

Evaluating functional connectivity with matrix behavior uncertainty for an endangered butterfly

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Abstract Understanding animal responses to landscape elements helps forecast population reactions to changing landscape conditions. The challenge is that some behaviors are poorly known and difficult to estimate. We assessed how uncertainty in behavioral responses to dense woods, an avoided landscape structure, impacts functional connectivity among reproductive habitat patches for Fender’s blue butterfly, an endangered prairie species of western Oregon, USA. We designed a factorial simulation experiment using a spatially explicit individual-based model to project functional connectivity for female butterflies across current and alternative landscapes. We varied the probability of dense woods entry and turning angle standard deviation for movements within the dense woods over a range of biologically reasonable and

observed values. Butterflies in the current landscape (46 % dense woods) and one with prairie encroached by forest (60 % dense woods) showed reductions in functional connectivity estimates consistent with the expectations of habitat fragmentation. Although dense woods entrance uncertainty impacted functional connectivity projections, uncertainty in the dense woods turning angle standard deviation had comparatively little impact on connectivity estimates. Reduction and reconfiguration of the current dense woods to 27 % cover (restored landscape) appeared to facilitate a corridor behavior in dispersing individuals, likely providing a functional connectivity estimate comparable to the historic landscape (<5 % dense woods). Our simulations suggest that additional study of butterfly movement within the dense woods is unnecessary and that a partial reduction in dense woods would be sufficient to achieve historic levels of functional connectivity for Fender’s blue across the study landscape.

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Introduction

A major challenge for conservation biologists is predicting how animals will persist within dynamic and anthropogenically impacted landscapes (Nathan

et al. 2008; Vos et al. 2008; Knowlton and Graham 2010). As an animal travels through a landscape, it responds to elements as they are perceived or encountered. Adopting a behavioral perspective enables a mechanistic-based understanding of how animals move through and settle across the landscape (Goodwin and Fahrig 2002; Revilla et al. 2004; Bélisle 2005; Baguette and Van Dyck 2007; Fahrig 2007; Hawkes 2009). For species occupying fragmented habitats, understanding the behavioral mechanisms that lead to successful between habitat patch movements enhances the efficacy of conservation planning for current and prospective landscapes (Fahrig 2007; McIntire et al. 2007; Vos et al. 2008; Knowlton and Graham 2010). Unfortunately, comparisons between different landscape studies are limited to coarse generalizations (Prevedello and Vieira 2010) due in part to inconsistencies in habitat and non-habitat/matrix definitions (Dennis et al. 2006; Andersson and Bodin 2009; Dover and Settele 2009), inaccurate assignment of landscape elements to study organism responses (Dennis et al. 2006; Andersson and Bodin 2009; Dover and Settele 2009; Eigenbrod et al. 2011) and landscape element response differences among similar species and between conspecific sexes (Uezu et al. 2005; Ovaskainen et al. 2008; Turlure et al. 2011; Schultz et al. 2012). For species that lack appropriate study, landscape level conservation is often challenging and limited to broad landscape prescriptions that are assumed to be pertinent to the focal species but may not necessarily be effective (Knowlton and Graham 2010).

If habitat is defined as the suite of conditions and species assemblages associated with reproduction and all other biotopes are considered to be variable matrix elements, then functional connectivity, the probability that an individual will move between different habitat patches (Vos et al. 2008), directly indexes immigration and indirectly colonization (Hanski 1998; Moilanen and Hanski 2001; Goodwin and Fahrig 2002; Baguette and Van Dyck 2007; Vos et al. 2008). However, it can be challenging to construct biologically meaningful individual-based landscape projections because behavioral responses within landscape elements and at element edges can vary in ways that are not fully understood (Lima and Zollner 1996; Mooij and DeAngelis 2003; Schooley and Wiens 2003; Ries et al. 2004; Bélisle 2005; Fahrig 2007; Kindlmann and Burel 2008; Nathan et al. 2008; Revilla and Wiegand

2008; Hawkes 2009; Prevedello et al. 2010). Some behavioral response parameters can be refined with direct experiments (e.g. Schultz 1998; Schultz and Crone 2001; Schultz et al. 2012) but others may be difficult or impractical to measure. For example, behavior while crossing and moving through the matrix is not well-characterized for most species (Ricketts 2001; Van Dyck and Baguette 2005; Ovaskainen et al. 2008) but understanding how species respond to key matrix elements is essential for developing a behaviorally mechanistic model of functional connectivity (McIntire et al. 2007; Ovaskainen et al. 2008; Hawkes 2009).

