Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds

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It is important to understand the relative effects of landscape habitat loss, habitat fragmentation, and matrix quality on biodiversity, so that potential management options can be appropriately ranked. However, their effects and relative importance may change with the size of the landscape considered because the multiple (and potentially conflicting) ecological processes that are influenced by landscape structure occur at different spatial scales (e.g. dispersal, predation, foraging). We estimated the relative effects of habitat loss, habitat fragmentation, and matrix quality (measured as the amount of forest, the proportion of forest area contained in large core forests, and the density of roads respectively) on fragmentation-sensitive forest birds in southern Ontario, Canada using a range of landscape sizes (0.8–310 km^2). We used three complementary statistical approaches to estimate relative effects of these correlated landscape factors – 1) multiple regression, 2) information theoretic (AIC) estimates of the most parsimonious model, and 3) multi-model inference to average effects across all supported models. We controlled for spatial autocorrelation, local habitat, roadside sampling bias, time of day, season, habitat heterogeneity, and the interaction between the effects of habitat amount and fragmentation. We found that relative effects of habitat amount and fragmentation were scale dependent; habitat amount had a consistently positive effect that was consistent over more than two orders of magnitude in landscape area ($\sim$1–300 km^2). In contrast, the effects of habitat fragmentation depended on the size of the landscape considered. Indeed, for veery *Catharus fuscescens*, habitat fragmentation had positive effects at one scale and negative effects at another. The effects of matrix quality were generally weak and changed little with scale. For the number of fragmentation sensitive species and the presence of veery, habitat amount was most important in large landscapes and habitat fragmentation in small landscapes but for the presence of ovenbird *Seiurus aurocapilla*, habitat amount was most important at all scales.

The amount of habitat in a landscape affects biodiversity through multiple processes including reproduction, mortality, dispersal, local extinction, and species interactions operating at various spatial and temporal scales (Addicott et al. 1987). Modelling and empirical studies (Rosenzweig 1995, Fahrig 2003, Ewers and Didham 2006) have shown that the effects of habitat amount on biodiversity are consistently positive and strong across regions, habitats, and taxa.

In addition to the direct effects of habitat loss, habitat fragmentation per se (i.e. breaking apart of habitat, independent of habitat amount) may affect biodiversity, particularly in regions with < 20–30% habitat cover (Andren 1994, Fahrig 1998). In empirical studies, the effects of habitat fragmentation per se (hereafter fragmentation) are about as likely to be positive as negative (Fahrig 2003). Negative effects may arise from a reduction in the proportion of patches that are large enough to support stable or productive (source) populations (Nol et al. 2005), or from negative edge effects (Chalfoun et al. 2002). Positive effects of fragmentation may arise through a reduced

probability of simultaneous extinctions of local populations (den Boer 1981), reduced inter-patch distances (Fahrig 2003), increased landscape complementation (access to resources in the matrix, Dunning et al. 1992, Law and Dickman 1998), or increased immigration rate (Bowman et al. 2002).

Beyond the amount and fragmentation of habitat in the landscape, the quality of the intervening space (the matrix) can also strongly affect biodiversity (Dunford and Freemark 2005). Matrix quality can influence species' abundances and distributions in suitable habitat through several processes (Kupfer et al. 2006): mortality during dispersal (Fahrig 2002); changes in movement, which in turn affect patch colonization (Ricketts 2001); influences on microclimate within habitat patches (Burke and Nol 1998); and changes in predators and parasites within the matrix that influence survival and reproductive success within habitat patches (Porneluzi and Faaborg 1999, Chalfoun et al. 2002).

Habitat amount, habitat fragmentation and matrix quality may all affect biodiversity but the relative effects

of these three landscape factors may be scale-dependent (Fahrig 1998, Krawchuk and Taylor 2003). Processes such as reproduction, dispersal success, mortality in the matrix, foraging, nest predation, and nest parasitism occur at different rates and within different ecological neighbourhoods (Addicott et al. 1987). Therefore, the effects of these processes should be apparent at different spatial scales. If fragmentation has positive effects on some of these processes and negative effects on others, then the net effect of fragmentation may be scale dependent. For species richness, the net effect of fragmentation on multiple processes may also depend on scale if different species respond at different scales. In contrast, the effects of habitat amount should be consistently positive because although habitat amount also represents multiple ecological processes, these processes all have positive effects. Similar to habitat amount, increasing matrix quality should have exclusively positive effects and should therefore be less scale dependent than fragmentation.

Assessing how the relative effects of landscape factors change with scale is vital to inform conservation decisions. Habitat amount, fragmentation, and matrix quality may be manipulated independently of one another to some degree (e.g. changes in fragmentation or matrix quality, for a given amount of habitat). Therefore, assessing the relative importance of these landscape factors allows the ranking of alternative management options by their relative potential benefits to biodiversity (Sutherland et al. 2004). However, if the relative effects are scale-dependent, then the relative ranking of potential management actions will depend on the spatial jurisdiction of the managing body (e.g. landowner, municipality, regional, or national organization) and the spatial extent of a management plan.

In this study we asked the question: do the effects of habitat amount, habitat fragmentation, and matrix quality on fragmentation-sensitive forest birds depend on the size of the landscape considered (i.e. are they scale-dependent)? We predicted that the effects of habitat amount and matrix quality would be consistently positive across all scales and that the effects of habitat fragmentation would be more scale-dependent.

