Landscape Ecol (2011) 26:7–18
DOI 10.1007/s10980-010-9549-z

LANDSCAPE ECOLOGY IN REVIEW

The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies

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Received: 20 March 2010 / Accepted: 18 October 2010 / Published online: 30 October 2010

Abstract Understanding the influence of large and small-scale heterogeneity on species distribution and abundance is one of the major foci of landscape ecology research in fragmented environments. Although a large number of studies have addressed this issue individually, little effort has been made to synthesize the vast amount of literature published in the last decade. We reviewed 122 focal patch studies on 954 species published between 1998 and 2009 to determine the probability of species responding significantly to landscape, patch, and within-patch variables. We assessed the influence of taxonomic, life history, and methodological variables on probability of response to these 3 levels. Species in diverse taxa responded at high rates to factors at all three levels, suggesting that a multi-level approach is often necessary for understanding species response in patchy systems. Mammals responded at particularly high rates to landscape variables and therefore may benefit more than other taxa from landscape-level conservation efforts in fragmented environments. The probability of detecting a species response to landscape context, patch, and within-patch factors was influenced by a variety of methodological aspects of the studies such as type of landscape metric used, type of response variable, and sample size. Study design issues rarely are discussed by authors as reasons why a particular study did not find an effect of a variable, but should be given more consideration in future studies.

Keywords Focal patch study · Isolation · Landscape · Patch quality · Presence–absence vs. abundance · Review · Multi-level · Sample size · Study design and methodology

Introduction

Identifying conditions under which local and landscape factors strongly influence ecological pattern and process is a central focus of landscape ecology (Levin 1992; Turner 2005). Multi-level studies, which simultaneously measure how factors operating at both local and regional levels influence species, are becoming increasingly common in landscape ecology research. In spatially heterogeneous or “patchy” landscapes, multi-level studies often focus on determining if species respond to within-patch (e.g., vegetation structure), patch (e.g., patch size and shape), and landscape variables (e.g., amount of habitat in the landscape). Results of these studies have been used to test hypotheses regarding which

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Electronic supplementary material The online version of this article (doi:10.1007/s10980-010-9549-z) contains supplementary material, which is available to authorized users.

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levels exert the strongest influence on species (Cushman and McGarigal 2004a). Because the vast majority of these studies are conducted in anthropogenically fragmented landscapes, results also may be used to guide management decisions regarding conservation of species in fragmented environments (Banks et al. 2005; Holland and Bennett 2009). In particular, whether management efforts should consider the landscape surrounding patches, or instead focus solely on managing patch-level attributes such as patch size or quality, is an important decision that is directly informed by these types of studies (Mazerolle and Villard 1999).

Several reviews of the fragmentation literature over the past decade have indicated that both patch (e.g., area) and landscape (e.g., isolation) variables impact species presence, abundance, or richness (Mazerolle and Villard 1999; Watling and Donnelly 2006; Prugh et al. 2008). In general, species are more likely to show a stronger response to patch-level effects (Watling and Donnelly 2006; Prugh et al. 2008). These reviews also found taxonomic and/or life history differences in how species responded to patch and landscape variables, although results were not consistent across studies. Methodological factors that may influence whether or not a particular study detects a response to variables operating at a particular level (e.g., sample size) have received little attention in previous reviews (but see McGarigal and Cushman 2002). Such methodological considerations may be particularly relevant for studies in patchy landscapes given the diversity of approaches taken to investigate the relative influence of patch and landscape variables. The influence of within-patch factors on species generally have not been examined in previous syntheses of multi-level studies.

We reviewed 122 focal patch studies published from 1998 to 2009 to determine the probability of a species' response to within-patch, patch, and landscape-level factors. Focal patch studies were defined as empirical field-based studies that examined species response (e.g., presence–absence) within discrete focal patches, and then related that response to characteristics of the focal patches and the surrounding landscape via statistical analysis. We determined if the probability of species responding to landscape, patch, and within-patch factors was influenced by taxonomic category of the study species, body size, landscape type, and several methodological variables (e.g., type of study design, sample size and type of response variable).