Methods to gather matrix related movements on larger animals, such as the use of transmitters (Douglas-Hamilton et al. 2005; Wikelski et al. 2006; Breed et al. 2009; Schofield et al. 2010; Fudickar et al. 2011; Hagan et al. 2011; Valentine-Darby et al. 2011) and harmonic radar for smaller flying animals (Cant et al. 2005), have provided information rich matrix movement data that are otherwise difficult to obtain. For some species, that either can not be fitted with transmitters or the financial cost of transmitter development is prohibitive (Wikelski et al. 2007), matrix movement information is often elusive and limited. Furthermore, the sub-meter accuracy and transmitter size required to track the movements of smaller organisms at the appropriate spatial scale is beyond what the current transmitting technology can reasonably provide (Wikelski et al. 2007; Bridge et al. 2011). In spite of recent technological tracking advances, there is a need to develop general analytic approaches that can account for poorly known and uncertain matrix behaviors in systems where transmitting technologies are not feasible.

Fender's blue butterfly, *Plebejus icarioides fenderi*, is considered a prairie-restricted species, but females occasionally enter and traverse the dense woods matrix (Schultz et al. 2012, Hicks, unpublished data). Butterfly behavior in prairies is well-described (Schultz and Crone 2001) but there is uncertainty at both the dense woods-prairie boundary and movement behavior within the dense woods, in large part because Fender's blues are infrequently observed to enter the dense woods and when they do they can not be followed (Schultz et al. 2012). We designed a factorial experiment using a spatially explicit individual-based simulation model (SEIBM) to investigate the influence of uncertainty in dense woods matrix-related behaviors on functional connectivity in

the current and three alternative landscapes (historic, encroached dense woods, and a restored landscape where dense woods are reduced and replaced by prairie matrix—grasslands without lupine host plants). We directly address uncertainty by identifying a minimal set of dense wood associated behaviors that are unknown and we vary these parameters over a range of biologically reasonable values. Combining the range of uncertain dense woods behaviors with the well-characterized prairie behaviors, we evaluate the impact of uncertainty in matrix associated behaviors on functional connectivity and simultaneously provide estimates of important butterfly responses to alternative landscapes. This provides an intuitively simple approach that evaluates the sensitivity of functional connectivity to behavioral uncertainties, enabling the assessment of habitat restoration on Fender’s blue butterfly prior to landscape modification.

Methods

Study species

Female Fender’s blues produce up to a few hundred eggs over their lifetime and oviposit one to several eggs on the underside of Kincaid’s lupine (*Lupinus oreganus*) leaflets over their 7–10 day average life span (Schultz et al. 2003). Fender’s blue egg laying movements are comparable to other lycaenid butterflies (Arnold 1983). They begin by laying one to several eggs on a host plant, then fly from ≈ 1 to many meters away (often bypassing lupines), where they select another plant for oviposition, and repeat the process until they are no longer motivated to lay eggs. With this behavior a butterfly broadly distributes eggs across natal and newly encountered lupine patches, although some localized egg concentration can occur if there are differences in host plant apparency (Severns 2008a). Male Fender’s blue behave differently than females, ranging more broadly across the landscape and often spend more time in prairie matrix (grassland without lupine host plants, Schultz et al. 2012), likely searching for females, nectar resources and new resource patches. Our simulations focus on females because they are required for colonization.

Study area

One of the largest of the 15 remaining Fender’s blue populations, Cardwell Hills (≈ 7 km west of