Methods

Study area

The study area was the 201 000 km^2 portion of North American Bird Conservation Region 13 that is located in Ontario, Canada (hereafter, BCR 13, Fig. 1). The study area is entirely within the Mixedwood Plains ecozone (Ecological Stratification Working Group 1996). This area is heavily affected by human activity, is dominated by agriculture and includes the country's largest urban centre. Forested, agricultural, and urbanized areas account for approximately 27, 60, and 8% of the landcover in the region, respectively. Agricultural activities in the region are diverse, ranging from low intensity pasture, and hay production to high intensity row crops such as soy and corn. Most of the larger, continuous areas of forest are near the northern boundary of the study area and to the south, near the shores of the Great Lakes. Forests are primarily

mixed deciduous-coniferous throughout the study area; coniferous species dominate in the more northern parts while deciduous species dominate in the south.

Predictor variables

We measured 3 primary predictor variables using ArcGIS 9.2 (ESRI, Redlands, CA), in landscapes of five different radii – 0.5, 1.0, 2.0, 5.0, and 10.0 km – centered on the plots where bird surveys were conducted. All predictors were standardized to a mean of 0 and a standard deviation of 1 to allow comparison of regression coefficients. The three predictor variables were: 1) habitat amount (Forest) – the percentage of the landscape area that was forested; 2) core forest (Core) – the percent of forest cover that is >100 m from a non-forest edge and >90 ha in total size (i.e. a subset of the area within Forest that represents large, compact forest patches, which are thought to sustain source populations of these fragmentation sensitive species, Nol et al. 2005); and 3) road density (Road) – the summed length per unit area of all paved roads within the landscape (km km^{-2}), log transformed so that it was normally distributed. Road data were from the 2005, Canadian National Topographic Data Base. These variables were chosen to represent the three key landscape factors; 1) habitat amount (Forest), 2) habitat fragmentation (Core), and 3) matrix quality (Road).

We used a binary classification of habitat/non-habitat, which combined all forested landcover types into a single habitat class. For each species, this definition of habitat is likely an over-simplification of their habitat requirements; however, since most recommendations for landscape management refer to the fragmentation or loss of forests in general (Ontario Partners in Flight 2005) and since we were also interested in a group of fragmentation-sensitive species, we feel this broad habitat definition is the most appropriate. Although, it is possible that a broad habitat definition may underestimate the absolute importance of fragmentation effects for individual species (Betts et al. 2006); this potential bias would be independent of the landscape size and therefore, will not affect our analysis of the change in relative effects with scale.

We used core forest to represent habitat fragmentation because it represents what are likely the two most important fragmentation-related mechanisms affecting forest birds in this region: 1) the presence and size of source populations in large areas of continuous forest (Nol et al. 2005) and 2) the inverse of the population's exposure to negative edge effects. These two mechanisms should combine for a strong positive effect of increasing percent core forest on fragmentation sensitive forest birds.

Road density was chosen to represent matrix quality because it both directly represents the potential increase in mortality due to collisions with vehicles and indirectly represents the increased mortality from collisions with human structures that are associated with roads (Erikson et al. 2005) as well as the increases in human activity, density of cats and other synanthropic predators, and human population density in areas with high road density. Agriculture is the dominant matrix type (i.e. non-forest landcover) in this region but spatially explicit measures of
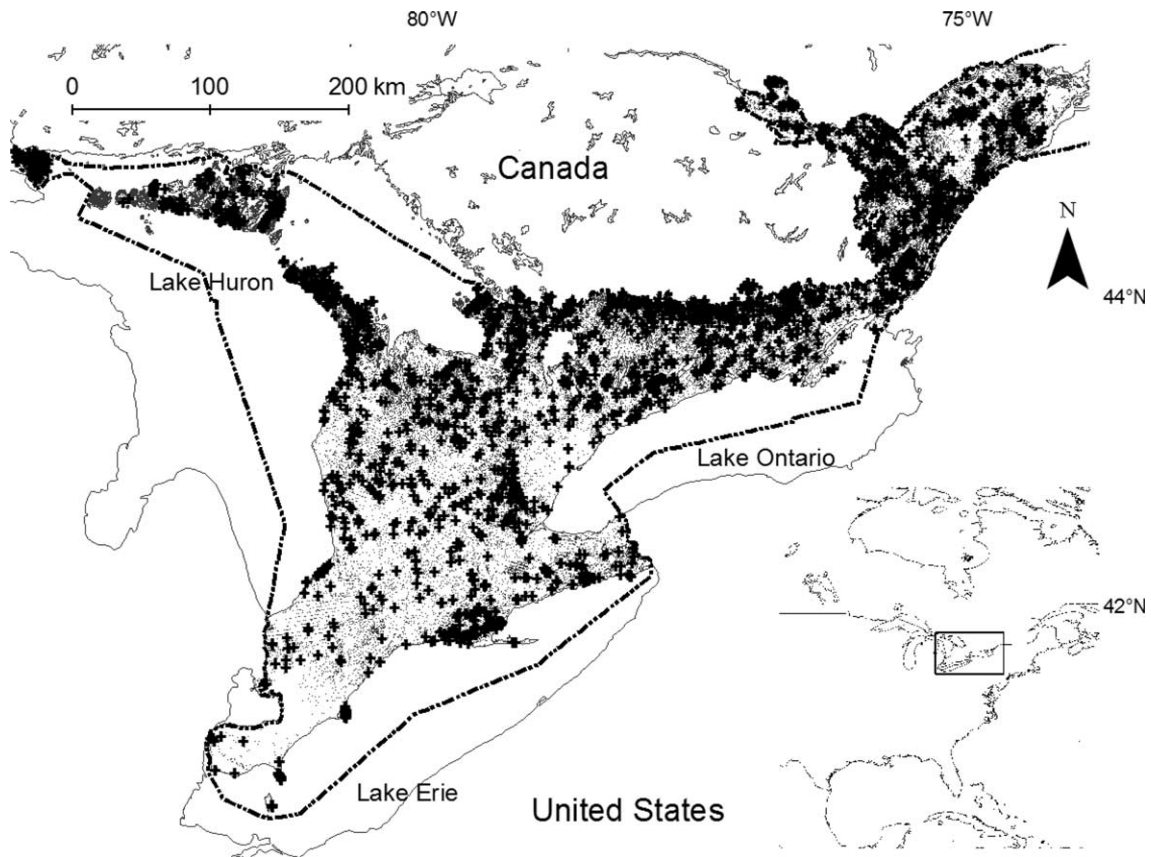
Figure 1. Distribution of forest cover (grey areas) and 2951 point count sampling stations with >95% forest cover inside the 100 m radius sampling area (crosses), within the study area (portion of Bird Conservation Region 13 in Ontario, Canada).