Methods

Literature search

We used the ISI Web of Science database to search for articles published between January 1998 and October 2009 with the search terms "patch" and "landscape". We used this range of publication dates to prevent overlap of sources with the Mazerolle and Villard (1999) review that also focused exclusively on focal patch studies. We confined results to articles in the ecology, conservation, biology, or forestry literature using the automatic filtering available in Web of Science. Our search yielded 3830 articles. We scanned through abstracts to further narrow our search to only those articles that were field-based, focal patch studies as defined above. We also included several ($n = 16$) studies from our own database of focal patch studies that were not found in the literature search, as well as one dataset from the first author (D. Thornton 2011). For this review, we only included focal patch studies that measured presence–absence, abundance, or density of species within patches. Studies examining species richness or diversity as the response variable were excluded. We only considered focal patch studies conducted in primarily terrestrial systems. This included studies of forest, open (e.g., prairie, meadows), and aquatic (e.g., marshes, wetlands, ponds) habitat patches embedded in anthropogenically fragmented environments. Several studies (10) conducted in naturally fragmented landscapes, but where patches could be clearly defined, also were included. We did not include studies where the patch was an island, and we excluded studies conducted on plants. We also excluded studies that used Principle Components Analysis to reduce dimensionality of predictors when it resulted in variables that were combinations of within-patch, patch, or landscape variables, and as such, not easily interpretable as solely belonging to one category. We included studies that evaluated species response to landscape-level variables and at least one other level (patch or within-patch) simultaneously. After excluding articles based on our criteria, we had a set of 122 focal patch studies on

954 species in the final analysis (see Appendix—electronic supplementary material).

Collection of data from studies

For each article in the final set for review, we determined if the species in the study displayed a significant response to landscape context, patch, and within-patch variables. Individual species in the studies were used as the unit of analysis. Landscape context variables included habitat composition and configuration measured in buffers around focal patches, and/or distance-based measures of isolation of the focal patch such as simple Euclidean distance (e.g., distance to the nearest patch, distance to nearest occupied patch) or connectivity metrics (e.g., Hanski's connectivity index). Patch variables were patch size and measures of patch shape, including perimeter, perimeter/area ratio, and fractal dimension. Within-patch variables were measures related to patch quality such as vegetation structure, level of disturbance, temperature, pH, etc.

Because authors used a diversity of statistical approaches to evaluate the influence of landscape, patch, and within-patch factors on species response, we developed a set of rules for defining a "significant" response. A particular variable was defined as having detected a significant influence on species response if it: (1) had a significant ($P < 0.05$) univariate or multivariate influence on the response (we chose only multivariate analyses when both were given), (2) appeared in a best-fit model based on stepwise multiple regression analysis, (3) appeared in the best fit model or a highly competitive model (within Δ2 AIC or AICc units of the best fit model), based on information-theoretical approaches.

We used a binomial response variable to indicate whether a species was found to respond significantly to each category of variable. For example, if a particular species in a study responded to landscape context and patch size, but not measures of within-patch quality, it would be coded as "1" for both response to landscape context and patch factors, but a "0" for response to within-patch factors. These data then formed the basis for three separate generalized linear mixed models that evaluated the influence of covariates on response to landscape context, patch, and within-patch factors (described below). Although we recognize that the vote-counting methodology that we employed has many limitations as a method for synthesizing the results of multiple studies (Hedges and Olkin 1980, 1985), the data from the studies in our review were not amendable to a more rigorous meta-analysis of effect sizes, which is a common problem in fragmentation syntheses (Mazerolle and Villard 1999; Mortelliti 2010).

Our review may have been biased toward those studies that found a significant response of species to within-patch, patch, or landscape-level variables. However, the majority of studies (60%) examined the response of multiple species, which may have increased the chance that both significant and non-significant results would be published. We cannot rule out the possibility that some studies may not have been published that did not find a significant effect for any within-patch, patch, or landscape variables for all species examined, although we think this unlikely to account for a large number of studies.

Data analysis

We use species, instead of the study, as the unit of analysis. The advantage of our approach is that not all species in a single study will respond the same to patch and landscape factors, and thus we do not lose this information by summarizing data at the study level. The disadvantage is that because we examined the response of multiple species within individual studies, correlations in the response of species to landscape, patch, or within-patch variables may be present (e.g., all the species in a particular study may have been more or less likely to respond to landscape context or patch or within-patch variables because of the selection of certain metrics, or unaccounted for peculiarities of sampling, analysis, or study system). To account for these correlations, we used generalized linear mixed models in Proc GLIMMIX (SAS 2008) to examine patterns in species response. GLMMs provide a flexible framework for analyzing non-normal data when correlations among observations are present. GLMMs account for these correlations by incorporating a random effect variable when analyzing the data, which in our analysis was a variable denoting the study from which the data were collected. The response variable in each GLMM was the presence, or lack thereof, of a significant response to landscape context, patch, and within-patch factors for each species.