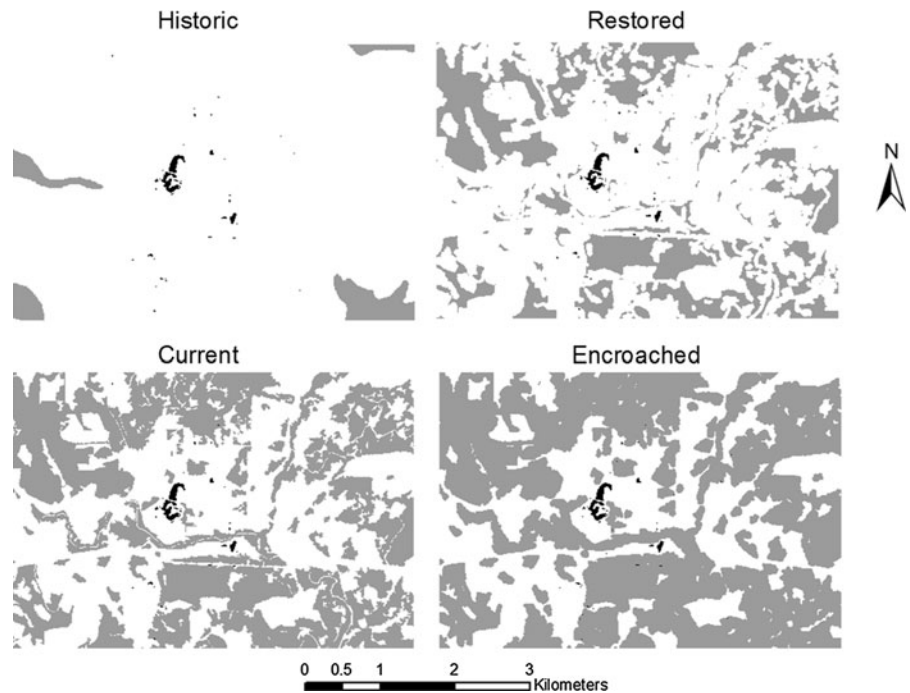
Corvallis, Oregon), is a group of privately owned properties with the potential to support a viable metapopulation required by the species’ recovery plan (U.S. Fish and Wildlife Service 2010). The area appears to support between 500 and 2000 butterflies annually (with potentially many more in a good butterfly year; Schultz pers. obs.), constituting 10–20 % of the range-wide annual adult Fender’s blue population size (U.S. Fish and Wildlife Service 2010). Cardwell Hills is a mosaic of remnant and degraded prairies, century old pasturelands, sparse deciduous and conifer trees, and stands of dense 20–50 year old *Pseudotsuga menziesii* (Douglas fir) trees (Fig. 1). Several large lupine patches, numerous smaller patches (3–20 m in radius) and non-reproductive prairie matrix are surrounded by a mixture of open and dense woods, riparian corridors and shrublands. In particular, the dense woods matrix obstructs the line-of-sight between lupine patches (habitat) and the non-reproductive prairie matrix.

Current and alternative landscapes

Functional connectivity projections were made for historic, current, dense woods encroached and restored landscape scenarios. We simplified the landscape to three elements; (1) reproductive habitat (hereafter habitat) contained prairie flora with lupine host plants and scattered trees with non-overlapping tree crowns, (2) the prairie matrix had sparsely distributed trees with non-overlapping crowns, lacked lupine host plants, and included pastures, shrublands and any other relatively open landscape element, and (3) the dense woods matrix had a closed tree canopy (>90 % canopy cover), a shade-dominated understory lacking grassland flora and no lupine host plants. Maps of forest cover were created with aerial photographs (3Di West Inc, Eugene, OR, July 2005) over which polygons of dense woods and prairie matrix were drawn to ≈ 5 m accuracy. The distribution of Kincaid’s lupine throughout Cardwell Hills was mapped to ≈ 2 m accuracy (provided courtesy of the Institute for Applied Ecology, Corvallis, OR, July 2007).

An all prairie landscape, composed of habitat and prairie matrix, served as a “null landscape” to which butterfly simulations in alternative landscapes were compared. The historic prairie (<5 % dense woods cover) was constructed from the interpretation of landscape survey data collected in the early 1850s

Fig. 1 Four landscapes of the Cardwell Hills study area (the all prairie landscape is not shown). *Black areas* represent habitat (prairie with lupine host plant), white areas are prairie matrix, and *gray areas* indicate the landscape distribution of dense woods matrix



from the Cardwell Hills area (Johannessen et al. 1970; Christy and Alverson 2011). In the current landscape, dense woods covered $\approx 46\%$ of the Cardwell Hills study area. To produce either the encroached dense woods (60% dense woods cover) or restored landscapes (27% dense woods cover), we added or subtracted 20 m from the edge of the current dense woods matrix (Fig. 1). We converted the former dense woods matrix to prairie in the restored landscape, keeping the habitat (0.38% cover) constant for all landscapes. It is highly likely that the historic and future distribution of lupine differs from the current landscape, but our focus was to investigate the impacts of changing dense forest cover on functional connectivity not permutations of habitat and matrix elements.

Spatially explicit individual-based simulations

Since we do not have long-term data on population dynamics, mark recapture and within dense woods movement data for Cardwell Hills, we cannot derive quantitative parameter estimates or project the effects of connectivity on metapopulation dynamics. Rather, our goal was to evaluate habitat connectivity given the behavioral uncertainty associated with dense woods. To do this, we used female only, spatially explicit individual-based landscape event simulations (Fall

and Fall 2001; Reuter et al. 2011) to examine functional connectivity responses to variation in dense woods matrix configurations with the program FendNet (McIntire et al. 2007). FendNet simulates butterfly movement through different virtual landscapes (GIS created landscape maps) from empirically derived per step estimates of within-habitat turning angle standard deviations, step lengths (the distance in meters between moves) and habitat edge responses from Fender's blue behavioral experiments (McIntire et al. 2007, 2013). Female movement was modeled as a biased correlated random walk (Turchin 1998, see McIntire et al. 2013 for specific details) when butterflies occurred within 10–22 m of lupine patch boundaries (the perceptual range for this species is variable, see Schultz and Crone 2001), reflecting the bias for female Fender's blue towards grasslands containing detectable host plants (Schultz 1998; Schultz and Crone 2001).