agricultural intensity are not available for our study area. Therefore, although it is possible that our analysis underestimates the absolute importance of matrix quality, our measure provides an unbiased estimate of how the relative importance of matrix quality varies across scales.

We used land cover data from the Ontario Land Cover Database (OMNR 1998), a Landsat TM-derived land cover classification with a 0.09 ha pixel resolution. The original 28 landcovers were reclassified into a binary habitat/non-habitat map where habitat was defined as forest cover, including 9 treed landcover types (including coniferous, deciduous, and mixed forest types). There has been little change in the distribution of forest cover and agriculture since the landcover data were collected in the mid-1990s (Dingle-Robertson 2007); however, some urban areas have expanded. Therefore, we updated the re-classified landcover using more recent information for urban development (OMNR 2007). The large size of our study area allowed us to sample larger landscapes, a greater range in variation for each landscape variable, and a more similar range of variation across all spatial scales than is usually possible (compare Dunford and Freemark 2005, Renfrew and Ribic 2008).

Response variables

We used Poisson regression to model the species richness of fragmentation-sensitive forest birds and logistic regression to model the occurrence (observed vs unobserved) of the two most common fragmentation-sensitive species (ovenbird *Seiurus aurocapilla* and veery *Catharus fuscescens*) as functions of habitat amount, habitat fragmentation, and matrix quality. These fragmentation-sensitive species included 13 species (ovenbird, veery and 11 others, Table 1), whose ranges overlap the entire study area and that have, in previous studies, shown significant negative responses to forest fragmentation after controlling for forest amount. We used the richness of this functional group – fragmentation-sensitive species – to represent the cumulative effects of increasing fragmentation (i.e. a decrease in Core) on forest bird diversity, because these species have shown similar responses to increasing forest fragmentation. We chose this cumulative response over individual species' responses for the remaining 11 species for two reasons. First, a Poisson regression model has greater statistical power than each of the single-species logistic models for the less common species, which maximizes our ability to measure changes in effects across scales. Second, because any management or modification of forest fragmentation in a landscape will presumably affect all of these sensitive species, their cumulative response is clearly important in a management/conservation context.

Forest bird data were taken from the point count database of the second Ontario Breeding Bird Atlas (OBBA). Point counts were conducted during peak breeding seasons from 2001 through 2005, by skilled volunteer observers using a standardized methodology (OBBA 2001).

Table 1. Species with previously demonstrated, significantly negative responses to increasing forest fragmentation, independent of the effects of habitat loss. *Four species showed significantly negative responses in more than one study.

Species	Response to fragmentation	Reference	Landscape size used in study (km^2)
Black-throated green warbler *Dendroica virens*	Positive effect of core area and patch size after controlling for habitat amount	Austen et al. 2001	12
Hairy woodpecker *Picoides villosus*	Negative effect of edge length	Villard et al. 1999	6
Hermit thrush *Catharus guttatus*	Negative effect of principle component representing increasing fragmentation	Trzcinski et al. 1999	100
Least flycatcher *Empidonax minimus*	Negative effect of edge length	Villard et al. 1999	6
Northern waterthrush *Seiurus noveboracensis*	Positive effect of core area and patch size after controlling for habitat amount	Austen et al. 2001	12
Ovenbird *Seiurus aurocapilla*	Positive effect of patch size after controlling for habitat amount	Betts et al. 2006	12
Pine warbler *Dendroica pinus*	Positive effect of patch size after controlling for habitat amount	Austen et al. 2001	12
Pileated woodpecker* *Dryocopus pileatus*	Positive effect of core area / Negative effect of mean nearest neighbour distance	Austen et al. 2001 / Villard et al. 1999	12 / 6
Purple finch *Carpodacus purpureus*	Negative effect of principle component representing increasing fragmentation	Trzcinski et al. 1999	100
Scarlet tanager* *Piranga olivacea*	Positive effect of patch size after controlling for habitat amount / Negative effect of mean nearest neighbour distance	Austen et al. 2001 / Villard et al. 1999	12 / 6
Veery* *Catharus fuscescens*	Positive effect of patch size after controlling for habitat amount / Negative effect of edge length	Austen et al. 2001 / Villard et al. 1999	12 / 6
Yellow-bellied sapsucker* *Sphyrapicus varius*	Positive effect of core area / Negative effect of principle component representing increasing fragmentation	Austen et al. 2001 / Trzcinski et al. 1999	12 / 100
Yellow-rumped warbler *Dendroica coronata*	Negative effect of principle component representing increasing fragmentation	Trzcinski et al. 1999	100

All birds seen or heard were recorded within a radius of 100 m, during a single 5 min period. Counts were conducted between dawn and 5 h after sunrise and only in suitable weather. Count locations for the atlas project either followed a stratified-random distribution along roads within cells of a 10 × 10 km grid (roadside counts) or were chosen by observers to ensure a representative sampling of landcover types with limited road access (off-road counts). Each location was sampled once over the 5 yr atlas project.