We considered several predictor variables (i.e., fixed effects) as potentially influencing the probability that a species would display a significant response to landscape, patch, and within-patch variables (Table 1). All variables were taken directly from the published studies included in the review except for body size. We determined average body size for all mammals and bird species using several different sources (Reid 1997; Nowak 1999; Sunquist and Sunquist 2002; Dunning 2007). Average weights were calculated by averaging male and female weights when both were presented. If only a range of weights was given, we took the mid-point of the range as the average. Body weights were only calculated for birds and mammals because of the strong relationship between mobility and body size in these species (e.g., Haskell et al. 2002; Carbone et al. 2005; Ottaviani et al. 2006), large sample size of species in these taxa in our review, and the limited availability of accurate information on body weight for other taxa.

When running GLMMs, we used a residual pseudo-likelihood as the estimation method and assessed degrees of freedom using the Kenward–Rogers method (Littell et al. 2006). Variables considered as potential predictors in the analysis of the full dataset were: taxonomic category, landscape type, type of study design, sample size, number of levels considered (whether the authors considered the influence of all three levels simultaneously, or just the influence of landscape and either patch or within-patch variables), and type of response variables. For statistical inference of fixed effects, we first fit a full model including all covariates, and then used a backward stepwise elimination procedure (P to remove <0.10, P to enter <0.05) based on Wald F-tests (Bolker et al. 2008). A likelihood-ratio test was used to test for significance of the random effect (Bolker et al. 2008). We used Tukey–Kramer adjustment for multiple comparisons to test for significant differences between levels of each predictor variable remaining in final models. We also ran the GLMMs without any covariates to get an estimate of the overall mean probability of species responding to landscape context, patch, and within-patch variables.

Several predictor variables could only be tested through subsetting and re-analysis of the data. To test the influence of studies employing multiple vs. single buffers on the probability of detecting a species response to landscape-level variables, we restricted our dataset to focal patch studies that used buffers and re-ran the GLMM. Instead of using the predictor variable "type of study design" (Table 1), we used a binomial variable that distinguished between studies employing single or multiple buffers. To test the influence of body size on probability of species response to the multi-level variables, we subset the data to include only birds or only mammals, and re-ran the backwards elimination procedure using body size in addition to all other predictors (except for taxonomic category) in the full analysis. We ran mammals and birds separately, as a 500g bird and 500g mammal differ markedly in mobility. To test the influence of the range of patch sizes on probability of species response, we used only those studies that presented this information ($n = 83$), and re-ran the backwards elimination procedure with all other variables included in the full analysis.

Results

Birds were by far the most common study species in the articles of our review (Fig. 1). Although this bias is not as pronounced when examining the percentage of the total number of *studies* that focused on birds, birds still account for the largest number of studies, followed closely by mammals. As noted by McGarigal and Cushman (2002), herpetofauna were the least common study species. In particular, reptiles were almost completely unstudied and were the focus of only 3 focal patch studies (Fig. 1).

GLMMs

Based on results of GLMMs without covariates, the mean probability of a species responding to landscape context was 0.55. The mean probability of species response to patch and within-patch factors was 0.59 and 0.71, respectively. Best-fit models for effects of predictor variables on the probability of species responding to landscape, patch, and within-patch variables are given in Table 2. Random effects were significant in all three models ($P < 0.001$), with parameter estimates (SE) of 0.50 (0.18), 1.4 (0.36), and 1.92 (0.50) for landscape, patch, and within-patch analyses, respectively. The probability of a species responding significantly to landscape context was