We assessed dense woods matrix and dense woods edge behavior uncertainty by constructing a factorial simulation experiment (96×4 landscapes plus 1 simulation with no dense woods behavior) that spanned a range of reasonable parameter values for the per-step probability of entering the dense woods and flight behavior (turning angle standard deviation and step lengths) while in the forest. Given the response of 22 females released on the dense woods/prairie matrix

edge (Schultz et al. 2012) the per-step probability of a female blue entering the dense woods if within 10 m of the woods boundary was 0.039 (0.014–0.106, upper and lower 90 % CI). Dense woods entrance probability is more uncertain than the boundary responses between prairie matrix and habitat (Schultz and Crone 2001; Schultz et al. 2012). Entering the dense woods is also likely to be conditional on the configuration of dense woods in the area immediately adjacent to the prairie (i.e. entrance probability increases with more surrounding forest). To address uncertain behavior at the dense woods edge we ran 12 simulations where the per-step dense woods entrance probability ranged from 0 to 0.10 (in increments of 0.009). We have no data for Fender's blue movement behavior within the dense woods but at least one marked female moved through dense woods to a new lupine patch (T. Hicks unpublished data) and observations of several females entering the dense woods suggests that they enter between 5 and 10 m above the ground and head relatively straight towards the canopy at $\sim 15^{\circ}$ – 30° angle (D. Roberts, A. Franco and C. Schultz, pers. obs).

We assessed the dense wood matrix turning angle standard deviation uncertainty over a range of known values, from 6° to 48° in 6° increments (6° is a relatively straight flight while 48° is more sinuous). These values encompass the turning angle standard deviations when butterflies are within lupine patches, outside lupine but within prairie, as well as nearly straight (6°) to account for potentially straight movement through a completely inhospitable habitat. The turning angle standard deviation in the prairie matrix was 23° (18° – 31° , upper and lower 90 % CI) and step length (the distance in meters between moves) was 8.8 m (6.5–8.8 m, upper and lower 90 % CI; Schultz and Crone 2001). We used the step lengths from the prairie matrix for the simulated dense woods movements. Turning angle standard deviation in habitat was 49° (46° – 52° , upper and lower 90 % CI) and step lengths were 2.1 m (1.9–2.4 m, upper and lower 90 % CI; Schultz and Crone 2001). Although we perform the whole factorial experiment, from a combination of observations and Fender's blue experience we considered 12° to be the most likely estimate of turning angle standard deviation within the dense woods.

We initiated 20,000 butterflies that were proportionately assigned to the area (m^2) of three large natal lupine patches that are likely to be the most persistent source patches due to host plant abundance. Since

each simulated butterfly acts independently, the butterfly is the unit of replication. Because we lack sufficient data to reasonably project population dynamics, we chose a large enough sample size to obtain precise estimates for output metrics. Thus, confidence intervals on means, which are sample size dependent, were essentially zero and are not presented. Individual butterfly longevity was drawn from a negative exponential distribution with mean of 2100 moves and an upper limit of 5880 moves.

Butterfly response projections to the current and alternative landscapes

We use three metrics to compare simulations between the historic, current, dense woods encroached and restored landscapes. First, functional connectivity was estimated as the number of simulated butterflies arriving at new habitat patches divided by the total number of butterflies in the simulation. For our purposes, a “new” habitat patch could not be the natal patch (in case butterflies ventured into the matrix and returned) and had to be separated by either dense woods or >30 m of prairie matrix. In our simulations individuals were free to explore the landscape under the biased correlated random walk conditions, regardless of whether they encountered a new habitat patch. Because we were interested in how the dense woods distribution could impact habitat connectivity, we calculated the relative functional connectivity as the ratio of functional connectivity with dense forest in the landscape to functional connectivity (absolute connectivity) in a landscape without dense woods (null landscape). A relative connectivity value >1 suggests that dense woods increases connectivity and a value <1 suggests that the dense woods reduce connectivity. Second, we calculated the percentage of time spent in habitat relative to the total life span of each simulated butterfly. Habitat residence time is a measurement reflecting reproductive effort because the time spent within lupine patches is proportional to the observed oviposition rate (Schultz and Crone 2005). Third, we calculated the 80th percentile of the straight-line travel distance from the natal lupine patch as dispersal distance. This number is less sensitive to stochasticity than the “furthest distance”, an extreme value of a distribution which can vary enormously.