To account for the effects of local habitat on bird distribution and detectability (i.e. probability of detecting a species given that it is present), we standardized the area of habitat within the point count plot and statistically controlled for differences between roadside and off-road counts. To standardize the area of forest sampled within each point count, we selected 2951 point counts (from among the >30 000 in our study area from the atlas database), for which >95% of the 100 m radius count area was forest (i.e. point counts were centered ca 100 m or more from a forest edge). This selection also controlled for potential variation among sites in species detectability because although detection probabilities are never = 1.0, they are generally similar among different forest types (Lichstein et al. 2002) and they are generally very high for most of the species tested here (Farnsworth et al. 2002). In addition, we tested for and found no relationship between the forest types inside the point counts and our landscape predictors, so that even if detectability had varied with forest type, it would not confound our analysis. Finally, we statistically controlled for differences between roadside

(n = 1221) and off-road counts (n = 1730), which should account for most other detectability or local habitat effects on the bird observations.

Although we have done much to limit any potential bias differential detectability among species may still confound our analysis because we cannot directly measure it with our dataset. However, no dataset currently exists that would allow us to test our hypothesis and concurrently account for varying detection probabilities. We modelled the unadjusted count of fragmentation-sensitive species observed at each count location. All methods for estimating detectability require multiple sampling events (either in space or time, Boulinier et al. 1998, Mackenzie et al. 2006). Combining observations from multiple locations in our dataset would make it impossible to test our hypothesis of scale dependence. Data of multiple counts over time at the same locations (such as the North American Breeding Bird Survey) simply do not exist with comparable spatial resolution (∼3000 forested count locations) and extent (spread across 210 000 km^2). Our estimate of the number of fragmentation sensitive species is better thought of as an index of the species present at individual sampling locations and not an estimate of the pure species richness of the bird community.

Statistical analyses

Estimating the relative effects of correlated predictor variables in a regression model requires a trade-off between statistical power and accurate estimates of effect strength.

Including correlated predictors increases type II errors by increasing the standard error of partial coefficients (Neter et al. 1990). However, removing predictors simply because they are highly correlated with others can lead to biased coefficient estimates and poor model fit (Neter et al. 1990, Smith et al. 2009). In addition, statistical approaches to dealing with correlations among landscape predictors, such as residual regression and variance partitioning approaches give biased estimates of relative importance (Smith et al. 2009). We have included correlated predictors because they represent distinct ecological mechanisms that likely influence forest birds in this region and removing one would lead to biased estimates of relative importance for the remaining predictors. We believe it is more appropriate to use a less powerful but unbiased design than to increase statistical power at the cost of biased and inaccurate estimates of effect strength.

We used three complementary analyses to ensure our results were not overly dependent on statistical artefacts (Koper et al. 2007, Smith et al. 2009). We compared results from 1) the global model, 2) the most parsimonious model, and 3) the average of all supported models in a multi-model inference framework (Burnham and Anderson 2002, hereafter MMI). For the global model, we compared the partial regression coefficients and statistical significance within a model including all three predictors, an interaction term between amount and fragmentation (Forest × Core), and the covariates listed in the following paragraph. For the most parsimonious model, we compared the partial regression coefficients of the model with the lowest AIC from among all possible combinations of the 3 predictors and the interaction (the covariates were retained in all models). For the MMI analysis, we compared the summed Akaike weights of each predictor and the averaged partial regression coefficients from all models within a 95% confidence set. Similar results from a global model, the most parsimonious model, and averaged results for all supported models give us extra confidence that our estimates of relative importance are meaningful (MacNally 2000). For example, if the coefficient of one variable changes a great deal with the inclusion or exclusion of another, differences among the results of the three approaches will reflect that variation. We chose these three approaches because they are relatively familiar statistical tools and with the exception of summed Akaike weights, they give unbiased estimates of relative effect strength even with highly correlated predictors (Smith et al. 2009). The partial coefficients from all three analysis methods can be directly compared because the original predictors were standardized to a mean of 0 and a standard deviation of 1.

We have presented plots only for the averaged coefficients from the MMI analyses because results from the three statistical analyses were so similar that the remaining plots of coefficients from the global and the most parsimonious models were almost indistinguishable. In addition, we have not reported confidence intervals associated with the coefficients in the most parsimonious models because they are very similar to those from the averaged MMI analyses that are shown in the plotted results.

Controlling for spatial autocorrelation and other covariates

We controlled for the effects of spatial autocorrelation, roadside survey biases, time of day, date, year, and habitat heterogeneity by including predictors representing these effects in all analyses (including all candidate models in the MMI and most parsimonious analyses). We controlled for the effects of spatial autocorrelation by using spatial eigenvector mapping to remove all significant autocorrelation from the residuals of global models (Griffith and Peres-Neto 2006). We also controlled for differences between off-road and roadside counts and for effects of time of day, date (both a linear and quadratic term), and differences among years. Finally, we controlled for habitat heterogeneity (number of forest classes) because it may influence our response variables through mechanism such as landscape complementation for individual species (Dunning et al. 1992) or habitat diversity for species richness, which act independently of habitat amount, fragmentation, or matrix quality. All of these covariates were somewhat correlated with at least one of the main predictors at some of the spatial scales. They were therefore included in all models at all scales to allow us to compare the primary predictors under similar conditions across scales.