Table 1 Covariates used in the generalized linear mixed models

Covariates	Categories (for categorical variables only)	Description
Taxonomic category of study species	(1) Birds (B)	Class Aves
	(2) Mammals (M)	Class Mammalia
	(3) Herpetofauna (H)	Includes Class Amphibia and Reptilia (considered together because of low sample size)
	(4) Invertebrates (I)	Includes Class Insecta, Arachnida, and Gastropoda
Body size	N/A-continuous variable	Mean body weights for species (birds and mammals only)
Type of study design	(1) Focal patch buffer study (FPBS)	Landscape context variables were measured in buffers around the focal patch (distances of buffers varied among studies) and included composition and configuration metrics
	(2) Focal patch buffer and isolation study (FPBIS)	Landscape context variables were measured in buffers around the focal patch and also included isolation metrics from the focal patch (Euclidean distances or connectivity measures)
	(3) Focal patch isolation study (FPIS)	Landscape context variables were only isolation metrics from the focal patch (Euclidean distances or connectivity measures)
Sample size	N/A-continuous variable	Number of patches surveyed in the study
Patch size range[a]	N/A-continuous variable	Absolute range of patch sizes sampled in the study
Number of levels considered	(1) Two	Two of the levels (landscape plus patch or within-patch) was considered in the analysis of the particular study
	(2) Three	All three levels (landscape, patch, and within-patch) were considered in the analysis of the particular study
Landscape type	(1) Forest–nonforest	Forest patches embedded within an agricultural or urban matrix
	(2) Forest-logging	Forest patches embedded in a managed forest matrix
	(3) Aquatic-human	Aquatic patches (e.g., ponds, wetlands) embedded within a human-dominated matrix
	(4) Open-human	Non-forest habitat patches embedded in human dominated matrix
	(5) Natural	Habitat patches embedded in naturally fragmented landscape
Response variable[b]	(1) Presence–absence (P)	Species presence-absence was assessed within patches
	(2) Abundance/density (A)	Species abundance or density was assessed within patches

[a] Patch size range could only be calculated for a subset of studies in the review that reported the range of patch sizes sampled

[b] For studies that measured and analyzed both abundance/density and presence–absence of the same species within patches, we randomly chose one of the response variables to consider in the review for each species and excluded the other

influenced by taxonomic category of the species, type of study design, and sample size of the study. Multiple comparison tests revealed that mammals had a significantly higher probability of responding to landscape-level variables than birds (Fig. 2b). Studies that examined a large number of focal patches had a higher chance of detecting a response of species to landscape variables. For every 10 additional patches studied, the odds of detecting a response to landscape-level variables increased by 2.3%. Studies employing buffers to measure landscape variables, or employing both buffer and isolation metrics, had a higher probability of detecting a response of species to landscape-level variables than those employing only isolation metrics (Fig. 2a). When considering only studies that measured landscape context in buffers, the use of multiple buffers around the focal patch did not increase the likelihood of detecting a response to landscape context ($P = 0.97$).

The probability of a species responding significantly to patch variables was only influenced by sample size. For every 10 additional patches studied, the odds of detecting a response to patch-level variables increased by 3.1%. The probability of a species responding significantly to within-patch variables was influenced by sample size and type of

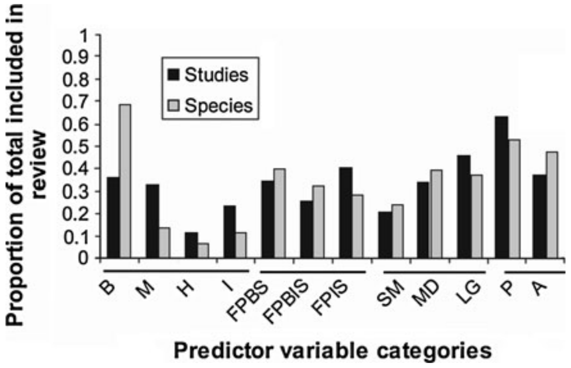

Fig. 1 Characteristics of the studies and study species included in the review organized according to categories of several predictor variables tested in the generalized linear mixed models. Abbreviations of categories of predictor variables along the x-axis are given in Table 1, except for SM, MD, and LG, which indicate studies sampling a small (<30), medium (>31–60), or large (>60) number of patches

response variable. A 3.4% increase in the odds of detecting a response to within-patch variables resulted from the addition of 10 patches to the study. Studies employing abundance/density as the response variables were more likely to detect a response to within-patch variables than studies measuring presence-absence (Fig. 3).

