

Patch characteristics and landscape context as predictors of species presence and abundance: A review¹

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Abstract: An increasing proportion of ecological studies examine landscape effects on the phenomena they address. We reviewed studies which simultaneously considered landscape-scale and patch-scale effects in order to answer the following question: does the inclusion of landscape characteristics as explanatory variables increase our ability to predict species presence and abundance when local (*i.e.*, habitat patch) conditions are known? The 61 studies selected cover a wide array of taxa, landscape types, and explanatory variables, but many (36%) focused on avian communities in forests fragmented by agriculture. Patch-scale variables (*e.g.*, habitat characteristics) had a significant effect on invertebrates, amphibians, reptiles, birds, and mammals in all landscape types. Landscape-scale characteristics (*e.g.*, area of suitable habitat within a certain radius of a patch) also were significant predictors of species presence and abundance for vertebrates, but not for the majority of invertebrates in the studies we reviewed. Thus, our results indicate that both patch and landscape characteristics should be included in models investigating the distribution and abundance of animals, at least for vertebrates. However, distinguishing between local (or patch) and landscape scales for particular taxa is often problematic. Analyzing movements of individuals and their influence on larger-scale population dynamics could potentially solve this dilemma, but other approaches, such as the analysis of context effects using nested sampling grids covering several different spatial scales may represent a more practical alternative. Results from this review suggest that the inclusion of landscape characteristics will enhance conservation strategies if the landscape scale is properly defined with respect to the taxon or taxa under investigation.

Keywords: landscape ecology, patches, spatial scales, species richness, abundance.

Résumé: Un nombre croissant d'études écologiques considèrent l'effet du paysage sur les phénomènes à l'étude. L'inclusion de caractéristiques du paysage dans des modèles de prédiction de présence ou d'abondance d'espèces augmente-t-elle la précision de ces prédictions lorsque les conditions locales (à l'échelle des parcelles) sont connues? Pour répondre à cette question, nous avons effectué une revue de littérature afin d'identifier des études considérant simultanément les variables à l'échelle des parcelles et du paysage. Les 61 études sélectionnées représentent plusieurs types de paysages différents et plusieurs taxons animaux, mais la majorité (36 %) portaient sur les communautés d'oiseaux de paysages forestiers fragmentés par des champs agricoles. Les variables à l'échelle des parcelles (caractéristiques de l'habitat) avaient des effets significatifs sur les invertébrés, les amphibiens, les reptiles, les oiseaux, ainsi que les mammifères, peu importe le type de paysage. Les caractéristiques du paysage (superficie d'habitat favorable compris dans un rayon donné autour d'une parcelle) avaient également un effet significatif sur la présence et l'abondance des vertébrés, mais ce n'était pas le cas pour la majorité des invertébrés. Ainsi, nos résultats indiquent que l'on devrait inclure à la fois les caractéristiques du paysage et des parcelles dans les modèles visant à prédire l'abondance et la répartition animale, au moins chez les vertébrés. La distinction entre les échelles locale et du paysage pour certains taxa et types de paysages peut s'avérer problématique. L'échelle du paysage doit être définie en fonction de l'espèce étudiée. On peut définir celle-ci en analysant les mouvements de dispersion des individus, ou encore en examinant l'influence du contexte spatial à plusieurs échelles. Cette revue de littérature suggère que l'inclusion de variables du paysage permettra d'améliorer les stratégies de conservation pour la plupart des taxons animaux.

Mots-clés: écologie du paysage, parcelles, échelles spatiales, richesse spécifique, abondance.

Introduction

Landscape ecology addresses the relationships among spatial patterns, temporal patterns, and ecological processes (Merriam, 1995). In contrast to traditional ecology, this field of ecology embraces heterogeneity instead of seeking the 'elusive homogeneous stand' (Noss, 1995; Hansson, Fahrig & Merriam, 1995). The object of study has effectively shifted from plots within stands deemed homogeneous, to complex habitat mosaics within which patches are embedded.