Results

Relative importance across scales

The effects of habitat amount were positive and excluded zero from the confidence intervals for all three response variables at almost all scales (Table 2). Forest amount became more important as a larger landscape was considered and was the most important predictor for all response variables in landscapes > 500 m in radius (Fig. 2–4). Habitat amount was present in the most parsimonious model at all scales and for all three response variables (Table 2). In fact, habitat amount was present in all supported models (summed Akaike weight = 1) for all responses and at all scales except for veery in 500 m landscapes (Table 3). Even in this case, when the average effect of amount was not particularly strong, its interaction with the effects of fragmentation (Core) was strong, which indicates that habitat amount may still be important in these small landscapes (Fig. 2).

The effects of fragmentation (Core) were more variable across scales and among responses. The relative ranking of fragmentation with other predictors changed with scale; for the number of fragmentation sensitive species and for veery, core forest area was the most important predictor at very fine scales (500 m radius, larger coefficients in the global and most parsimonious models, Table 2, and larger averaged coefficients across all supported models, Fig. 2 and 4, as well as higher Akaike weights, Table 3) but was less important at broader scales (2–10 km radius). For ovenbird occurrence, Core was not important at any scale (Table 2, 3). For veery, even the qualitative effect of fragmentation was scale dependent; core forest had a strong

Table 2. Standardized coefficients from the most parsimonious model (lowest AIC) within landscapes of 5 different sizes. Predictors included 3 landscape variables – total amount of forest (Forest), the proportion of forest area within the core of large forests (Core), and the density of roads (Road) – plus the Forest × Core interaction. Models predicted the number of fragmentation sensitive species observed (Poisson regression) and the occurrence (logistic regression) of ovenbird and veery at 2951 forested point counts in southern Ontario Canada. Candidate models included all 8 possible combinations of the 3 landscape predictors, plus the Forest × Core interaction. All models included covariates controlling for spatial autocorrelation, time of day, season, habitat heterogeneity, and roadside survey biases.

	Landscape radius	Standardized regression coefficients				AIC	Weight
		Forest	Core	Road	Core × Forest		
Number of	500 m	0.06	0.10	−0.04	−0.08	8256	0.893
fragmentation	1 km	0.12	0.05	−0.03	−0.06	8256	0.683
sensitive	2 km	0.24	0.002	−0.07	−0.08	8253	0.980
species	5 km	0.30	0.01	−0.06	−0.07	8239	0.871
	10 km	0.31	0.05	−0.05	−0.07	8206	0.613
Ovenbird	500 m	0.23		−0.07		3879	0.216
	1 km	0.26				3877	0.234
	2 km	0.41	−0.14			3866	0.230
	5 km	0.53				3869	0.238
	10 km	0.55				3864	0.184
Veery	500 m	0.10	0.15			2970	0.246
	1 km	0.22	−0.02		−0.16	2960	0.602
	2 km	0.37	−0.19	−0.08	−0.22	2943	0.555
	5 km	0.54	−0.27	−0.20	−0.13	2942	0.458
	10 km	0.49	−0.22	−0.20		2937	0.376

positive effect at fine scales and a strong negative effect at broad scales (Fig. 4).

The effects of matrix quality were relatively weak and not strongly scale dependent. The standardized coefficient for road density was generally smaller than for either habitat amount or fragmentation (Fig. 2), it was absent from the most parsimonious model for ovenbird at all scales, for veery at two of the five scales (Table 2), and was almost always missing from one or more of the supported models (summed Akaike weight <1, Table 3). Road density was somewhat important for the number of fragmentation sensitive species and for this response, its effects were generally consistent across scales. It had a consistently negative effect and it was included in the most parsimonious model at all scales (Fig. 2, Table 3).

In all cases, the interaction between habitat amount and fragmentation (Forest × Core) had the expected qualitative effect; increasing core forest had a stronger positive effect when amount was low (Fig. 2). The interaction was only scale dependent for veery. It was important in landscapes 1–5 km in radius (Fig. 4), where it was included in the best model (Table 2) and its summed Akaike weight was highest (0.91–1, Table 3) but not important in very small or very large landscapes (Fig. 4). For the number of species it was important at all scales (Fig. 2, included in the best model and most of the supported models at all scales Table 2 and 3). For ovenbird it was not important at any scale (Fig. 3, Table 2, 3).

Predictor variance and covariance

The overall correlation among the predictors increased slightly at broader landscape scales (Table 4). Average VIF was <3 at all scales and VIF for single predictors was always <4 (VIF >10 indicates severe collinearity, Neter et al. 1990). The increase in collinearity in larger landscapes is also reflected in the larger error bars around coefficient estimates at broad scales (Fig. 2). Most of the increasing collinearity with scale (and therefore the increasing error around coefficient estimates) seems to be due to an increase in the strength of correlation between Core and Road (from −0.19 to −0.62). We are confident that this increasing correlation has not strongly influenced our results because the level of correlation is not particularly high even in large landscapes and the confidence limits around the coefficients for Core and Road do not increase with scale at similar rates (Fig. 2–4).