Considering only birds species in GLMMs, body size was not selected as a variable in best-fit models, nor did body size have a significant univariate correlation with response to landscape, patch or within-patch factors. Considering only mammals in GLMMs, body size did not influence the probability of a species responding significantly to landscape context or within-patch variables, but body size did influence the probability of response to patch-level variables ($P = 0.06$). A 1 kg increase in body weight resulted in a 11.8% increase in the odds of responding to patch-level variables. Considering only those studies that published information about the range of sizes of focal patches examined, mean range size of patches in a given study did not influence the probability of detecting a response to landscape, patch, or within-patch variables.

Discussion

When considered together, over half of the species included in this review (56%) were influenced significantly by at least one measure of landscape context. This corresponds closely with the results of the early review by Mazerolle and Villard (1999), which found that 59% of studies detected a response to landscape context. Moreover, none of the individual taxa analyzed in our review had a probability of response to landscape context less than 0.4. Landscape variables were therefore important in determining distribution and abundance of species and conservation efforts in patchy landscape will often need to consider characteristics of the surrounding landscapes. Our review focused only on focal patch studies, which are fairly common in the published literature. True landscape-level studies (e.g., studies using landscape replicates as the unit of study; McGarigal and Cushman 2002; Fahrig 2003) should provide additional insights into landscape influences on species, although such studies are difficult to implement for most species and thus relatively rare.

Mammals had a significantly higher probability of responding to landscape-level variables than birds,

Table 2 Results of backward stepwise regression (based on three separate generalized linear mixed models) to investigate the influence of covariates on probability of response to landscape, patch, and within-patch level variables

Variable	Landscape context		Patch		Within-patch	
	F-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
Taxonomic category of study species	3.07	0.03	–	–	–	–
Type of study	6.23	>0.01	–	–	–	–
Sample size	3.66	0.05	4.80	0.03	2.77	0.09
Number of levels considered	–	–	–	–	–	–
Landscape type	–	–	–	–	–	–
Response variable	–	–	–	–	3.88	0.05

Dashes indicate variables that were not selected in the best-fit model

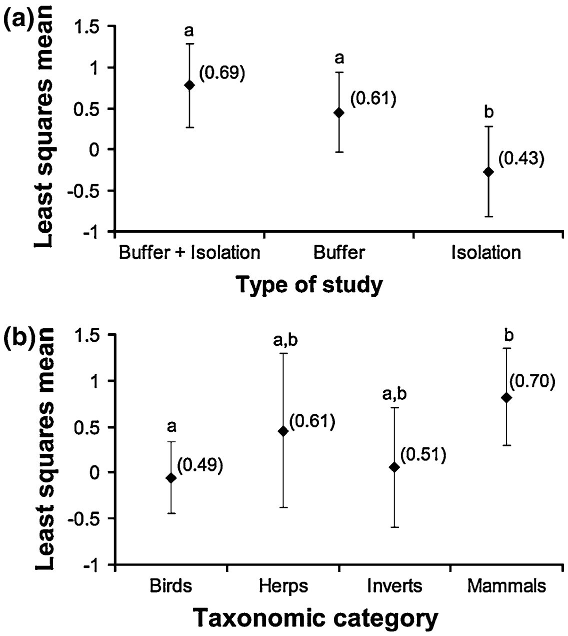

Fig. 2 The probability of response to landscape-level variables according to type of study (**a**) and taxonomic category (**b**). Description of x-axis categories is given in Table 1. The y-axis provides the least squares mean estimate (±95% CI) of the response on the logit scale. *Numbers in parentheses* have been converted from the logit scale to probabilities and indicate the mean probability that a species in each category would respond significantly to landscape context. *Means with different letters* above the error bars are significantly different

