ELSEVIER

Biological Conservation 98 (2001) 179–190

BIOLOGICAL
CONSERVATION

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Species diversity and the scale of the landscape mosaic: do scales of movement and patch size affect diversity?

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Received 15 April 2000; received in revised form 10 August 2000; accepted 18 August 2000

Abstract

We use a combination of a model and empirical data to examine the relationship between the scale of the landscape mosaic and individual movement patterns on the measurement of local butterfly species diversity. In landscapes where patch sizes are smaller, the type of patch adjacent to the patch surveyed can influence both local species richness and incidence. In landscapes composed of larger patches, adjacency has no effect on species richness or incidence. We hypothesize that the mechanism for species enrichment is the potential for movement of individuals between habitats, resulting in either (a) spillover of species from the higher-diversity patches into other habitats, or (b) habitat sampling by species that benefit from the resources in adjacent patches. In order to determine whether landscape configuration alone can account for the observed patterns of diversity, we employ a simulation model. Simulation results suggest that both specialist and generalist butterflies can sample a much more diverse array of habitat types in a more fine-grained landscape. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Spillover; Edge effects; Biodiversity; Dispersal; Landscapes

1. Introduction

Species diversity at any one point in a landscape is determined by multiple factors acting at multiple scales (Turner and Gardner, 1991; Turner, 1989; Wiens, 1989). At the landscape scale, the frequency and spatial distribution of critical habitats and resources determines species distribution patterns (Swingland and Greenwood, 1983; Pearson, 1993), while historical accidents, community interactions, and spatio-temporal variability further limit the distribution that is realized at any given time. At finer scales, populations may be separated on patches of habitat within a landscape of less suitable habitat (e.g. Arnold and Weeldenburg, 1990; Merriam et al., 1991; Opdam, 1991). Species dispersal patterns may interact with patch size and patch context to determine species distributions within and among patches (van Dorp and Opdam, 1991).

'Patch context' describes the habitat directly adjacent to a patch, and also the larger neighborhood of nearby landscape elements (Forman, 1995). Patch context may be important to species that must access different resources at different stages of their life history. For example, most butterfly species require at least two distinct resources, a larval host plant and an adult nectary. A butterfly that lays its eggs in a sedge meadow may need to move into a drier meadow to nectar on forbs. Less mobile species may not be able to locate sufficient resources if the scale of the landscape mosaic does not facilitate habitat sampling.

Hypotheses concerning the effects of patch context on local species diversity have received little study (Palmer, 1992; Forman, 1995; but see Harrison, 1999). However, some guidance is available from other areas of investigation, including studies of metapopulation dynamics (Levins, 1970; Hanski and Gilpin, 1997; Holt, 1997), source-sink dynamics (Pulliam, 1988; Pulliam and Danielson, 1991), and mass effects (Shmida and Wilson, 1985; Auerbach and Schmida, 1987; Kunin, 1998). Shmida and Wilson (1985) define mass effects as "the flow of individuals from areas of high success (core areas) to unfavorable areas." Mass effects can dilute the species-habitat relationship by increasing the frequency of species outside of their core habitats (e.g. Shmida and

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PII: S0006-3207(00)00153-1

Whittaker, 1981). Cody (1993) notes that species in their core habitats are rarely the source of local species 'turnover' (species addition or loss). Instead, turnover generally involves rare species that invade from adjacent habitats. He calls this effect of patch context on local diversity a 'spillover effect'. Holt (1997) uses the term 'spillover' to describe how metapopulation dynamics (Gilpin and Hanski, 1991) can maintain a species' presence in unsuitable habitat patches. He notes that "species with high colonization or low extinction rates in their preferred habitat should exhibit a high occupancy in this habitat and can secondarily have a high incidence in habitats where they cannot persist." This mechanism is described at the population level in models of source-sink dynamics (Pulliam, 1988; Pulliam and Danielson, 1991), in which local populations are maintained in unproductive habitats through dispersal of individuals from productive habitats. At the community level, spillover can enrich diversity in species-poor habitats that are scattered among species-rich habitats (Holt, 1997).

Here, we consider the potential for fine-scaled patchiness in the landscape to enhance the spillover effect. Simulation studies by Palmer (1992) explore spillover in landscapes that differ in 'fractal dimension', a measure of patch scale. These studies predict that landscapes comprised of smaller patches exhibit higher average local diversity. We propose that the enrichment of local diversity in highly fractal landscapes may derive from scale effects alone, regardless of species population dynamics within distinct habitats. The spillover effect described above (Palmer, 1992; Cody, 1993; Holt, 1997) requires that species have some probability of surviving across generations within sub-optimal habitat. This requirement is not necessary for effects of landscape scale on local diversity. If the scale of patches or 'grain' of a landscape is fine relative to the movements of individuals, then individuals may cross patch boundaries within a single generation. Movement across patch boundaries allows 'habitat sampling', which may be an important feature of the population dynamics of many species. These within-generation movements or habitat sampling events may affect local diversity estimates.

As an empirical example, we assess the effects of patch scale and patch context on patterns of butterfly diversity (species richness and incidence). We then use field data to guide and parameterize a simulation model, to determine whether the movement of individuals within a season can interact with landscape structure to create the patterns of diversity that we observe. The empirical study focuses on montane meadow butterflies within the Greater Yellowstone Ecosystem. As one of the largest, relatively intact ecosystems in the United States, this site is particularly appropriate for the study of species-habitat relationships. The ecosystem hosts over 100 butterfly species and a variety of meadow habitat types. As a taxonomic group, butterflies display many levels of specialization and sensitivity to habitat characteristics (Pollard and Yates, 1993; Pullin, 1995). This variation facilitates an inclusive study of landscape effects on butterflies of varying habitat specificity.

There are two distinct landscapes within the study system. Both landscapes support similar meadow types and butterfly diversity, while differing in average patch size. Meadows in the northern landscape (the 'Gallatin' landscape) are smaller and lie in relatively narrow valleys between forested hillsides within the Gallatin mountain range. Meadows in the southern landscape (the 'Teton' landscape) are larger and lie in the broad Jackson Hole Valley, with fewer intervening ridges and forests. The meadow habitats fall into seven categories along a moisture gradient, from hydric (M1) to xeric (M7) (Fig. 1; Debinski et al., 1999). We observed that mesic (M3) meadows support a slightly higher butterfly species richness than meadows at the wetter and dryer extremes. Mesic meadows tend to be located near streams and have the highest species richness of grasses, shrubs and forbs (Debinski et al., 2000). Forbs constitute the primary plant coverage, providing abundant nectar sources. This pattern holds across both Gallatin and Teton landscapes.