The recent popularity of the landscape approach has resulted in an explosion of publications on the response of

various animal taxa to landscape variables. The premise of these studies is that local phenomena cannot be fully understood without considering the influence of the surrounding landscape. Statistically, this concept could be expressed as follows: the fraction of local variability in a response variable that can be explained by variables measured at the local scale is too small to allow meaningful predictions on the species' response; one has to consider landscape-level variables. For example, one could think of a system where variables measured at specific sites (*e.g.*, atmospheric humidity, ground vegetation density, percent cover of forest canopy) are insufficient to predict the presence of a focal animal species with reasonable accuracy owing to the influence of larger-scale variables (*e.g.*, isolation from similar habitat, nature of adjacent habitat types).

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If the premise of landscape ecology is valid, then this discipline has important implications not only for the traditional practice of ecology, but also for conservation. With the pressing need for efficient conservation strategies applicable to ever larger areas, it is tempting to interpolate information available from local studies to identify priority conservation areas at broader scales. This type of approach (e.g., gap analysis; Scott *et al.*, 1993) is currently being applied across the United States to identify biodiversity 'hotspots' that require priority attention from environmental protection agencies.

A basic assumption of a mapping approach such as gap analysis is that species presence or absence can be reliably predicted from a knowledge of habitat affinities and range boundaries of each target species, and mapped using satellite imagery (Scott *et al.*, 1993). This assumption has been challenged by a number of authors (Merriam, 1988a; Hansson, Fahrig & Merriam, 1995), who point out that availability of suitable habitat is insufficient to predict species presence. Furthermore, multi-scale studies have shown that habitat associations tend to vary with the spatial scale considered (Wiens, Rotenberry & Van Horne, 1987). Landscape ecology should help assess the degree to which the context of a site influences the presence or abundance of particular taxa. Enough landscape ecological studies have now been published to allow a first investigation of the response of various animal taxa to landscape context.

In this review, we assess the influence of patch-scale and landscape-scale characteristics on the presence and abundance of species. We ask the following question: should ecologists consider landscape context in addition to patch-scale characteristics in their models of species presence and abundance? We also address methodological issues that influence our ability to make inferences from separate landscape ecological studies.

Material and methods

COMPILATION OF STUDIES

Our review was restricted to studies that simultaneously considered the effects of patch characteristics and landscape context on various response variables. Studies meeting this criterion were included in our survey, irrespective of the taxon (or taxa) and landscape type considered (*i.e.*, agricultural, heathland/agriculture, forest/agriculture, managed forest, subalpine forest/tundra, suburban, scrub). The main response variables examined in the studies were species richness, abundance, and presence/absence of focal species. We also included studies using a variety of other response variables such as indices of species diversity, home range size, and predation rate to provide a broader perspective on the sensitivity of animal taxa to patch and landscape-scale characteristics. Various explanatory variables were included in the studies we reviewed. These variables were classified as referring to either patch (area, habitat) or landscape (configuration and cover) characteristics (see Table I for details). For landscape-scale explanatory variables, we use the term 'cover' to designate the amount of a certain habitat type within a given radius around a patch, while 'configuration' refers to the particular spatial arrangement of this habitat type in the landscape.

Only variables having a significant effect ($P = 0.05$) on the response variable are shown in the summary table (Table II). Studies examining patch-scale and landscape effects on several different taxa (family or higher) were treated separately for each taxon.

The studies reviewed herein represent a wide variety of experimental designs, response and explanatory variables, and statistical approaches (e.g., multiple linear regression, logistic regression, correlation). Basic descriptive statistics for the variables measured were not provided in all studies, which prevented us from performing a meta-analysis. However, we chose to provide proportions of studies detecting significant patch-scale effects, landscape effects, or a combination of these. This type of 'vote counting' may be misleading, since it does not take into account the variation in the statistical power of the studies considered (Gurevitch *et al.*, 1992). Therefore, the proportion of studies showing similar effects should be considered with caution, as a first approximation of general tendencies across studies. We hope that future studies will be conducted or published in a manner that will make them more amenable to meta-analyses.

Results

ALL LANDSCAPE TYPES COMBINED

Nearly half (25) of the 61 studies selected for this review included birds as a focal taxon (Table II). Several invertebrate taxa, as well as amphibians, reptiles, and mammals were also represented. Potential biases arising from this non-random taxonomic selection must be kept in mind when examining results of this review.