Discussion

Habitat amount in the surrounding landscape had an important and consistently positive effect on forest birds regardless of the size of the landscape considered but the strength of the effect increased with the size of the landscape. For most of the scales tested here, our results agree with previous studies, which have shown that habitat amount is more important than fragmentation in determining species distributions (Betts et al. 2006, Smith et al. 2009; and others reviewed in Fahrig 2003). The novel contribution of this study is that the positive effect of habitat amount (at least for fragmentation sensitive forest birds) is consistent over more than one order of magnitude in landscape radius (0.5–10 km) or more than two orders of magnitude in landscape area ($\sim$1–300 km^2) but this is not the case for the effects of fragmentation. Even considering the interaction between habitat amount and fragmentation, which complicates a simple interpretation of relative importance, the effects of habitat amount were more important and more consistent across a wide range of values of fragmentation; while the effects of fragmentation tended to be weaker or even change direction depending on the value of habitat amount (e.g. for species richness, the effects of core forest were positive at low levels of forest
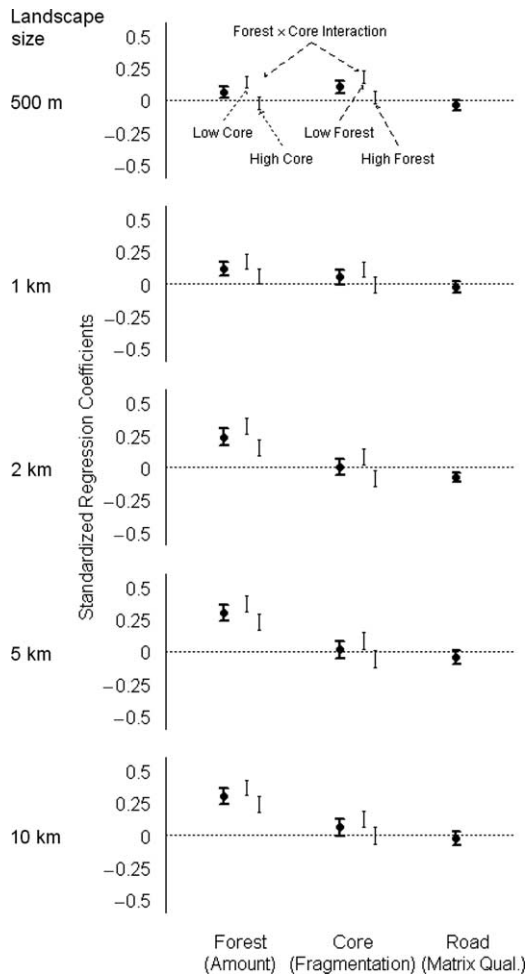
Figure 2. Poisson regressions coefficients for the effects of the total amount of forest (Forest), the proportion of forest area in large core forests (Core), and the density of roads (Road) in landscapes of 5 different radii on the number of fragmentation sensitive bird species observed at forested point counts in southern Ontario Canada. Points are the standardized, averaged coefficients (weighted by the model's Akaike weight) from all models in a 95% confidence set and error bars are the associated unconditional confidence limits. An interaction between Forest and Core, is demonstrated by the error bars without points. These error bars represent the confidence limits around the coefficient for Forest at low and high levels of Core (−1 and +1 standard deviation of Core) and for Core at low and high levels of Forest (−1 and +1 standard deviation of Forest). All models accounted for the effects of spatial autocorrelation, time of day, season, surrounding habitat diversity, and roadside survey biases.
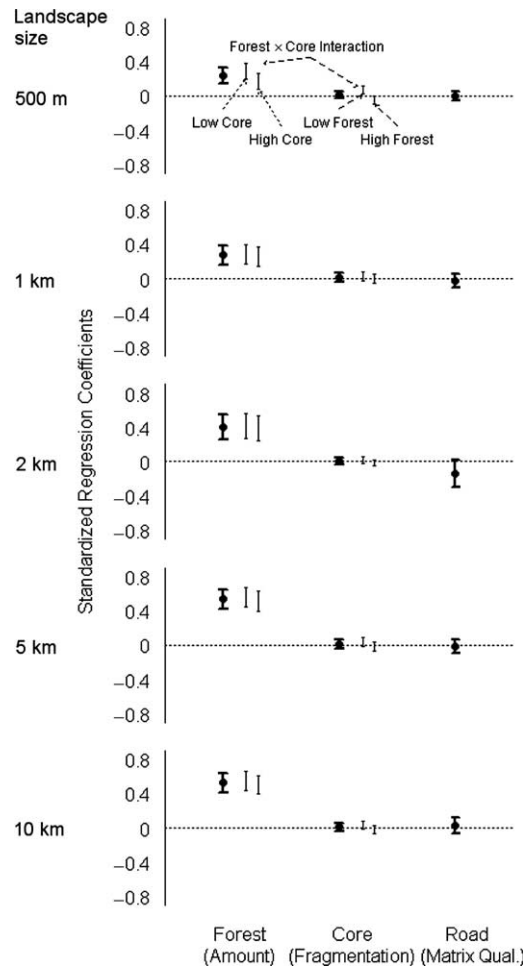
Figure 3. Logistic regressions coefficients for the effects of the total amount of forest (Forest), the proportion of forest area in large core forests (Core), and the density of roads (Road) in landscapes of 5 different radii on the occurrence of ovenbird at forested point counts in southern Ontario Canada. Points are the standardized, averaged coefficients (weighted by the model's Akaike weight) from all models in a 95% confidence set and error bars are the associated unconditional confidence limits. An interaction between Forest and Core, is demonstrated by the error bars without points. These error bars represent the confidence limits around the coefficient for Forest at low and high levels of Core (−1 and +1 standard deviation of Core) and for Core at low and high levels of Forest (−1 and +1 standard deviation of Forest). All models accounted for the effects of spatial autocorrelation, time of day, season, surrounding habitat diversity, and roadside survey biases.

amount and neutral or negative at high levels, Fig. 2). With a correlative study such as this it is difficult to tell whether the process(es) through which habitat amount influences biodiversity are constant across these scales or that the processes change but their resultant effects are constant; however, the general implications are clear – a reduction in habitat amount will likely have a negative effect on fragmentation sensitive forest bird species at all these scales.