Based on these observations, we make several predictions. These predictions concern the distribution of species within a landscape, assuming there is sufficient habitat available to support all species.

1. Point-estimates of butterfly species diversity will be higher where the habitat mosaic is fine-grained relative to the movements of individuals, due to within-generation 'spillover' or undirected movement of species between habitats.
2. The incidence of certain butterfly species will be higher in sub-optimal habitats when the scale of the habitat mosaic is fine relative to the movements of individuals, due to the potential for 'habitat sampling' or the use of resources from multiple habitats.
3. The difference between species diversity patterns observed in Gallatin and Teton landscapes may be explained adequately by effects of scale, without invoking more complex species-habitat relationships.

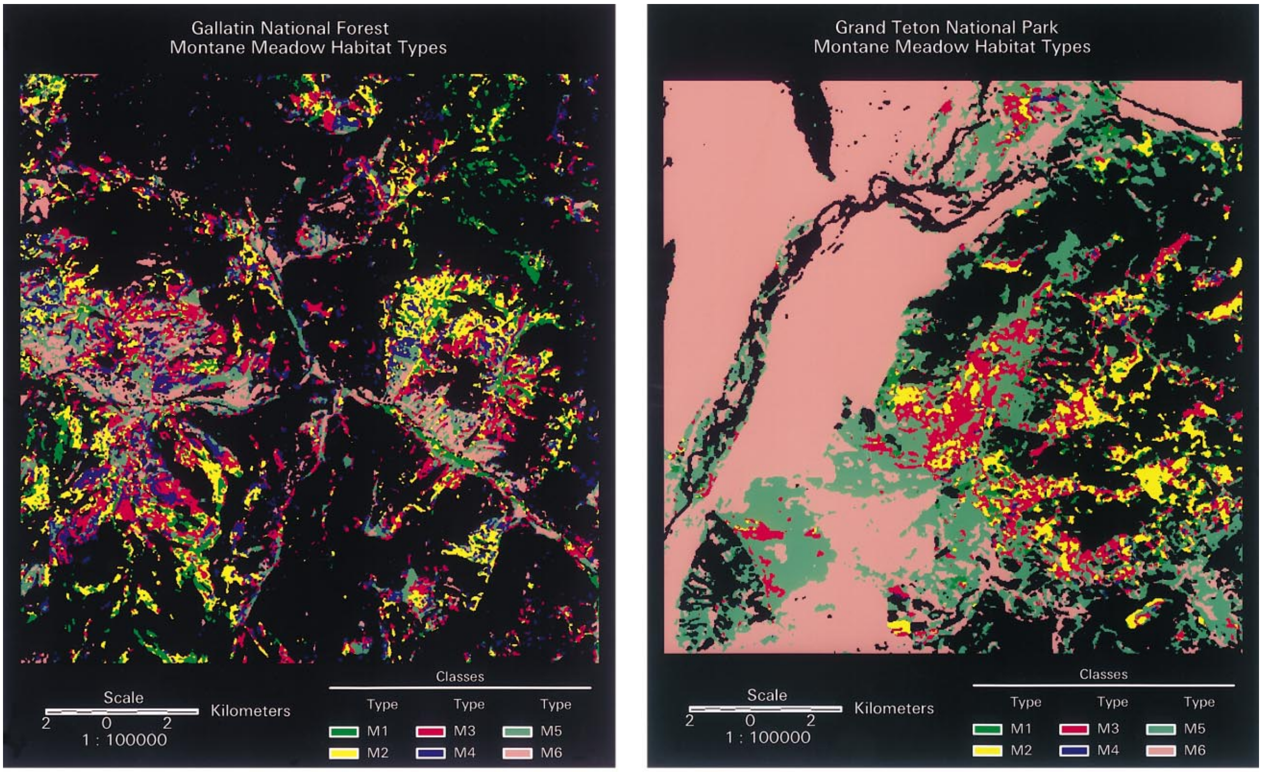
In order to test whether these predictions are consistent with our data, we develop a model that simulates individual movements across a patchy landscape. We apply the model to landscapes that differ in patch size, similar to the difference in average meadow size between Gallatin and Teton landscapes. Individuals differ in movement behaviors, according to degree of habitat specialization. Individual movement behaviors are drawn from several empirical studies. We explore the potential for scale-dependent spillover and habitat sampling in these systems for both specialist and generalist species, and compare model results with observed patterns.

2. Methods

2.1. Field study

Landsat satellite data (30×30 m pixel resolution) were used to classify seven montane meadow types along a moisture gradient ranging from extremely hydric wetlands (M1 and M2) to mesic, forb-rich meadows (M3) to xeric, sagebrush meadows (M6 and M7) in both Gallatin and Teton landscapes (Kindscher et al., 1998; Jakubauskas et al., 1998; Debinski et al., 1999). Field investigations in 1993, 1994 and 1995 confirmed distinct vegetation in each meadow type (Debinski et al., 1999). M4 meadows do not exist in the Teton landscape and M7 meadows do not exist in the Gallatin landscape (i.e. native meadow communities of these types are not identifiable using satellite imagery). To facilitate location of study sites during fieldwork, maps were converted to vector format and plotted on translucent Mylar for overlay onto 1:24,000 scale United States Geological Survey (USGS) topographic maps of the study regions. Field sampling was conducted at sites within polygons selected from the meadow classes. Sites were considered suitable for sampling if they were at least 100×100 m in size, a distance of 500 m or farther from other sites, and within 8 km of a road or trail. Five or six sites for each of the meadow classes were sampled (total study sites = 30 in each landscape). Particular care was taken to ensure that sampling sites were located in the center of a given class polygon on the satellite classification map.