For all landscape scenarios the “off-map” areas were converted to 100 % dense woods. When simulated

butterflies traveled to the map edge, they responded to and moved through the off-map areas as they would through dense woods.

Results

Absolute connectivity in the all prairie (null landscape) was estimated at 0.389; i.e., 38.9 % of simulated individuals arrived successfully at a new patch. Historic prairie had high relative connectivity, 0.95–1.08 regardless of dense woods boundary behavior or dense woods turning angle standard deviation (Fig. 2). In spite of a broad range of uncertain dense woods behavioral parameters, relative connectivity values in the restored landscape were similar to the historic landscape, ranging between 0.91 and 1.04 (Fig. 2). However in both the current and encroached landscapes, uncertain dense woods behaviors and the dense woods interacted to generate a broader range of connectivity responses that were <0.93 (Fig. 2). Relative connectivity contours were similar between the current and encroached landscapes but connectivity estimates were lower in the encroached landscape (<0.82 ; Fig. 2). Thus, the impact of dense woods behavior uncertainty on functional connectivity variation increases as the landscape cover of dense woods increases. In both the current and encroached landscapes, relative connectivity was more sensitive to the uncertainty of entering the dense woods than the turning angle standard deviation uncertainty (Fig. 2), suggesting a strong isolating property of the dense woods matrix.

The 80th percentile of the simulated butterfly population travelled 1.03 km from their natal patch in the all prairie landscape. In general, dispersal distance decreased as the dense woods increased and distances were most impacted by movement uncertainty (more contours) in the encroached and current landscapes (Fig. 3). Among the encroached, current and restored landscapes, only butterflies that entered the dense woods frequently and flew with a relatively straight trajectory dispersed >1.0 km, and these long flights occurred exclusively in the encroached landscape (Fig. 3). Dispersal distance in the historic prairie varied between 0.8 and 1.2 km with the greater distances occurring when the turning angles were relatively straight and the probability of entering the dense woods was either low or high (Fig. 3). Simulated butterflies in the current landscape traveled, from

0.8 to 1.0 km, when individuals frequently entered the dense woods and flew relatively straight (Fig. 3). Dispersal distances in the restored landscape ranged from 0.6 to 1.0 km, which were slightly higher than the current and encroached landscapes over most parameter space (Fig. 3).

Simulated female butterflies spent 69.3 % of their total life in reproductive habitat when the landscape contained only habitat and prairie matrix. Habitat residence times in the historic and restored landscapes were similar to that of the all-prairie landscape, ranging from 67 to 71 % (Fig. 4). As the amount of dense woods in the landscape increased, habitat residence times also tended to increase regardless of the combinations in uncertain behavior parameters (Fig. 4), suggesting that individuals spent more time in their natal habitat patches. Similar to connectivity and dispersal distance estimates, the encroached landscape had the greatest variation in the percentage of time spent in reproductive habitat (69–81 %) and responses varied more with the uncertainty of the probability of entering the dense woods than the uncertainty in the dense woods turning angle standard deviation (Fig. 4).

At the most likely parameter values (intersections of crosshairs on Figs. 2, 3, 4) an increase in the cover of dense woods corresponded broadly with a reduction in relative connectivity, a decrease in dispersal distance and an increase in the proportion of life spent in reproductive habitat (Fig. 5), suggesting that as dense woods cover increases habitat isolation also tends to increase.

Discussion

In our simulations, functional connectivity was more sensitive to variation in landscape configuration, in both the current and encroached landscapes, than to variation in uncertain dense woods behaviors provided that butterflies entered the dense woods frequently (the right halves of the Fig. 2 panels). When butterflies did not enter dense woods frequently, the uncertainty in the dense woods entrance probability generated a wider range of functional connectivity projections (the left halves of the Fig. 2 panels). Once butterflies were in the dense woods, turning angle standard deviation uncertainty had only a minimal impact on functional connectivity projections in any of the simulated

Fig. 2 Relative connectivity estimates for four different landscape scenarios. The *dotted line* on the *x*-axis indicates empirically derived maximum likelihood estimate for the per move probability of entering the dense woods (0.039) and the *dotted line* on the *y*-axis represents the likely within dense woods turning angle standard deviation (12°)