As predicted, fragmentation effects depended more on landscape scale. Our results lend support to the hypothesis that the multiple processes through which fragmentation

affects populations and communities act at different scales and therefore; the relevant positive, negative, or neutral effects of fragmentation are evident at the different scales (Addicott et al. 1987). The size of the landscape considered affected the relative importance, absolute importance (significance, inclusion in the best model), and even the qualitative effect of increasing fragmentation. Interestingly, the effects of fragmentation changed with scale for a group of forest bird species that are generally considered sensitive to the effects of fragmentation. If fragmentation sensitive species can appear tolerant of fragmentation at some spatial
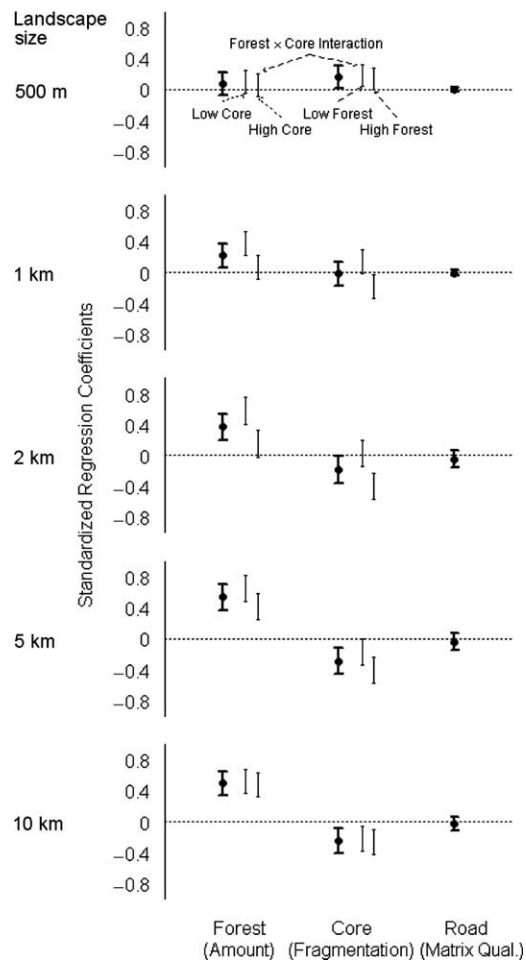
Figure 4. Logistic regressions coefficients for the effects of the total amount of forest (Forest), the proportion of forest area in large core forests (Core), and the density of roads (Road) in landscapes of 5 different radii on the occurrence of veery at forested point counts in southern Ontario Canada. Points are the standardized, averaged coefficients (weighted by the model's Akaike weight) from all models in a 95% confidence set and error bars are the associated unconditional confidence limits. An interaction between Forest and Core, is demonstrated by the error bars without points. These error bars represent the confidence limits around the coefficient for Forest at low and high levels of Core (-1 and $+1$ standard deviation of Core) and for Core at low and high levels of Forest (-1 and $+1$ standard deviation of Forest). All models accounted for the effects of spatial autocorrelation, time of day, season, surrounding habitat diversity, and roadside survey biases.

scales, it suggests that species previously thought to be tolerant may need to be reassessed. Further, if the direction of a species' response to habitat fragmentation depends on the scale of the landscape considered, the very notion of classifying species by their sensitivity to fragmentation may be unproductive.

If fragmentation effects are generally more scale dependent than those of habitat amount, it may explain some of the conflicting results around the relative effects of habitat loss and fragmentation in the literature (Fahrig 2003, Koper et al. 2007, Smith et al. 2009). Previous studies on forest birds have used landscapes ranging in size from

0.25 km² (McGarrigal and McComb 1995) through 100 km² (closest in area to our 5 km radius landscapes, Trzcinski et al. 1999, Radford and Bennett 2007, Table 1). Additionally, this scale dependence may partly explain why particular species have shown conflicting responses to fragmentation in different studies. For example, the scarlet tanager showed a significant negative response to increasing fragmentation within 6 and 12 km² landscapes in Villard et al. 1999 and Austen et al. 2001, but a significant positive response within the 100 km² landscapes in Trzcinski et al. 1999.

However, scale dependence cannot definitively explain all differences among studies. Fragmentation effects may also depend on other study-specific factors such as the metric used to quantify fragmentation (McGarigal and Cushman 2002) or the statistical method used to estimate the effects (Smith et al. 2009). For example, we did not find a significant response to increasing fragmentation for ovenbirds at any scale; which contrasts with a significantly negative response to increasing fragmentation in the 12 km² landscapes of Betts et al. 2006 and a significantly positive response in the relatively similarly sized 6 km² landscapes of Villard et al. 1999. Different fragmentation metrics may be better or worse representations of the important ecological processes that are sensitive to fragmentation. In our study we used core forest area to represent relatively broad scale processes such as the presence of source populations and negative edge effects. However, if conspecific attraction is an important process (Fletcher 2009), then a patch-related variable such as patch size may have given different results. Ultimately, our finding that fragmentation effects depended more on spatial scale than those of habitat amount supported our hypothesis: The potentially conflicting processes influenced by fragmentation, which act at different spatial scales, create a greater scale dependency for fragmentation effects than for habitat amount effects. However, we have only sampled a small number of forest bird species and it remains to be seen if there is broad support for this hypothesis in other taxa.