Butterfly surveys followed the protocol of Debinski and Brussard (1992). Surveys were conducted on sunny days when the temperature was above 70°F, with low to moderate wind. Presence/absence data were collected by netting and releasing butterflies. A species was deemed present if it was observed during any of the sampling times. In the Gallatin landscape, surveys were conducted during 1993 and 1995, using three randomly selected 50×50 m plots within each 100×100 m sampling site. During the survey period, a total of three, 20-min surveys were conducted in each plot, except in rare cases where adverse weather prevented a survey. In the Teton landscape, surveys were conducted in 1996 under a modified sampling regime designed to accommodate a short field season and new information on sampling efficiency. Because multiple sampling plots per site did not increase the number of species observed (unpublished analysis of Gallatin data), Teton sites were surveyed in



(a) (b)

Fig. 1. A comparison of landscape mosaics found in the (a) Gallatin National Forest and (b) Grand Teton National Park . These images show the diversity of meadow types (M1–M6) as classified by SPOT imagery. M1 meadows are the most hydric and M6 meadows are the most xeric (M7 meadows are not shown). Note that M4 meadow types are classified in Teton scene, but were not used in our sampling because field investigation indicated that they were aspen (*Populus tremuloides*) stands. Forested habitats are masked out and shown as black. Note the striking difference in meadow size between the Gallatin and Teton landscapes, especially in M5 and M6 meadows.

one 50×50 m plot per sampling site. Each plot was surveyed twice for 30 minutes. Thus, the two landscapes differed in the number of samples taken to determine a species' incidence (frequency of presence). There were nine samples of each meadow in the Gallatin (three surveys of three plots within each meadow), and just two in the Teton (two surveys of one plot in each meadow). In order to assess whether the detection of species differed significantly between sampling regimes, we constructed a species accumulation curve for each landscape using PC ORD (McCune and Mefford, 1997) and estimated total species richness for each landscape using a first-order jackknife estimator (Heltshe and Forrester, 1983; Palmer, 1990).

Gallatin and Teton landscapes were characterized using spatial analysis of meadow statistics. FRAGSTATS spatial analysis program (McGarigal and Marks, 1993) was applied to a geographic information system meadow habitat coverage to calculate landscape statistics for each polygon in which at least one sampling site resided. A 500-m buffer was drawn around each polygon of interest. Parameters calculated within this buffer included the area and number (coverage) of all surrounding habitat types. These parameters were used to calculate average landscape indices. Wilcoxon Rank Sum tests were used to test for differences in indices between Gallatin and Teton landscapes.

Low-diversity meadows (M1, M2, M5, M6, and M7 in the Teton landscape; M1, M2, M4, M5, and M6 in the Gallatin landscape) were characterized as either adjacent to an M3 or not, with adjacency defined as any edge-to-edge contact between meadows. A *t*-test was used to determine whether species richness differed between landscapes based upon this meadow context (M3 adjacency). Finally, a signed-rank test was applied to determine whether the incidence of individual species was higher in meadows adjacent to M3 meadows.

2.2. Model

Our model is designed to illustrate how species distributions can be influenced by 'spillover' within a generation, and how 'habitat sampling' can increase the effect of spillover in some species and landscapes. The model focuses on two butterfly species (*a* and *b*) in a landscape containing patches of two habitat types (*A* and *B*) embedded in a non-habitat matrix. Habitat *A* represents meadows on an extreme end of the moisture spectrum (xeric or hydric), while habitat *B* represents intermediate, mesic meadows. Species *a* prefers habitat *A*, and cannot distinguish habitat *B* from the non-habitat matrix. This species is a strict specialist. Species *b* prefers habitat *B* but also distinguishes habitat *A* as marginal, or containing some resource worth sampling. For brevity, we call species *b* a generalist. In reality, species *b* also exhibits some degree of habitat specialization (Table 3). We intend results obtained from our model of specialist *a* to illustrate effects of within-generation spillover on species distribution, and results obtained from 'generalist' *b* to illustrate additional effects of habitat sampling.

Species preferences are conferred by rules governing the movement of individuals across the landscape. When in preferred habitat, individuals move once each time step, turning a random angle (distributed uniformly among all compass directions) and traveling one unit of distance in a straight line. Movements that would cause an individual to exit a patch of preferred habitat are 'reconsidered' with probability X. Individuals reconsider leaving marginal habitat with probability Y, where $Y < X$. Probabilities X and Y are inversely related to the 'permeability' of habitat boundaries (Stamps et al., 1987), defined as the probability that an individual approaching a habitat edge will exit the habitat. Individuals in the process of reconsidering exit from a patch remain stationary until the next time step, when a new movement (new angle of travel) is considered. When in non-habitat, individuals travel in relatively straight lines, turning small angles ($\leqslant 10$ degrees) between time steps, as observed in several studies (Baker, 1984; Odendaal et al., 1989). Movement into patches is random, and the boundaries of *A* and *B* habitats are perfectly permeable to entering individuals. Individuals cluster in patches of preferred habitat because they avoid leaving, not because they are attracted from afar. The resulting movement patterns (Fig. 2) generally mimic published accounts of daily butterfly movements (reviewed in Baker, 1984).

Model Teton and Gallatin landscapes differ only in the size and quantity of habitat patches. Total landscape size and the amount of each habitat type are held constant. Model Teton patches (diameter = 2.83 km) are 50 times larger and 50 times less numerous than Gallatin patches (diameter = 400 m). In reality, Teton meadows (average diameter ≈2.89 km) are about 47 times larger than Gallatin meadows (average diameter ≈422 m; Table 1). Model Teton landscapes include four patches of each type, while model Gallatin landscapes include 200 of each type.

Across these model landscapes, we track the movement of a single cohort of each species over a single flight season, approximated by 60 time steps or 'days' that are suitable for butterfly flight (i.e. sunny with low to moderate wind). At the beginning of each season, 1000 individuals of each species are distributed at random locations in preferred habitat. Distance moved per time step and probabilities of exiting a patch are drawn from the range of field observations (see below) and are identical in Gallatin and Teton landscapes. Each landscape is modeled as a torus, so that individuals exiting one side enter the other, equalizing immigration and emigration rates. Reproduction and mortality are not modeled. Periodically, we tally the number of individuals of each species occurring in each landscape element.