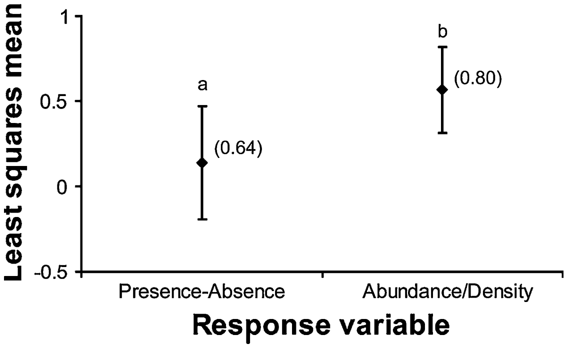

Fig. 3 The probability of response to within-patch variables according to type of response variable measured. Description of x-axis categories is given in Table 1. The y-axis provides the least squares mean estimate (±95% CI) of the response on the logit scale. *Numbers in parentheses* have been converted from the logit scale to probabilities and indicate the mean probability that a species in each category would respond significantly to within-patch variables. *Means with different letters* above the error bars are significantly different

but not a higher probability of response than invertebrates or herpetofauna. However, the low sample size of studies conducted on invertebrates and herpetofauna may have resulted in low power to detect any differences between these taxa and the others included in the review. For example, both of these taxa had large errors in parameter estimates. The difference in how birds and mammals responded to landscape-level variables may be driven by a couple of factors. Higher mobility of birds may enable them to move freely among fragments in some cases (Fraser and Stutchbury 2004; Churchill and Hannon 2010), resulting in a low response to isolation, which was the most common measure of landscape context in our review. However, this clearly does not apply to all birds, as some species are reluctant to cross small gaps and show altered movement behavior in fragmented landscapes (e.g., Belisle and Desrochers 2002; Robertson and Radford 2009). Moreover, some larger species of mammals are extremely mobile. Another possibility is that the coarse-scale habitat maps used to estimate landscape context variables in focal patch studies (usually vegetation maps derived from aerial or satellite imagery) were better at depicting habitat for mammals than for birds, and, consequently, were more accurate representations of landscape context for mammals. Vegetation types have been found to be poor predictors of habitat for birds in forested systems (Cushman et al. 2008b). However, whether or not this same problem would apply to birds in other systems, or if mammal distribution/abundance tends to be better predicted by vegetation types is unknown.

Species in all taxa also responded at high rates to patch-level variables, which concurs with previous reviews that have found patch-level variables to be important predictors of species distribution, abundance or richness (Mazerolle and Villard 1999; Watling and Donnelly 2006; Prugh et al. 2008). No significant differences in probability of response to patch-level variables were detected among taxonomic categories. Considering mammals alone, body size exerted a positive influence on the probability of response to patch-level variables. Because the most commonly measured patch-level variable was patch size, larger area requirements for large bodied species, and a resulting greater sensitivity to patch area, may explain this result. Although studies on larger bodied species tended to sample a larger mean patch size, they also sampled a larger range of patch sizes (correlation coefficient between body size and mean and range of patch sizes; $r = 0.23$ and 0.29, respectively). The greater range of patch sizes sampled may have increased the chance of detecting a significant response to patch-level variation for larger-bodied species.

Our review also found that species had an especially high probability of response to within-patch variables, as has been noted in several studies using other approaches such as variance partitioning (e.g., Cushman and McGarigal 2002; Fletcher and Hutto 2008; but see Grand and Mello 2004). Species distribution or abundance patterns may be influenced more strongly by fine-scale features of the environment (such as vegetation structure) with which they interact most directly rather than more diffuse influences as coarser-scales (Cushman and McGarigal 2004a). The high likelihood of response to within-patch factors also may be expected given that fragmentation results in not only increased isolation of patches and a reduction in patch size, but also in some cases to changes in habitat quality of patches over time (Holland and Bennett 2009). Long-term changes in patch quality in fragmented landscapes, such as edge-related vegetation changes, or degradation from cattle, logging, or fire can have a marked effect on species presence or abundance (e.g., Hannah et al. 2007; Michalski and Peres 2007). The high frequency of response of species to within-patch variables that we found in our review highlights the need to incorporate patch quality in metapopulation models (e.g., Schooley and Branch 2009). Regression models of occupancy and extinction-colonization dynamics typically rely on area and isolation as predictor variables, but the addition of patch quality as a predictor may substantially improve the fit of such models (Schooley and Branch 2009).