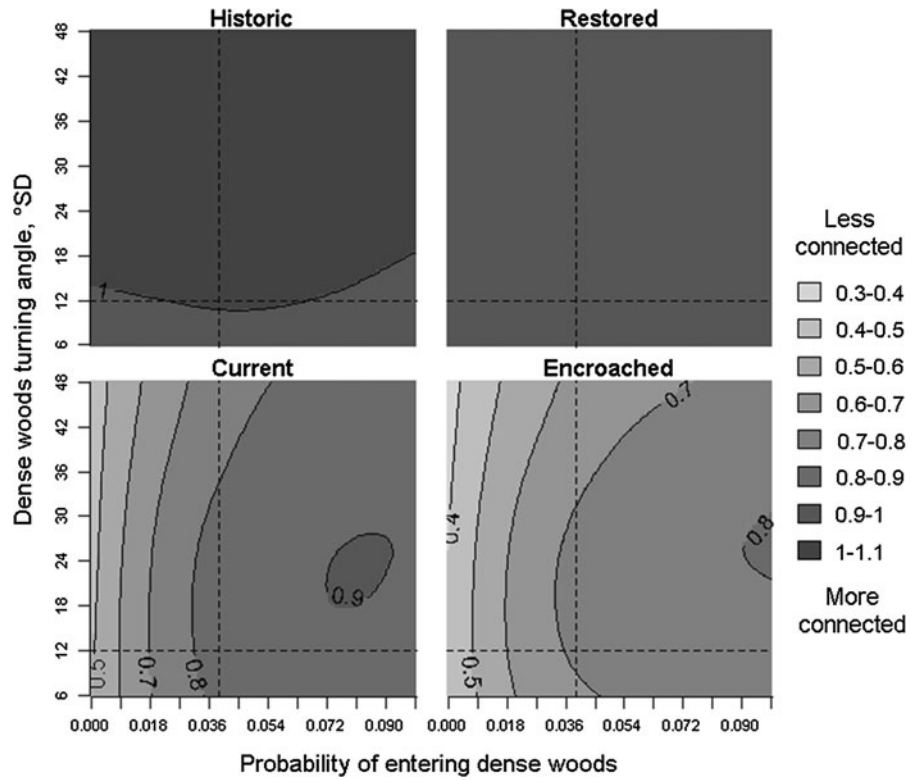


Fig. 3 The distance traveled in kilometers by the 80th percentile of 20,000 individuals. The *dotted line* on the *x*-axis indicates empirically derived maximum likelihood estimate for the per move probability of entering the dense woods (0.039) and the *dotted line* on the *y*-axis represents the likely within dense woods turning angle standard deviation (12°)

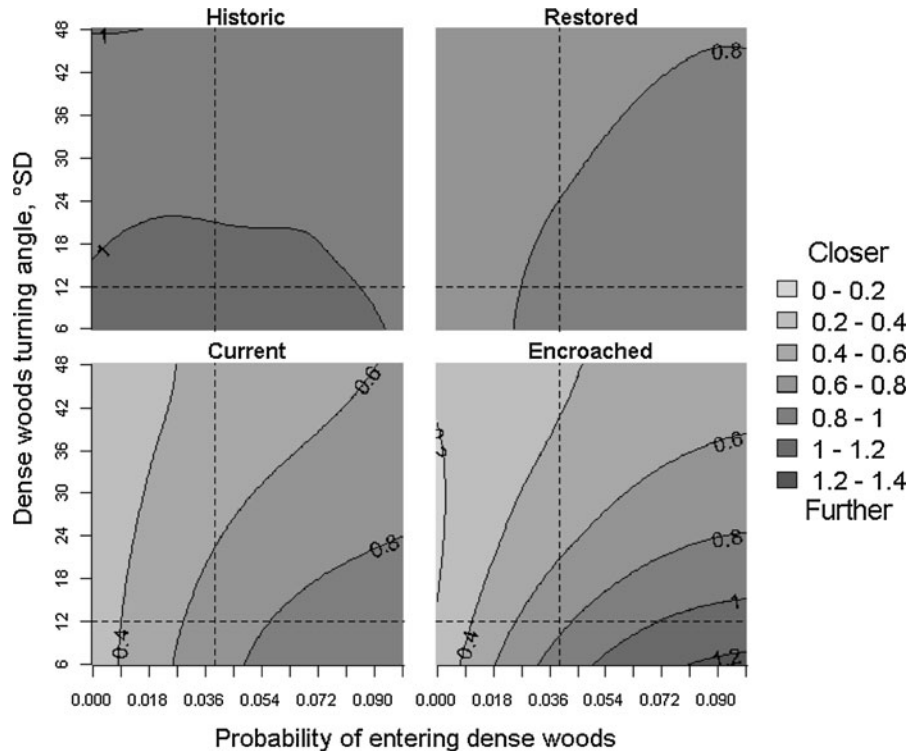
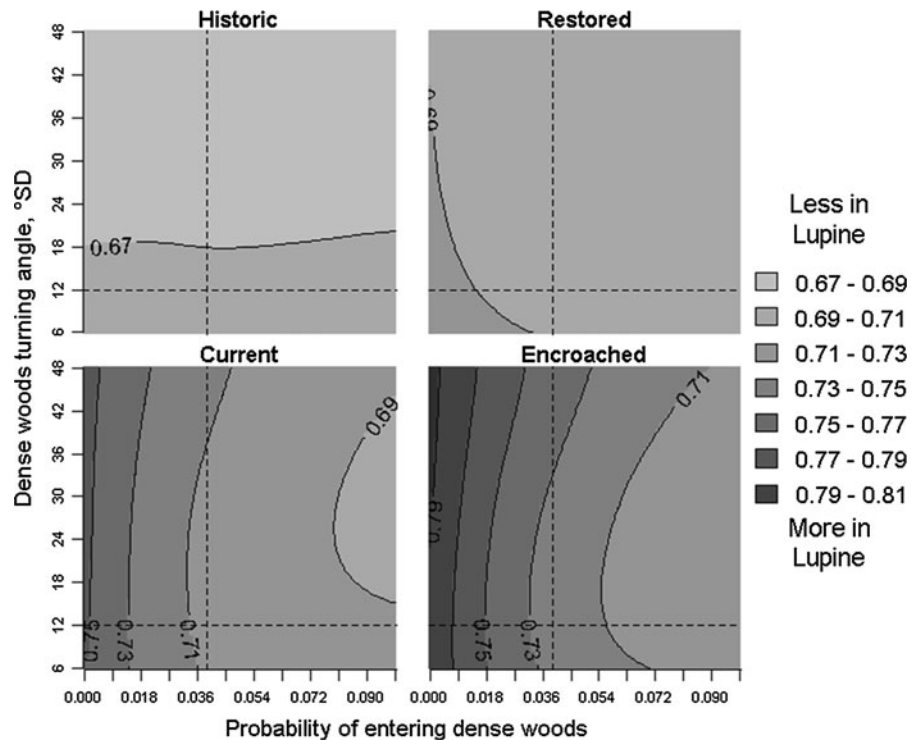