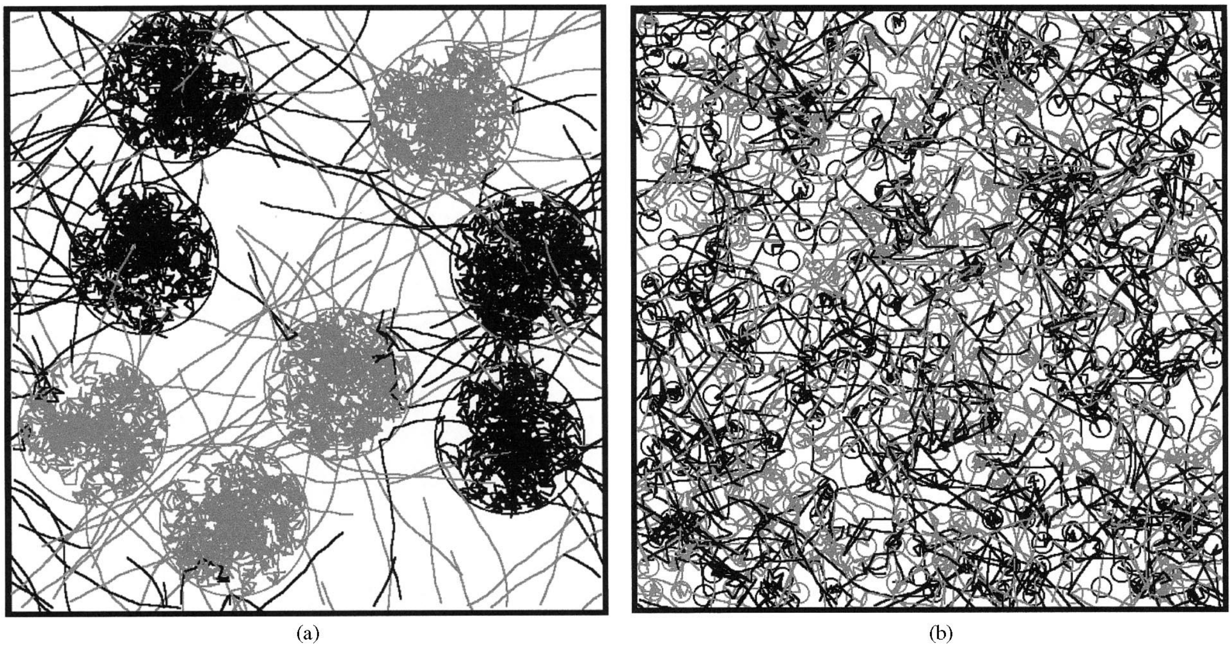


Fig. 2. Tracks of 500 butterflies moving for 25 days across model Teton (a) and Gallatin (b) landscapes. 'Generalists' and habitats of type *B* are represented in black; strict specialists and habitats of type *A* are in gray. Patch diameters are 400 m and 2830 m in Gallatin and Teton landscapes, respectively. Flight distance per time step is 200 m for both species in both landscapes. The permeability of preferred habitat is 0.4 (40% will cross an encountered boundary leading to non-habitat), and 'generalists' will exit marginal (*A*) habitat with probability 0.8 . (See Table 3 for our definition of generalism).

Results are averaged over 100 simulations of the flight season in each landscape type.

We employ simulation models because our questions involve effects of landscape structure on the non-equilibrial distribution of species, which is difficult to address using analytical models. The equilibrial density of species in different habitats depends on the permeability of edges in the landscape rather than the amount of edge in the landscape. If edge permeabilities and the total amount of each habitat type are identical between landscapes, the equilibrial distribution of species between habitats will be identical; given enough time, model Gallatin and Teton landscapes will achieve equivalent equilibria. However, the amount of edge or size of patches within a landscape influences the rate of approach to equilibrium, by increasing the rate at which individuals encounter edges. Individuals encounter edges more often in the more fine-grained Gallatin landscape, resulting in a faster approach to equilibrial densities. Our simulations reveal the potential for butterfly distributions to reach equilibrium in a single season. This potential is determined by landscape structure and butterfly movement rates.

Empirical estimates of butterfly movement rates are extremely variable, both among and within species (Baker, 1984). Among species, per-season displacement ranges from several thousand kilometers for migratory species, down to nearly zero. For example, a transplanted colony of *Euphydryas* remained within an area of 100×150 m for four generations (Ehrlich, 1984). Some average per-season displacements for non-migratory species are 500 m for *Euphilotes enoptes* (Peterson, 1996), 1.3 km for *Colias alexandra* (Ehrlich, 1984) and 200 km for *Pieris rapae* (Baker, 1984). Thomas and Hanski (1997) estimate maximum colonizing distances of 1.0 km for *Plebejus argus*, 8.65 km for *Hesperia comma*, 2.25 km for *Thymelicus acteon*, 2.5 km for *Mellicta athalia* and 1.40 km for *Satyrium pruni*. Movement rates were measured by Auckland and Debinski (unpublished) for *Parnassius clodius* butterflies in the Teton landscape. After correcting for marking and resight effort and fitting the data to several skewed distributions, we found the average daily movement rate was approximately 200 m. Under this rate, 60 favorable (sunny, low-wind) days would result in a maximum seasonal displacement of 12 km. This estimate is used as a baseline in the modeling study, which explores daily displacements such that the maximum seasonal displacement ranges from 360 m to 48 km. This range should encompass the movement capacities of butterflies resident within the study landscapes, which span up to 48 km in length (see Section 4). It is unnecessary to model movement capacities outside this range because our goal is to compare the potential for spillover and habitat sampling between these two landscapes. Butterflies with extremely high or low displacement rates would perceive no difference between the average patch sizes in these landscapes, and would sample each habitat at a rate independent of landscape structure.

Table 1
Comparison of average landscape parameters for Gallatin and Teton meadows for polygons in which survey sites were located[a]

	N	Area (ha)	Perimeter (km)	Proximity (m)
M1 Meadows				
Teton	2	58.0	111.6	36.0
Gallatin	5	12.7	29.0	53.4
M2 Meadows				
Teton	5	8.6	1.9	168.5
Gallatin	5	5.2	2.2	68.2
M3 Meadows				
Teton	5	13.6	3.0	86.9
Gallatin	6	16.6	4.1	44.6
M5 Meadows				
Teton	4	840.0	96.0	56.1
Gallatin	6	17.8	4.3	98.9
M6 Meadows				
Teton	4	2393.7	62.2	45.0
Gallatin	5	15.9	4.1	56.0
All above meadows				
Teton	20	658.1	33.98	65.4
Gallatin	27	14.0	4.1	60.0

[a] Proximity is the distance to the nearest patch of similar type (moisture classification). Differences in average parameters between landscapes are not significant when comparing only sites sampled using a Wilcoxon Rank Sum tests. However, these same trends in area hold for all meadow types except M1 across the entire landscape and are highly significant for all comparisons ($P<0.001$) using a *t*-test (degrees of freedom are on the order of thousands in each case).