Landscape variables were significant predictors of species response in more than half (59.0%) of the studies. Patch variables were significant predictors of species presence or abundance in nearly all (93.4%) of the studies. Both landscape and patch variables were significant predictors of response variables in 32 studies (52.5%). Landscape context was a significant predictor of invertebrate species response in only 20% of the studies. Vertebrates, however, appeared to be more sensitive to landscape context, as 79.5% of vertebrate studies reported a significant response. In the 44 studies where both configuration and cover were measured, configuration was significantly related to animal response in 47.7 % of these, whereas cover was a significant predictor in 34.1 % of the studies reviewed.

FOREST/AGRICULTURE LANDSCAPES

Forty-nine studies were conducted in forests fragmented by agriculture. In this landscape type, patch-scale variable(s) had a significant effect on the organisms studied (Table II). Vertebrates responded significantly to landscape characteristics (Figure 1). This was not the case for most invertebrate taxa, where only 16.7% of the studies detected significant landscape effects (scorpions and ants, and parasitoids of forest tent caterpillars: Table II).

Of the 12 avian studies conducted in forests fragmented by agriculture where both cover and configuration of suitable habitat were measured, birds were sensitive to configuration in eight (66.7%) of these, while cover was significant in six studies (50%). Four studies (33.3%) detected a significant

TABLE I. Variables considered as patch and landscape features in the present review of patch- and landscape-scale effects on species presence and abundance.

Patch characteristics		Landscape characteristics	
Variables	Description	Variables	Description
AREA	patch area	CONFIG	configuration, or spatial arrangement of focal habitat type (<i>e.g.</i> , isolation measures, distance to nearest patch, degree of connect edness, degree of fragmentation)
AGE	patch age (<i>i.e.</i> , stand age, pond age)		
ELEV	patch elevation		
HAB	habitat characteristics (<i>e.g.</i> , vegetation composition and structure, water and soil characteristics)		
Host ABUN	abundance of hosts (parasites)	COVER	total cover of focal habitat type (<i>e.g.</i> , amount of suitable habitat within given distance, nature of the mosaic)
ORIE	patch orientation		
PERIM	patch perimeter		
PERIM/AREA	ratio of patch perimeter to patch area		
SHAPE	patch shape		

effect of both habitat cover and configuration. Of the 17 invertebrate studies which included both cover and configuration variables, 11.8% reported a significant configuration effect, while none of the studies reported a significant effect of cover. Too few studies were conducted on the other taxa to allow a quantitative assessment of cover *versus* configuration effects.

TAXON RESPONSE IN OTHER LANDSCAPE TYPES

Of the two invertebrate studies conducted in agricultural or heathland/agriculture landscapes, one detected significant landscape effects. Significant effects of landscape context were reported in all five amphibian studies from agricultural, scrub, or suburban landscapes, and both reptile studies (from scrub or suburban landscapes). Birds were sensitive to landscape context in a study conducted in a managed forest landscape, while no such effect was detected in a subalpine forest/tundra landscape. Two out of the three mammal studies (scrub, suburban landscapes) showed significant landscape effects. Patch-scale variables were significant for

all taxa in these other landscape types. In the six studies where both cover and configuration were considered, neither characteristic clearly emerged as a more important predictor of the response variables.

Discussion

Our results indicate that landscape characteristics can be significant predictors of species presence and abundance for a wide variety of taxa and landscape types. The generality of landscape effects revealed by this review indicates that models predicting species distribution based only on local environmental conditions may be inadequate for most taxa.

The apparent inconsistency in the responses of vertebrates and invertebrates may be an artefact of the sampling designs, especially the definition of habitat patches. Patch structure may not influence an organism when habitat heterogeneity is beyond the scale it can perceive (With, 1994). When the range in patch area of a given study extends many orders of magnitude above and below the home range of the species studied (Lynch & Whigham, 1984; Askins, Philbrick & Sugeno, 1987; Robbins, Dawson & Dowell, 1989; de Vries, den Boer & van Dijk, 1995), the patch itself can actually represent a landscape attribute for the organism.

