster in lower-quality habitat. This latter result sets up an interesting tradeoff for landscape planners who want to promote connectivity. Higher quality habitat (by definition) leads to higher population growth rates, but lower quality habitat increases permeability, if animals need to track moving habitat windows. The costs and benefits of including sink habitat in landscapes will depend on their effects on movement speed, as well as vital rates and habitat selection. We plan to continue to explore this result in the future.

Finally, all of our conclusions about the effects of habitat restoration were modified in one way or another by biotic interactions at higher trophic levels. Restoration ecologists typically adopt a bottom-up approach, and assume that, if suitable habitat for animals is created, they will be able to persist there. Our three case studies included one in which the effects of restoration depended on a mutualist-consumer, one in which the effects were moderated by the increase in habitat quality for generalist predators, and one in which population dynamics appear to be driven strongly by intra-specific competition and population cycles (boom-bust dynamics even in optimal environments). These effects are implicitly included in field-measured vital rates, but the mechanisms help us evaluate the consequences of specific restoration practices, and how they may play out in novel circumstances.

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