Parameters for the permeability of patch boundaries are drawn from Ries (1998), who tracked the movements of two species in patches of Iowa prairie. The first species (*Speyeria idalia*) is a specialist found only in prairie habitat. The second species (*Danaus plexippus*) may be considered a habitat generalist for our purposes, because it uses a host plant that is found both within and outside of prairie patches. Square plots were established in several prairie patches, such that individuals crossing one of the four plot boundaries would enter non-prairie habitat, while individuals crossing the other three plot boundaries would remain in prairie. Individuals were tracked until they crossed a boundary. Of 433 *Speyeria idalia* tracked, 42 crossed into non-prairie habitat. If all four plot boundaries were equally permeable, then ≈108 *Speyeria idalia* should have crossed into non-prairie habitat. Instead, permeability of prairie boundaries averaged 0.388 for the specialist (range ≈0.0–0.8), and 0.825 for the generalist (range ≈0.2–1.0). From these data, it is reasonable to assume that habitat permeability may differ by a factor of two between specialist and generalist species. This estimate is varied in a sensitivity analysis of the model.

3. Results

Both empirical and model results show that the scale of the landscape mosaic, relative to the scale of individual movements, can have significant effects on local species incidence and richness.

3.1. Empirical data

Teton and Gallatin landscapes differ primarily in patch size (Table 1). Of the meadows surveyed, hydric (M1) meadows averaged five times larger and xeric (M5 and M6) meadows averaged hundreds of times larger. Because of the high variance among polygons and the small sample size (some sampling sites occurred in the same polygon), only M5 meadows showed a significant difference between landscapes (although M6 meadows showed the largest difference in mean size). With the exception of M3 meadows, all Teton meadows averaged larger than Gallatin meadows. Results for meadow perimeter and distance between meadows of similar type were mixed between habitat types (Table 1). The larger overall perimeter observed for Teton meadows is mostly explained by the larger overall area of Teton meadows (observed ratio between Teton and Gallatin meadow perimeters = 8.29; expected ratio assuming perfectly circular meadows = 6.86). This result may be taken as evidence that the edges of Teton and Gallatin meadows share a similar fractal dimension. If the fractal dimension of edges differed significantly between landscapes, we would suspect different movement patterns across edges.

There was no significant difference between landscapes in total butterfly diversity. A total of 58 species were observed overall, 43 in the Gallatin landscape and 42 in the Teton landscape. Twenty-eight species were common to both landscapes. Ten species were found in all meadow types, while the remainder showed a peak in frequency at some point along the moisture gradient. In the Gallatin landscape, 16 sites were adjacent to an M3, and 9 sites were not; in the Teton landscape, 10 sites were adjacent to an M3, and 15 were not. There was no significant difference between landscapes in the mean butterfly species richness in M3 meadows (Teton $S=13$, Gallatin $S=14.5$; $P=0.462$, d.f. = 9). There also was no significant difference between landscapes in the average number of habitats in which a species was found (Teton 3.64, Gallatin 3.52; $t=0.291$, $P=0.77$, d.f. = 82).

Gallatin meadows were significantly higher in species richness when adjacent to a mesic meadow (mean = 12.8 species when adjacent to an M3 versus mean = 9.1 species when not; t = 2.69, d.f. = 23, $P<0.01$ by *t*-test and variances were equal). Species richness in Teton meadows showed no significant effect of patch context (mean = 12.8 species when adjacent to an M3 versus mean = 11.6 species when not; t = 0.665, d.f. = 12.8, $P=0.518$ and variances were equal). Species incidence was also significantly higher in Gallatin meadows adjacent to M3 meadows (t = 171.5, d.f. = 37, $P = 0.0018$; Table 2). The Teton data again showed no effect of patch context on species incidence (t = 328.5, d.f. = 40, $P = 0.095$). Statistical tests for effects of patch context on the subset of species that specialize on mesic meadows were precluded by small sample sizes.

Because we sampled less intensively in the Teton landscape, it is possible that we detected fewer of the total species there, compromising our ability to detect effects of patch context on species diversity. We assessed this possibility using a first order Jackknife estimate of the total species present in each landscape (Heltshe and Forrester, 1983; Palmer, 1990). By these estimates, we observed 86% of the 50 species expected in the Gallatin landscape, and 91% of the 46 species expected to occur in the Teton landscape. We conclude that our sampling efficiency was high in both landscapes, and results were not likely the outcome of different sampling regimes.

The observed results of patch context on species diversity could be due to spillover and/or habitat sampling. If due to spillover alone, we should observe a group of mesic meadow specialists (species occurring with highest abundance in mesic meadows), and these species should be found in other habitats only when mesic meadows are nearby. If due to habitat sampling, we could observe the same pattern (if mesic meadow 'specialists' were sampling other habitats). Alternatively, habitat sampling could produce a group of species occurring with relatively high abundance in meadows of type X and in mesic meadows near meadows of type X. Because of the similar patterns of diversity expected under both mechanisms, and because peak abundance may not reveal optimal habitat (van Horn, 1983; Pulliam and Danielson, 1991), it is difficult to determine the relative importance of spillover and habitat sampling in this system.

However, several observations hint that habitat sampling by 'specialists' is an important determinant of species diversity near mesic meadows. First, we saw little evidence of pure spillover. Most of the species occurring in high abundance *near* mesic meadows could not be considered mesic meadow specialists, because they did not occur with highest abundance *in* mesic meadows. Second, the pattern of species diversity near mesic meadows was not linked to generalist species. Most of the common species with generalist tendencies (e.g. *Euchloe ausonia, Plebejus saepiolus, Plebejus icariodes, Erebia epipsodea* and *Vanessa cardui*) showed no differences in distribution related to patch context (proximity of mesic meadows) (Table 2). Finally, butterflies generally exhibit behaviors suitable for habitat sampling, with larval host plants restricted to one habitat and adult nectar sources more widely distributed. Pure spillover should be more common in organisms with passive dispersal or in territorial species that can saturate optimal habitats (Pulliam 1988, Pulliam and Danielson, 1991).