Fig. 4 The proportion of lifetime spent in habitat (lupine patches). The *dotted line* on the *x*-axis indicates the empirically derived maximum likelihood estimate for the per move probability of entering the dense woods (0.039) and the *dotted line* on the *y*-axis represents the likely dense woods turning angle standard deviation (12°)



landscapes (Fig. 2). Although we are unaware of any other studies that directly assess the impact of matrix edge response and matrix movement uncertainty on functional connectivity, there are several studies that estimate the influence of perceptual range uncertainty on functional connectivity. In comparison to our study with Fender's blue, Graf et al. (2007) and Pe'er and Kramer-Schadt (2008) suggest that individual-based models may be more sensitive to variation in uncertain behavioral parameters than landscape configuration. Graf et al. (2007) observed that responses to the same landscape elements with unknown perceptual range parameter values yielded highly variable functional connectivity estimates for the capercaillie grouse, *Tetrao urogallus*. Pe'er and Kramer-Schadt (2008), for Eurasian lynx (*Lynx lynx*), demonstrate that connectivity is heavily influenced by variation in unknown perceptual range distances. The impact of perceptual range uncertainty on functional connectivity was proportionally greater than the loss of estimate precision due to a 4-fold decrease in landscape element map resolution. For Fender's blue, the well-described prairie behavior responses facilitated the evaluation of functional connectivity for butterflies over a range of uncertain dense woods behaviors in the

historic, current and alternative future landscapes. Because butterflies responded with more variation to uncertainty in entering the dense woods than uncertainty in the turning angle standard deviation (Fig. 2) supplementary study of behavior inside the dense woods is unlikely to improve functional connectivity projections. Likewise, if restoration work proceeds, additional study of dense woods entrance probability is unnecessary as its influence disappears with the reduction in dense woods (Fig. 2). Fortunately, Fender's blue dense woods edge behavior can be experimentally studied (e.g. Schultz et al. 2012) so it is possible to obtain more refined connectivity estimates with additional field studies if it is necessary to project to landscape alternatives outside of those considered in this study.