The effects of matrix quality, as measured here (road density), were generally weak; therefore, it is difficult to derive any strong inferences on their scale dependence. Our results differ from those of a previous study that showed an increasing importance of matrix quality with landscape size (Dunford and Freemark 2005). This may be because we did not include sufficiently broad spatial scales (i.e. >10 km radius) for our particular measure of matrix quality and/or our measure of matrix quality may not represent the same agricultural processes measured in Dunford and Freemark (2005). We chose road density as a variable that should represent the increased probability of mortality within poor-quality matrix – both directly through increased collisions with vehicles and as a proxy for factors that are associated with roads such as the density of buildings and towers that increase bird mortalities (Erikson et al. 2005). However, because many of these mortalities occur during migration, when many of these forest birds are moving at very large spatial scales, their effects may only be apparent at even broader spatial scales than those measured here. Additionally, many different measures of matrix quality are possible and some may not represent the matrix-dependent

Table 3. Summed Akaike weights for the 3 landscape predictors – total amount of forest (Forest), the proportion of forest area within the core of large forests (Core), and the density of roads (Road), plus the Forest × Core interaction – measured within landscapes of 5 different sizes. Models predicted the number of fragmentation sensitive species observed (Poisson regression) and the occurrence (logistic regression) of ovenbird and veery at 2951 forested point counts in southern Ontario, Canada. Weights were summed across the 95% confidence set of supported models from among the same competing models as in 2.

	Landscape radius	Summed Akaike weights			
		Forest	Core	Road	Core × Forest
Number of	500 m	1	1	0.89	1
fragmentation	1 km	1	1	0.70	0.97
sensitive	2 km	1	1	1	1
species	5 km	1	1	0.87	1
	10 km	1	1	0.62	1
Ovenbird	500 m	1	0.51	0.75	0.34
	1 km	1	0.40	0.36	0.08
	2 km	1	0.88	0.36	0.38
	5 km	1	0.42	0.43	0.16
	10 km	1	0.47	0.43	0.14
Veery	500 m	0.71	0.96	0.26	0.32
	1 km	1	1	0.29	1
	2 km	1	1	0.56	1
	5 km	1	1	0.49	0.91
	10 km	1	0.98	0.38	0.40

processes that are important for forest birds. For example, road density likely does not represent the same processes measured by an estimate of agricultural intensity in Dunford and Freemark (2005). Agricultural activities influence the density of nest parasites (Hoover and Brittingham 1993), predators (Burke et al. 2004), or the rates of chemical inputs from agricultural activities (Stinson et al. 1994). Unfortunately, data on agricultural activities that might better represent these processes are not available in the study area at spatial resolutions comparable to the road or landcover data used here.

Our findings also support the existence of a fragmentation threshold, where the negative effects of fragmentation become more important when the amount of habitat is low (Andren 1994). This threshold has been supported by theoretical work (Fahrig 1998) but has not been frequently demonstrated in empirical systems (Fahrig 2003, but see Betts et al. 2007). In our study, whenever fragmentation effects were somewhat important and in the expected direction (positive effect of increasing core forest), there was evidence of a statistical interaction between amount and fragmentation. The direction of the interaction indicated that the effects of core forest were more positive (i.e. the effects of fragmentation were more negative) when forest amount was low.

In this study, we have shown that the effects of fragmentation on forest birds appear to be more scale dependent than the effects of habitat amount. However converting the quantitative results (standardized coefficients) of this focal-plot study into specific landscape recommendations is not simple. In our analyses, we used the same response variable measured at a central plot for all landscape scales. This was necessary so that the response variable remained constant across the different spatial scales and we could therefore be sure that a change in effect across scale truly was a function of changes in the landscape measures. However, these effects on a response measured in a focal plot may not directly translate to effects on the bird community measured within an entire landscape, which is ultimately the goal of landscape management. For example, our response variables were measured only within forest areas that were >100 m in radius (to control for local habitat and sampling effects); however, the landscape of southern Ontario includes a great deal of forest that does not fulfil this criterion. It remains to be seen whether bird populations and communities measured over the entire landscape will respond similarly to measures of habitat amount, fragmentation, and matrix quality in landscapes of varying size.

Table 4. Collinearity among the landscape predictors increased with landscape size. Variance inflation factors (VIF) and pair-wise Pearson correlation coefficients for predictors: total amount of forest (Forest), the proportion of forest area within the core of large forests (Core), and the density of roads (Road). VIF represents the predictor's overall collinearity in a regression model with all other landscape predictors, the interaction between Forest and Core, and all covariates (see Table 2 for a list of covariates). Values above the diagonal are for large landscapes (10 km radius) and below are for small landscapes (0.5 km radius). Values for intermediate scales are intermediate to those shown here.

		Largest landscapes (radius = 10 km)		
		Forest (VIF = 2.5)	Core (VIF = 3.2)	Road (VIF = 1.2)
Smallest landscapes	Forest (VIF = 1.9)		0.64	−0.25
(radius = 500 m)	Core (VIF = 1.9)	0.68		−0.62
	Road (VIF = 1.1)	−0.16	−0.19	

Although translating the quantitative results here into specific recommendations for management is complicated, these results do suggest three broad conclusions relevant to managing scale-dependent landscape effects. First, if fragmentation effects are only apparent at some scales then these effects should only be managed or considered at that scale. Second, if the relative ranking of fragmentation and amount changes with scale (e.g. as it did for the number of fragmentation-sensitive species in this study), then the ranking of conservation options will depend on the scale of influence of the managing organization. Third, if fragmentation has positive effects at one scale and negative effects at another (e.g. veery in this study), then in this context, managing fragmentation may not be an effective use of conservation resources.

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