Table 2
Comparison of butterfly species incidence in Gallatin and Teton meadows adjacent to mesic meadows (near M3) or not adjacent to mesic meadows (no M3)[a]

	Teton Data		Gallatin Data	
	Near M3	No M3	Near M3	No M3
Anthocharis sara			0.333	0.400
Boloria epithore	0.100	0.067	0.800	0.700
Boloria frigga			0.267	0.200
Boloria selene	0.500	0.133	0.200	0.000
Coenonympha haydenii	0.500	0.733	0.800	0.300
Coenonympha inornata	0.200	0.667	0.600	0.200
Cercyonis oetus	0.400	0.733	0.067	0.000
Chlosyne palla	0.300	0.133		
Colias eurytheme			0.000	0.100
Colias pelidne			0.133	0.100
Colias philodice			0.067	0.200
Colias sp.	0.500	0.067	0.200	0.100
Erebia epipsodea	0.400	0.333	0.000	0.500
Euchloe ausonides	0.200	0.000	0.933	0.900
Euphydryas editha	0.100	0.133		
Euphydryas gillettii	0.200	0.067	0.067	0.100
Gaeides xeditha	0.100	0.267	0.200	0.000
Glaucopsyche lygdamus	0.200	0.267		
Glaucopsyche piasus	0.000	0.133		
Harkenclenus titus	0.100	0.067		
Limenitis weidemeyerii	0.700	0.133		
Lycaena cupreus	0.100	0.067	0.067	0.100
Lycaena helloides	0.300	0.400	0.067	0.300
Lycaena heteronea	0.400	0.733	0.333	0.200
Lycaena nivalis	0.300	0.267		
Nymphalis milberti	0.300	0.133	0.267	0.100
Nymphalis vau album			0.133	0.100
Oeneis chryxus			0.267	0.000
Oeneis uhleri			0.267	0.000
Papilio eurymedon	0.100	0.067		
Papilio glaucus	0.400	0.267		
Papilio zelicaon	0.200	0.067	0.067	0.100
Parnassius clodius	0.300	0.200		
Parnassius phoebus	0.000	0.067	0.133	0.100
Parnassius protodice			0.133	0.300
Phyciodes pulchella	0.400	0.200	0.067	0.100
Phyciodes coctya	0.900	0.667	0.400	0.300
Pieris napi	0.100	0.133	0.667	0.700
Pieris occidentalis	0.000	0.133		
Plebejus acmon	0.500	0.600	0.333	0.400
Plebejus glandon	0.300	0.267	0.400	0.100
Plebejus icarioides	0.600	0.867	0.867	0.800
Plebejus saepiolus	0.700	0.333	1.000	0.900
Polygonia faunus			0.067	0.100
Speyeria callippe	0.100	0.133		
Speyeria cybele	0.100	0.000		
Speyeria egleis	0.000	0.067		
Speyeria hesperis	0.000	0.067	0.267	0.000
Speyeria hydaspe	0.200	0.067		
Speyeria mormonia	0.700	0.933	0.133	0.100
Vanessa atalanta			0.067	0.000
Vanessa cardui			1.000	0.900
Vanessa carye			0.067	0.000

[a] Incidence is measured over all meadows sampled, including M3 meadows. In the Gallatin landscape, species occur with significantly higher frequency in meadows adjacent to mesic meadows ($X_{\text{near M3}} = 0.31$ vs. $X_{\text{no M3}} = 0.25$, T = 171.5, d.f. = 37, $P = 0.0018$). This relationship is not significant in the Teton landscape ($X_{\text{near M3}} = 0.29$ vs. $\mathrm{X}_{\text{no M3}} = 0.27$, T = 328.5, d.f. = 40, $P = 0.095$). P values are based on a Sign Rank Test for significant differences.

3.2. Model

Fig. 2 shows how these model species spread across the two landscapes under identical movement parameters. Note that butterflies explore preferred habitats more thoroughly than other habitats, due to differences between habitats in the consistency of flight direction. Patch exploration time reflects both habitat specificity (permeability of patch boundaries) and patch size (area-perimeter ratio). Strict specialists spread faster across the landscapes, because they do not explore patches of habitat *B*. Both species spread faster across the more fine-grained Gallatin landscapes, where they encounter patch boundaries more often and have more frequent opportunities to travel in a consistent direction through non-habitat. In Teton landscapes, most individuals remain within natal meadows throughout the flight season. Large turning angles combine with large patch sizes to create low average displacements within a season.

After 60 flight days, species incidence patterns differ markedly between landscapes (Figs. 3 and 4, Table 3). Incidence in non-preferred habitat reflects the potential for habitat sampling. Habitat sampling is more likely in Gallatin landscapes for nearly all parameterizations of the model. Individuals in Teton landscapes must move almost eight times farther per time step in order to realize the same incidence patterns observed in Gallatin landscapes (Fig. 3). Species that travel much less than 100 m per sunny day would not be able to sample multiple habitat types in the Teton landscape without some sort of directed movement. This result is not substantially affected by the permeability of habitat boundaries, because