Several methodological variables had pronounced effects on the probability of detecting a significant response of species to landscape, patch, and within-patch factors. This finding suggests that focal patch studies may fail to detect an effect of within-patch, patch, or landscape variables because of the approach that was used, not necessarily because species were not responding to a particular level. Studies that measured landscape variables within buffers around the focal patch had a higher probability of detecting a response to the landscape level than studies that measured landscape variables by calculating Euclidean distance or connectivity measures of the focal patch to surrounding patches. Simulated animal movement patterns are more highly correlated with buffer-based measures of isolation than Euclidean distance or connectivity measures (Bender et al. 2003; Tischendorf et al. 2003). Buffer-based measures thus may be better proxies of overall isolation of the focal patch. Buffer-based measures also provide rich information beyond simple measures of isolation. They allow calculation of the full suite of landscape metrics such as patch density, contrast weighted edge density, contagion, proximity index, etc. This enables buffer-based analysis to provide a much more comprehensive evaluation of the effects of landscape context, in addition to patch isolation. In our analysis, we lumped all studies employing Euclidean distance or connectivity measures into one category to reduce the number of levels of the predictor variable. We cannot comment on whether certain distance measures were more likely than others to result in detection of a response of species to the landscape-level (e.g., nearest-neighbor distance vs. distance to nearest occupied patch). These differences have been noted elsewhere (Prugh et al. 2008).

The use of multiple buffers did not appear to have a marked effect on the probability of detecting species response to landscape context, which was surprising considering that many studies have found that spatial scale influences the strength of response of species to landscape variables (e.g., Cooper and Walters 2002; Thompson and McGarigal 2002; Boscolo and Metzger 2009). Moreover, a recent simulation study found that performance of buffer measures as predictors of connectivity were sensitive to measures of buffer radius (Moilanen and Nieminen 2002). Thus, all buffers are not equivalent and studies that use multiple buffers should have a better chance of detecting a significant response to landscape-level variables. The lack of effect of multiple buffers may indicate that researchers employing single buffers did a good job of identifying the most influential spatial extent for their particular species. However, researchers are unlikely to know beforehand what spatial extents are most important for calculating landscape variables, especially given that even closely related species can respond most strongly to landscape variables measured at drastically different scales

(Kolozsvary and Swihart 1999; Kadoya et al. 2008; Klingbeil and Willig 2009). For example, over 50% of single buffer studies of birds in our review used either a 1- or 2-km buffer. However, focal patch studies employing multiple buffers consistently show that birds respond most strongly to both larger and smaller buffers than this size (e.g., Hinsley et al. 1995; Sallabanks et al. 2006; Renfrew and Ribic 2008). A more likely explanation for the lack of relationship between use of multiple buffers and detection of response to landscape-level variables is the binary nature of our measure of response (i.e., significant or non-significant). Estimates of significance do not take into account variation in the strength of response to landscape variables (Hedges and Olkin 1980, 1985). Measures of landscape context within multiple buffers often are correlated because larger buffers encompass smaller buffers. A significant response of a species to landscape context therefore may be found at more than one spatial extent. However, the overall strength of the response could be quite different (Thompson and McGarigal 2002).

Studies that measured species response in a larger number of focal patches were more likely to detect effects of landscape, patch, and within-patch variables on species presence or abundance than studies that measured response in a smaller number of patches. Sample size has been found to influence detection of changes in species prevalence or population size (Ward et al. 2008; Nielsen et al. 2009), accuracy of large-scale species distribution modeling (Wisz et al. 2008), and has been implicated as a critical limiting factor in fragmentation studies (McGarigal and Cushman 2002). The power of statistical tests to find a significant effect of a variable is related to sample size (Quinn and Keough 2002). However, authors of focal patch studies rarely discuss sample size constraints as a possible reason for why they did not detect a response to landscape, patch, or within-patch factors. This may be a significant oversight because many focal patch studies are conducted on a limited number of patches. Almost 40% of the studies included in this review examined species presence or abundance in fewer than 40 focal patches.

Studies were more likely to detect a response of species to within-patch factors when abundance or density were used as the response variable rather than presence–absence. Our findings support a recent community-level study on birds that found that abundance data explained more of the total variation in species–environment relationships than did presence–absence data (Cushman and McGarigal 2004b). This may be driven by the fact that for common species, which are present at most sites (e.g., present within most focal patches), variation in response will only be seen in abundance data, not presence–absence data. In addition, Cushman and McGarigal (2004b) found that the relative importance of within-patch variables increases when analyses are based on abundance data, while landscape context appears to be more important in studies that are based on presence–absence data.