The criteria used to distinguish patches were rarely provided in the articles we reviewed. Moreover, some studies did not include descriptive statistics (*e.g.*, mean, median or standard deviation) providing information on the shape of the frequency distribution of patch area. If for a particular species, the landscape scale is considered to be somewhere between the home range and regional distribution (Dunning, Danielson & Pulliam, 1992), these statistics would be critical to distinguish local and landscape scales in studies where maximum patch area greatly exceeds the home range size of the taxon under consideration.

One would intuitively expect that patch conditions would be better predictors of species presence or abundance than landscape context (*i.e.*, habitat must be favourable in order for the species to be present). Indeed, results show that when both patch and landscape scales were considered, landscape-scale variables were the only significant predictors of species presence and abundance in only 6.6% of the studies, suggesting that their influence is complementary to that of patch characteristics. In fact, when combined with significant patch variables, landscape variables were significant

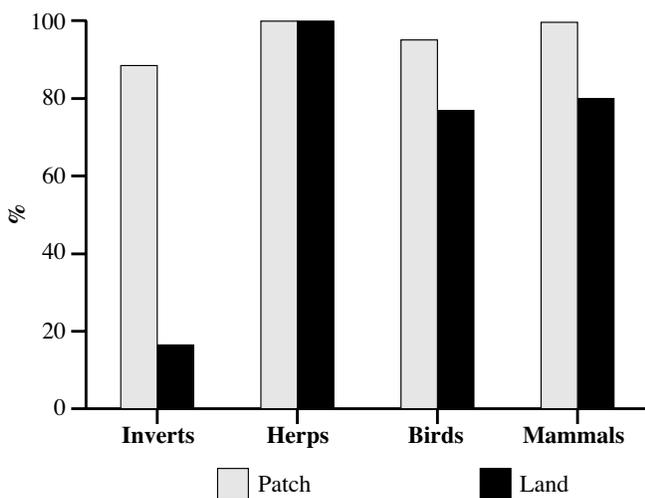


FIGURE 1. Proportion of studies conducted in the forest/agriculture landscape type reporting significant ($P < 0.05$) effects of patch and landscape characteristics on the response variable. Herps corresponds to amphibians and reptiles, while inverts designates invertebrate taxa. Inverts ($n = 18$ studies), herps ($n = 3$), birds ($n = 22$) and mammals ($n = 5$).

TABLE II. Patch and/or landscape effects on presence and abundance of animal taxa. Land corresponds to landscape scale. See Table I for meaning of other variable codes

Response variable	Taxa considered	Landscape type	Range of patch area (ha)	Explanatory variables	Results(significant predictors, $\alpha=0.05$)	Reference
Abundance	Arachnids (scorpions)	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Land (CONFIG)	Abensperg-Traun <i>et al.</i> , 1996
	Arachnids (spiders) ^o	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (HAB)	Abensperg-Traun <i>et al.</i> , 1996
	Arachnids (spiders) ^o	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (HAB)	Abensperg-Traun <i>et al.</i> , 1996
	Arachnids (spiders) ^o	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (HAB)	Abensperg-Traun <i>et al.</i> , 1996
	Amphibians	Agricultural	0.61±1.36(pres) 0.21±0.22(abs), (\bar{x} ±SD)	AREA, HAB, CONFIG, COVER	Patch (HAB) Land (COVER)	Vos & Chardon, 1998
	Birds	Forest/Agriculture	5- >1000	AREA, HAB, CONFIG	Patch (AREA, HAB), Land (CONFIG)	Lynch & Whigham, 1984
	Birds	Forest/Agriculture	0.1-3000	AREA, HAB, COVER	Patch (AREA, HAB), Land (COVER) ¹	Robbins, Dawson & Dowell, 1989
	Insects (ants)	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (HAB)	Abensperg-Traun <i>et al.</i> , 1996
	Insects (beetles)	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (HAB)	Abensperg-Traun <i>et al.</i> , 1996
	Insects (cockroaches)	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (HAB)	Abensperg-Traun <i>et al.</i> , 1996
	Insects (termites)	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (HAB)	Abensperg-Traun <i>et al.</i> , 1996
	Isopods	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (AREA)	Abensperg-Traun <i>et al.</i> , 1996
	Species richness	Mammals	Forest/Agriculture	0.05-4.45	AREA, HAB, CONFIG, COVER	Patch (HAB), Land (CONFIG, COVER)
Mammals		Suburban	0.16-20	AREA, HAB, CONFIG, COVER	Patch (HAB)	Dickman & Doncaster, 1987
Amphibians		Forest/Agriculture	0.014±0.02 (old ponds) 0.003±0.003 (new ponds) (\bar{x} ±SD)	AREA, AGE, HAB, CONFIG, COVER	Patch (AREA, HAB, AGE), Land (CONFIG)	Laan & Verboom, 1990
Amphibians		Forest/Agriculture	0.66 (\bar{x})	AREA, AGE, HAB, CONFIG, COVER	Patch (AGE), Land (CONFIG, COVER) ²	Hecnar, 1997
Amphibians and Reptiles		Suburban	0.16-20	AREA, HAB, CONFIG	Patch (AREA), Land (CONFIG)	Dickman, 1987
Amphibians, Reptiles Mammals		Scrub	< 10-200	AREA, HAB, CONFIG, COVER	Patch (AREA), Land (CONFIG)	McCoy & Mushinsky, 1994
Arachnids (scorpions)		Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (HAB)	Abensperg-Traun <i>et al.</i> , 1996
Birds		Forest/Agriculture	1.5-2600	AREA, HAB, COVER	Patch (AREA, HAB), Land (COVER) ³	Askins, Philbrick & Sugeno, 1987
Birds		Forest/Agriculture	0.02-30	AREA, HAB, PERIM, SHAPE CONFIG,COVER	Patch (AREA, HAB, PERIM), Land (CONFIG, COVER) ⁴	Bellamy, Hinsley & Newton, 1996
Birds		Forest/Agriculture	1.8-600	AREA, HAB, CONFIG	Patch (AREA, HAB) ³	Blake & Karr, 1987