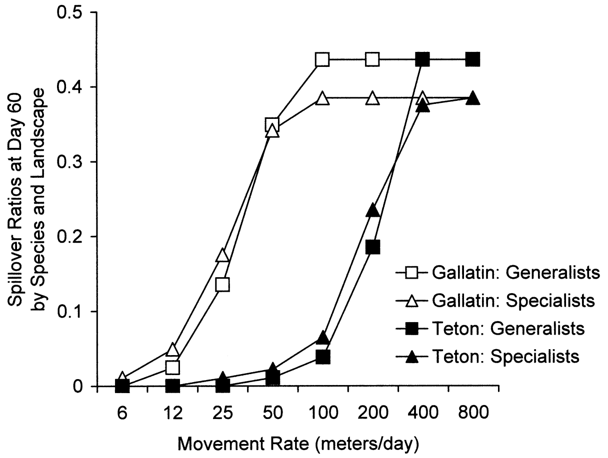
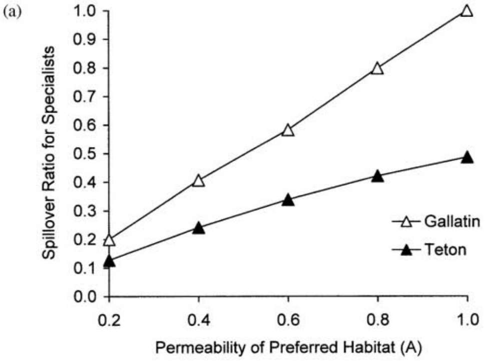
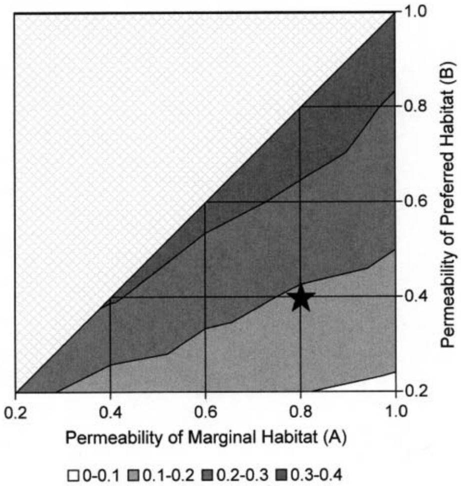


Fig. 3. Effect of movement rate on the potential for spillover in each model species and landscape, assuming preferred habitat permeability = 0.388 and marginal habitat permeability (for 'generalists') = 0.825. The 'spillover ratio' is the incidence of a species in non-preferred habitat divided by its incidence in preferred habitat (e.g.% specialists in *B*/% specialists in *A*). All individuals are in preferred habitat at day zero. The potential for spillover into other habitats is higher for both species in the more fine-grained Gallatin landscapes, provided that individuals move less than 400 m/day.



(b) **Spillover Ratio for Generalists in Teton Landscapes**



(c) **Spillover Ratio for Generalists in Gallatin Landscapes**

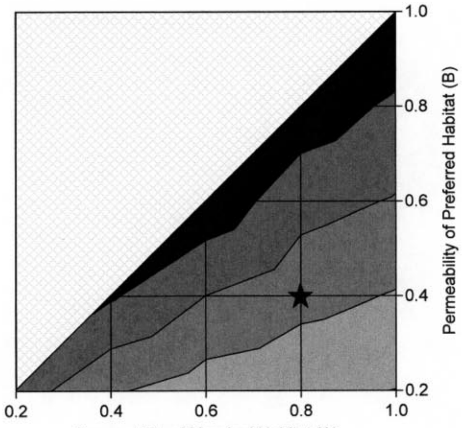


Fig. 4. Effect of habitat permeability on the potential for spillover in each model species and landscape, assuming a daily movement rate of 200 meters for both species. For strict specialists (a), only the permeability of preferred habitat affects species incidence patterns. For 'generalists' (b) and (c), incidence patterns are affected by the permeability of both preferred and marginal habitats. The contour plots show spillover ratio as a function of both permeabilities, where the permeability of marginal habitats is never less than the permeability of preferred habitats. Note the different scales for plots b and c. In the more fine-grained Gallatin landscapes, the spillover ratio is usually larger by a factor of two or more. Stars indicate parameter combinations supported by field data (see Section 2). At the star in (b), the spillover ratio is 0.188. At the star in (c), the spillover ratio is 0.467.

Table 3
Effects of landscape structure and the permeability of marginal habitats on species distributions[a]

		Gallatin landscapes			Teton landscapes		
Strict specialist	% In preferred (A) habitat		38			50	
	% in non-habitat (B)		15			12	
	% in non-habitat (matrix)		47			38	
	Mean displacement		3276			2123	
	Permeability of marginal habitat	0.4	0.6	0.8	0.4	0.6	0.8
'Generalist'	% In preferred (B) habitat	34	36	38	51	52	53
	% In marginal (A) habitat	28	22	18	16	12	10
	% In non-habitat (matrix)	38	42	44	33	36	37
	Mean displacement	2048	2092	2145	1830	1789	1798

[a] Simulations are initialized with 1000 individuals (500 of each type) in preferred habitat. Individuals move 200 m per time step, and results are given after 60 time steps. Each result represents the average of 100 simulations, each using a different random landscape. There are 200 small patches of each habitat type in the Gallatin landscapes, and four of each in the Teton landscapes. The permeability (see Section 2) of preferred habitat is 0.4. Results are given for three different levels of 'generalist' behavior, determined by the permeability of marginal habitat. Mean displacements from initial locations are given in meters. Displacements are higher in Gallatin landscapes because individuals spend more time in the non-habitat matrix, where they travel in relatively straight trajectories. The more fine-grained Gallatin landscapes create a more equitable distribution of species between habitat types.

individuals who move short distances rarely reach patch boundaries in Teton landscapes. For more vagile species (e.g. *Parnassius clodius*, moving 200 m/day), permeability has a large effect on habitat sampling, especially in Gallatin landscapes (Fig. 4). However, the permeability of marginal habitat has a relatively small effect on generalist incidence patterns, compared to the effect of patch scale (Figs. 4b,c; Table 3). Permeability of preferred habitat and the scale of the landscape mosaic have the largest influence on patterns of biodiversity in this model.

Although no modeling was necessary to predict that a species can sample more habitats in a more fine-grained landscape, this model quantifies the degree to which Gallatin and Teton landscapes may differ from a butterfly's perspective. A typical species may explore non-preferred meadows nearly twice as often in the Gallatin landscape (Figs. 3 and 4; Table 3). Species less vagile than *Parnassius clodius* can sample alternative meadow types up to 17 times more often in the Gallatin landscape (e.g. a butterfly moving 50 m/day under the model in Fig. 3). This model also quantifies how habitat sampling (observed in the 'generalist') can boost the effects of spillover in the Gallatin landscape (Figs. 3 and 4; Table 3).

These estimated differences between landscapes depend on the assumption that butterflies never reach equilibrial distribution among the large meadows in the Teton landscape during a single flight season. This assumption is based on the observation that most butterfly species have a very short flight season of three weeks to two months (Scott, 1986), of which only some days are sunny and suitable for long-distance flight.