Mechanistic models of animal movement should provide sound estimates of functional connectivity when landscapes and behaviors are well-characterized (Tischendorf and Fahrig 2000; Revilla et al. 2004; Bélisle 2005; Fahrig 2007; Nathan et al. 2008; Hawkes 2009; Marucco and McIntire 2010). Our simulations suggest, like other studies (Ricketts 2001; Baum et al. 2004; Revilla et al. 2004; Castellón and Sieving 2006), that matrix configuration influences landscape processes and that matrix arrangement can either enhance or

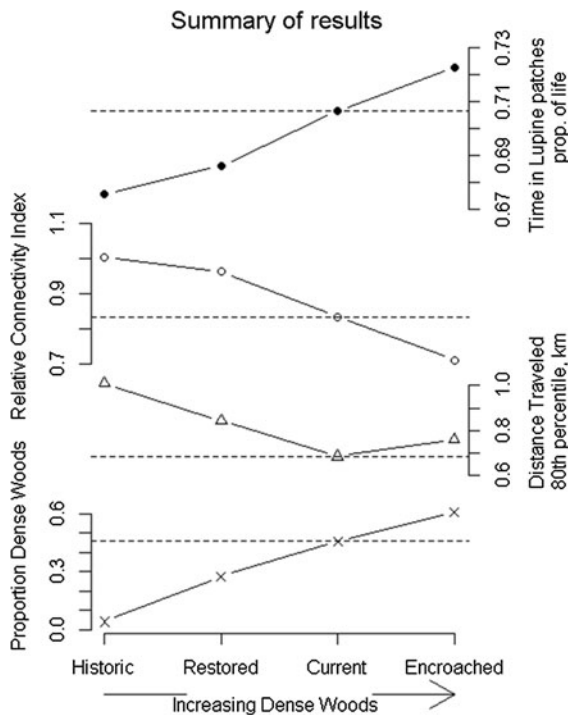


Fig. 5 A summary of butterfly response estimates at the most likely parameter values of the uncertain dense woods behaviors (intersection of *dashed lines* from Figs. 2, 3, 4) for each landscape in order of increasing dense woods cover. The *dotted horizontal line* indicates the response value for the current landscape

reduce functional connectivity. Fender's blue responded to the encroached landscape with reduced connectivity, the hallmark of habitat fragmentation (Tschamtko et al. 2002; Fischer and Lindenmayer 2007). However, functional connectivity for butterflies in the restored landscape was comparable to that of the historic landscape even though the restored landscape contained >5 times the cover of historic dense woods (Fig. 2). The behavior at the dense woods boundaries results in a large portion of the butterflies being reflected back towards prairie areas. When the dense woods cover is too extensive, this reduces connectivity and increases habitat fragmentation. With a decrease in the cover of dense woods, such as the restored landscape scenario, this dense woods reflecting behavior can create a corridor effect (*sensu* Haddad 1999; Pe'er et al. 2005) because fewer butterflies spend time exploring the low quality areas of the landscape. Consistent with these simulation observations, butterflies in nature often move along linear boundaries (reviewed by Dover and Settele 2009) such as forest edges (Haddad 1999), hedgerows

(Dover and Fry 2001; Severns 2008b), along the margins of grass sward that differ in height (Summerville et al. 2002; Severns 2008a) and even pieces of flagging (Dover and Fry 2001). The response of Fender's blue to changes in the dense forest matrix configuration was reasonable but somewhat unexpected given that dispersal corridors were not intentionally introduced into the restored landscape.

We gained insight into how Fender's blue might behaviorally respond to alternative future landscapes given uncertainty about dense woods matrix behavior through individual-based simulations. Although these types of projections are important for developing landscape conservation strategies (Knowlton and Graham 2010), the interpretation of simulation results should be carefully weighed against model assumptions. First, butterfly responses were relativized to a hypothetical all-prairie landscape for comparison. Second, we did not make projections concerning population persistence, colonization or extinction for the Cardwell Hills landscape. However, in selecting the historic level of functional connectivity as a conservation benchmark, we implicitly assumed that historic levels of functional connectivity were sufficient for metapopulation persistence (otherwise Fender's blue would not have survived centuries ago). Third, it is very likely that there were more lupine patches historically than there are today (Wilson et al. 2003). Therefore, estimates of functional connectivity, dispersal and habitat residence time only reflect the dense woods component of the historic landscape.

In ecosystems dominated by invasive species and intensive anthropogenic modifications, the efficacy and perceived necessity to restore ecosystems to historic conditions has been challenged as being unrealistic and biologically intractable for the persistence of both rare and common species (Shapiro 2002; Shochat et al. 2005; Severns and Warren 2008; Tepedino et al. 2008). Our simulations suggest that butterflies at Cardwell Hills would likely experience historic levels of functional connectivity if the dense woods were reduced rather than restored to the historic dense woods distribution. Given the challenges and unpredictability in restoring Fender's blue reproductive habitat (Schultz 2001; Severns 2003; Carleton and Schultz 2012), enhancement of connectivity through the reduction of dense woods offers an important and realistic alternative to recreation of the historic landscape.

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