TABLE II. (Continued)

Response variable	Taxa considered	Landscape type	Range of patch area (ha)	Explanatory variables	Results(significant predictors, $\alpha=0.05$)	Reference
	Birds	Forest/Agriculture	0.1-32.3	AREA, HAB, CONFIG, COVER	Patch (AREA, PERIM/AREA, HAB) Land (COVER)	Gutzwiller & Anderson, 1987
	Birds	Forest/Agriculture	0.1-32.3	AREA, HAB, PERIM/AREA, SHAPE, ORIE, CONFIG, COVER	Patch (AREA, PERIM/AREA, HAB, ORIExAREA), Land (COVER)	Gutzwiller & Anderson, 1992
	Birds ^B	Forest/Agriculture	0.1-7	AREA, HAB, CONFIG, COVER	Patch (AREA, HAB) Land (CONFIG)	Howe, 1984
	Birds ^B	Forest/Agriculture	0.1-7	AREA, HAB, CONFIG, COVER	Patch (AREA, HAB) Land (CONFIG)	Howe, 1984,
	Birds	Forest/Agriculture	5- >1000	AREA, HAB, CONFIG	Patch (AREA)	Lynch & Whigham, 1984
	Birds	Forest/Agriculture	0.7-14.5	AREA, SHAPE, HAB, CONFIG, COVER	Patch (AREA, SHAPE), Land (CONFIG, COVER) ³	McCollin, 1993
	Birds	Forest/Agriculture	0.09-304	AREA, HAB, CONFIG	Patch (AREA), Land (CONFIG)	McIntyre, 1995
	Birds	Forest/Agriculture	< 50	AREA, CONFIG, COVER	Patch (AREA), Land (CONFIG, COVER)	Opdam, van Dorp & ter Braak, 1984
	Birds	Forest/Agriculture	<1-20	AREA, SHAPE, HAB, COVER, CONFIG	Patch (HAB) Land (CONFIG, COVER)	Opdam, Risjdijk & Hustings, 1985
	Birds	Scrub	<10->200	AREA, HAB, CONFIG, COVER	Patch (AREA)	McCoy & Mushinsky, 1994
	Birds	Subalpine Forest/Tundra	0.8-5.0	AREA, HAB, CONFIG, COVER	Patch (HAB)	Turchi <i>et al.</i> , 1995
	Gastropods	Agricultural	0.0001-0.0213	AREA, HAB, CONFIG	Patch (AREA, HAB) Land (CONFIG)	Brönmark, 1985
	Insects (ants)	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Land (CONFIG)	Abensperg-Traun <i>et al.</i> , 1996
	Insects (beetles)	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (HAB)	Abensperg-Traun <i>et al.</i> , 1996
	Insects (beetles)	Heathland/Agriculture	<0.4- >1600	AREA, HAB, COVER, AGE	Patch (HAB)	de Vries, den Boer & van Dijk, 1996
	Insects (cockroaches)	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (HAB)	Abensperg-Traun <i>et al.</i> , 1996
	Insects (termites)	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (HAB)	Abensperg-Traun <i>et al.</i> , 1996
	Reptiles (lizards)	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (AREA, HAB), Land (CONFIG)	Smith <i>et al.</i> , 1996
	Mammals	Suburban	0.16-20	AREA, HAB, CONFIG	Patch (HAB), Land (CONFIG)	Dickman, 1987
Presence	Amphibians	Agricultural	0.05±0.06(pres), 0.04±0.04(abs), ($\bar{x}\pm SD$)	AREA, HAB, CONFIG, COVER	Patch (HAB), Land (CONFIG, COVER)	Vos & Stumpel, 1995
	Amphibians	Agricultural	0.61±1.36(pres), 0.21±0.22(abs), ($\bar{x}\pm SD$)	AREA, HAB, CONFIG, COVER	Patch (AREA, HAB), Land (COVER)	Vos & Chardon, 1998
	Birds	Managed forest	3.96±0.57(pres), 9.76±0.44(abs), ($\bar{x}\pm SE$)	AREA, PERIM, ELEV, CONFIG, COVER	Patch (AREA), Land (CONFIG, COVER)	Coker & Capen, 1995
	Birds	Forest/Agriculture	3-14	AREA, HAB, CONFIG	Land (CONFIG) ⁵	Enoksson, Angelstam & Larsson, 1995