4. Discussion

Landscape structure influences the distribution of butterfly species in both empirical and model results. Model results show that most species of butterfly should move more easily between habitats in the Gallatin landscape, providing the mechanism through which point species diversity can be increased in some meadow contexts. We predicted that the mechanism for species enrichment in locations adjacent to mesic meadows is the potential for movement of individuals between habitats. This movement can result in (a) spillover of species from the higher-diversity mesic meadows into other habitats, and (b) habitat sampling by species that benefit from the nectar in mesic meadows. Either or both of these mechanisms may be operating in the Gallatin landscape, where individuals can move frequently between habitats. In the Teton landscape, neither mechanism is likely to produce significant enrichment of species diversity near mesic meadows, because meadows are so large that the potential for individuals to leave their natal meadow is limited during the short flight season.

Our empirical data did not support the hypothesis that the observed species enrichment is due to spillover in the traditional sense. Instead, our data and model results support a more complex interplay between patch scale and movement patterns, potentially including both spillover and habitat sampling, as follows. Species in both landscapes occur in the same number of habitat types, yet species are concentrated near mesic meadows only in the fine-grained landscape. This pattern suggests that movement in a fine-grained habitat mosaic more often results in the discovery of resources that can be locally exploited. In a fine-grained mosaic, individuals that discover the nectar resources in mesic meadows need not stray far from other necessary resources (e.g. larval host plants). In a coarse-grained mosaic, individuals may not be able to move easily between necessary resources, and may not opt to linger near mesic meadows. In general, the finer the scale of the landscape mosaic, the closer an individual is to every habitat type in the landscape, and the easier it is to access an optimal resource base with minimal movement. When patches are small enough to be easily sampled during daily movements, and large enough to accommodate multiple species, then species diversity should increase near resources that are used by multiple species.

These effects of landscape scale can also be described as edge effects. Given that the maximum colonizing distance for many butterfly species is no more than several kilometers (Thomas et al., 1992), most non-migratory butterflies probably spend their whole lifetimes within areas no larger than a single average meadow in the Teton landscape. In this situation, only individuals that eclose near meadow edges have the potential to sample multiple habitats. Of these individuals, only a fraction are in a position to sample nectar from mesic meadows. In the Gallatin landscape, smaller meadows mean more edge habitat, more contact between mesic meadows and other habitats, and more potential for edge effects on species diversity. In addition, random sampling techniques necessarily record species from edge and core habitats according to the ratio of these habitats. In meadows as large as those in the Teton landscape, the ratio of edge to core habitat is relatively small, so random samples will necessarily include a smaller proportion of species outside their core habitat. For these reasons, landscapes with a coarse-grained habitat mosaic should exhibit lower evidence of edge effects such as spillover and habitat sampling. Our study cannot differentiate between the effects of patch scale and edge density on species diversity, because the location of our sample plots was not stratified by distance to patch edges.

Our aim here is to provide alternative hypotheses for certain effects of landscape structure on patterns of biodiversity. To this end, we have extended previous models of spillover (Pulliam, 1988; Palmer, 1992; Holt, 1997) to include within-generation dynamics. We have demonstrated that spillover effects may be important even when there is no detectable spillover between generations. Note that we begin each simulation with each species present only in its preferred habitat, which is analogous to assuming total reproductive failure or extirpation in other habitats. Under this assumption, Holt's (1997) metapopulation model for spillover in a heterogeneous landscape predicts that species will occur only in preferred habitat; i.e. there will be no spillover effect. However, most species counts must occur between the instants or seasons in which local extinction or reproductive failures occur. We suggest that modeling efforts aimed at explaining patterns of species diversity should address the potential for within-generation movements, and the potential that biodiversity will be censused in non-equilibrial situations.

Our results have profound implications for conservation planning. Many conservation efforts are based upon species–habitat relationships determined through surveys of incidence and/or abundance. We have shown that the species–habitat relationships revealed in such surveys are potentially confounded by landscape effects. However, the potential effects of patch scale and context can be determined using simple models like the ones outlined here. Another challenge for conservation planning is the fact that mobile species may use a range of habitats. In fact, habitat sampling may be more important for the persistence of certain species than is currently recognized. For such species, conservation units should not be habitats, but landscape complexes. As the ecological understanding of species–habitat relationships improves, there should be a move towards more complex, landscape-level analyses of species–habitat relationships rather than simple surveys of incidence and/or abundance.

5. Conclusion

We have shown that patterns of species diversity and abundance may differ according to the scale of the landscape mosaic, regardless of the habitat affinities or population dynamics of individual species. The finer the scale of the landscape mosaic, the more habitats can be sampled by each species. This trend may benefit species with restricted movement that require multiple resources to complete a complex life cycle. However, this effect of scale may obscure important species–habitat associations. In order to translate expected patterns of species diversity between landscapes of different scale, we must address the interaction between movement and patch scales. Our data indicate that fine-grained landscapes may reveal effects of patch context on butterfly incidence and diversity, while coarse-grained landscapes may not. Our models explain this observation, illustrating that species distributions can be altered in fine-grained landscapes by ephemeral 'spillover' movements and by opportunistic 'habitat sampling'. The potential for these mechanisms to alter species–habitat relationships presents a real challenge for species conservation. The potential for species–habitat associations to differ between landscapes, and the potential for species to require access to more than one habitat type, must be considered in future conservation efforts.

Acknowledgements

This research was supported by the US Environmental Protection Agency (Grant 96-NCERQA-1A to Debinski et al.), the University of Wyoming National Park Research Station, Grand Teton National Park, and Iowa State University. Although the research described in this article has been funded in part by the EPA (through Grant 96-NCERQA-1A to Debinski et al.), it has not been subjected to the Agency's peer review and therefore does not necessarily reflect the views of the Agency, and no official endorsement should be inferred. Mark Jakubauskas analyzed the remotely sensed imagery. Martin Cody, Susan Harrison, Bob Holt, Brent Danielson, Kirk Moloney, Julia Auckland, Leslie Ries and Jens Roland provided comments on earlier drafts of the manuscript. Alan Vandiver, Ron Krager and Nancy Hallstrom of the Gallatin National Forest provided data, maps of the area and housing. We thank James Pritchard, Liesl Kelly, Camille King, Katie Horst, Michelle Wieland, Danielle Slaterly, John Clark and Paul Rich for assistance in the field. This is Journal Paper No. J-18320 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa, Project 3377, and supported by Hatch Act and State of Iowa Funds.

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