We did not find an effect of landscape type on the probability of detecting a response to landscape, patch, or within-patch variables. This result is contrary to results of a previous review which found that area sensitivity (a patch-level factor) was higher in human-dominated vs. naturally fragmented systems (Prugh et al. 2008). This same review found that isolation sensitivity (a landscape-level factor) was greater in forestry systems (forest patches surrounded by clear-cuts). However, we detected no influence of landscape type on response to landscape or patch variables, although our ability to detect a difference between naturally and anthropogenically fragmented systems was limited because of the small number of studies in our review that were conducted in naturally fragmented areas.

Focal patch studies in our review employed a variety of approaches to analyze data and reach conclusions regarding the importance of landscape, patch, and within-patch factors. However, we noted several common analytical problems that could be addressed in future studies of this kind. Only 20 of the 125 studies in our review tested for spatial autocorrelation in their datasets (i.e., the residuals of regression models). Autocorrelation is problematic for classic statistical test such as regression that rely on independently distributed errors (Legendre 1993) and may lead to erroneous conclusions regarding the significance of covariates in studies of species–environment relationships (Lichstein et al. 2002; Christman 2008). Forty of the 125 studies in our review did not measure correlations between predictor variables (landscape context, patch, and within-patch factors), although the problem of multicollinearity for regression models in ecology and conservation biology has been acknowledged for quite some time (Mac Nally 2000). Finally, only 34% of studies that employed a buffer approach to measuring landscape context variables used multiple buffers. Although our own analysis showed that use of single vs. multiple buffers does not impact on the probability of finding a significant response to landscape context, use of single vs. multiple buffers may have a major effect on the strength of the response to landscape context (i.e., overall effect size). We thus list this as a potential deficiency, with the caveat that more work must be done to determine the utility of multiple vs. single buffers in focal patch studies. Use of multiple buffers may also suffer from some limitations, such as the possibility for data-dredging if a large number of buffers is employed.

Our review is limited by our use of a vote-counting procedure to synthesize results. Meta-analysis of effect sizes would provide a more rigorous way to combine information from multiple studies (Osenberg et al. 1999a). If data could be published in a form more amenable to meta-analysis, this would greatly aid future reviews. For example, focal patch studies could be commonly published with standardized effect sizes, instead of just significance tests of no effect, or with raw data available in appendices for a re-analysis of datasets in a form more amenable to meta-analytical approaches (Osenberg et al. 1999b). Additionally, more work could be done to narrow down the diverse set of landscape metrics (e.g., Cushman et al. 2008a) to just a few that are of primary relevance and that could be applied repeatedly across studies and ecosystems. Another approach would be for studies to consistently employ a variance or hierarchical partitioning approach in multi-level studies that would enable a comparison of the “amount of variation explained” across all three levels as a measure of relative influence (e.g., Cushman and McGarigal 2002; Grand and Cushman 2003; Grand and Mello 2004).

Conclusions

The literature on species response to patchiness and fragmentation already is so large and diverse that substantial opportunities exist to synthesize information and look for general trends in species response (Lindenmayer and Fischer 2006). Despite the large number of multi-level studies that have been published, relatively little work has been done to synthesize the available information to arrive at a better understanding of species response to within-patch, patch, and landscape-level characteristics. Our review of focal patch studies revealed that the probability of species responding to landscape-level, patch and within-patch factors was influenced by a variety of methodological aspects of the studies. Such study design issues rarely are discussed by authors as reasons why a particular study did not find an effect. Although focal patch studies do not represent the full range of approaches to studying fragmentation or response to spatial heterogeneity, the focal patch methodology is one of the most commonly employed approaches. Given that results of such studies are often used to inform conservation or management decisions, a better understanding of how methodology influences the conclusions of such studies may be of substantial practical importance.

Our review also confirmed the general importance of the multi-level approach in focal patch studies, as species responded at high rates to landscape, patch, and within-patch variables. Mammals responded at a particularly high rate to landscape-level variables compared to other taxa. However the degree to which this difference reflects differences in the biological response of the different taxa to habitat fragmentation, or to differences in methodology is not known. Our review also indicates that more multi-leveled studies of species response to fragmentation should focus on herpetofauna, particularly reptiles, given the under representation of these groups in our review and others (e.g., McGarigal and Cushman 2002).

Acknowledgements We thank A. Thornton for assistance with literature searches and data collection. We thank Mary Christman for assistance with statistical analyses.

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