TABLE II. (Concluded)

Response variable	Taxa considered	Landscape type	Range of patch area (ha)	Explanatory variables	Results(significant predictors, $\alpha=0.05$)	Reference
	Birds	Forest/Agriculture	0.1-32.3	AREA, HAB, PERIM/AREA, CONFIG, COVER	Patch (AREA, HAB, PERIM/AREA), Land (CONFIG) ⁶	Gutzwiller & Anderson, 1987
	Birds	Forest/Agriculture	3.0-129.8	AREA, HAB, CONFIG, patch-scale abundance in preceding year	Patch (AREA, HAB), Land (CONFIG), + patch-scale abundance in preceding year ⁷	Villard, Merriam & Maurer, 1995
	Mammals	Forest/Agriculture	0.05-4.45	AREA, HAB, CONFIG, COVER	Patch (HAB), Land (COVER) ⁸	Fitzgibbon, 1997
Index of species diversity	Birds	Forest/Agriculture	5- >1000	AREA, HAB, CONFIG	Patch (HAB)	Lynch & Whigham, 1984
	Birds	Forest/Agriculture	0.09-304	AREA, HAB, CONFIG	Patch (AREA), Land (CONFIG)	McIntyre, 1995
	Insects (ants)	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (HAB)	Abensperg-Traun <i>et al.</i> , 1996
	Insects (beetles)	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (HAB)	Abensperg-Traun <i>et al.</i> , 1996
	Insects (termites)	Forest/Agriculture	0.5-174	AREA, HAB, CONFIG, COVER	Patch (HAB)	Abensperg-Traun <i>et al.</i> , 1996
Index of biotic integrity	Fish	Forest/Agriculture	n/a	HAB, COVER	Land (COVER)	Roth, Allan & Erickson, 1996
Home range size	Mammals	Forest/Agriculture	0.8-32.2	AREA, COVER, SEASON, SEX, ABUN	Patch (AREA), +SEASON	Sheperd & Swihart, 1995
Nest abundance	Birds	Forest/Agriculture	0.1-32.3	AREA, HAB, PERIM/AREA, CONFIG, COVER	Patch (AREA, HAB) ⁹	Gutzwiller & Anderson, 1987
	Birds	Forest/Agriculture	0.1-32.3	AREA, HAB, PERIM/AREA, SHAPE, ORIE, CONFIG, COVER	Patch (AREA, ORIExAREA)	Gutzwiller & Anderson, 1992
	Mammals	Forest/Agriculture	0.55-13.78	AREA, HAB, CONFIG, COVER	Patch (AREA, HAB), Land (CONFIG, COVER)	Verboom & Apeldoorn, 1990
Predation	Birds (artificial nests)	Forest/Agriculture	7->50	AREA, HAB, CONFIG, COVER	Patch (HAB), Land (CONFIG) ¹⁰	Huhta, Mappes & Jokimäki, 1996
	Mammals	Forest/Agriculture	0.2-30	AREA, PERIM, CONFIG, COVER	Patch (PERIM/AREA), Land (CONFIG, COVER)	Brown & Litvaitis, 1995
Parasitism	Insects (dipteran parasitoids on moths)	Forest/Agriculture	n/a	COVER, Host ABUN	Patch (Host ABUN), Land (COVER)	Roland & Taylor, 1997

¹ COVER was significant in 40 of 75 species investigated² data analyzed separately each year, COVER and CONFIG significant both years³ slight variations among ecological classes⁴ COVER and CONFIG significant in different ecological classes⁵ of 6 spp., 3 were significantly related to CONFIG⁶ of 4 spp., 3 were related to AREA, 2 to HAB, 1 to CONFIG⁷ of 4 spp., 3 were significantly related to CONFIG⁸ of 2 spp., 1 was significantly related to COVER⁹ of 2 spp., 1 significantly related to HAB¹⁰ CONFIG was significant for nests close to an edge^a families analyzed separately^b bird assemblages on different continents analyzed separately

predictors of response variables in half of the studies reviewed. This raises the issue of the interaction among patch-scale and landscape-scale variables, as certain patch characteristics for a given taxon might enhance landscape effects (and *vice versa*).

Using a simulation model, Fahrig (1997) found that habitat loss had a greater effect on the probability of population extinction than habitat configuration. In our review, a slightly greater proportion of studies that measured both cover and configuration reported significant configuration effects on animal response variables (*i.e.*, 47.7% versus 34.1% for cover). This trend can be seen for birds and invertebrates in forests fragmented by agriculture.

Conservation strategies tend to be more difficult to design and implement as the spatial scale increases due to the multiple land ownership that characterizes large territories (Arnold, 1995). In spite of this, Noss (1983) suggested that management of the landscape mosaic would provide a more efficient conservation strategy than the management of single sites. This review supports the notion that efficient management of vertebrate species should be conducted both at the patch and landscape scales.

Landscape conservation planning requires the definition of ecologically-meaningful landscape units. Danielson (1992) and With (1994) proposed to first define the 'perceptive resolution' of an organism, or to determine the scales over which the organism perceives the landscape as being heterogeneous, in order to present an organism-centered view of the landscape. Furthermore, a species may consider a landscape to be fragmented whereas for another species it is continuous, depending on its response to factors of the environment and the spatial extent of its movements during its life cycle (Diffendorfer, Gaines & Holt, 1995).

To determine the perceptive resolution of an organism, one can record movement patterns of individuals and their response to habitat heterogeneity (With, 1994). Movement patterns can then be analyzed using fractals to detect at what scale the species perceives and responds to heterogeneity (With, 1994). However, monitoring movement patterns of individuals can become impractical for some species, especially those (*e.g.*, small songbirds) whose movement range is extensive, and for which current technology does not yet permit long-term tracking. For such species, the use of nested sampling grids (*e.g.*, Roland and Taylor 1997) may be useful in revealing patterns of response to habitat heterogeneity over a variety of spatial scales. This approach helps the researcher to identify scales where landscape context is relevant to local phenomena.

This review, although qualitative in nature, suggests that the consideration of landscape effects in ecological studies is not a mere bandwagon, but represents an important progress toward the prediction of species presence and abundance. Furthermore, we submit that the consideration of landscape effects will greatly increase the efficiency of conservation strategies, as suggested by many authors (Noss, 1983; Urban, O'Neill & Shugart, 1987; Merriam, 1988b), if the landscape scale is properly defined with respect to the taxon or taxa under investigation.

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