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RESEARCH ARTICLE

# Residuals cannot distinguish between ecological effects of habitat amount and fragmentation: implications for the debate

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**Abstract** Habitat amount and fragmentation usually covary in natural and simulated landscapes. A common way of distinguishing between their effects is to take the residuals of the fragmentation index or indices regressed on habitat amount, as the index of habitat fragmentation. We used data on prairie songbird relative abundances from southern Alberta, Canada to compare this approach with the reverse: taking the residuals of habitat amount regressed on habitat fragmentation as the index of habitat amount. We used generalized additive models (GAMs) to derive residuals, and modeled relative abundances using linear mixed-effects models. The modeling approach used strongly influenced the statistical results. Using residuals as an index of fragmentation resulted in an apparently stronger effect of habitat amount relative to habitat fragmentation. In contrast, habitat fragmentation appeared more influential than habitat amount when residuals were used as an index of habitat amount. Regression of residuals may eliminate statistical collinearity, but cannot distinguish between the ecological effects of habitat amount and fragmentation. Habitat fragmentation may therefore have a larger effect on species than previously studies have shown, but experimental manipulations of underlying mechanisms are ultimately required to address this debate.

**Keywords** Canada · Generalized additive models · Grasslands · Habitat amount · Habitat fragmentation · Residuals · Songbirds

## Introduction

Recent literature emphasizes the need to distinguish between the effects of habitat loss and fragmentation (McGarigal and Cushman 2002; Fahrig 2003; Turner 2005). Habitat loss indicates a reduction in habitat amount, while habitat fragmentation describes the configuration of the remaining habitat. Ecological theory suggests that habitat amount and fragmentation have distinct effects on species. Habitat loss has strong and usually negative effects on populations, such as loss of individuals from the population (Schmiegelow and Mönkkönen 2002) and increasing isolation among populations inhabiting separate patches (Fahrig 2003), whereas habitat fragmentation may reduce connectivity (Schmiegelow and

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Mönkkönen 2002), cause edge effects, or result in patches that are too small to support individuals or populations (Johnson and Igl 2001; Fahrig 2003). From a conservation perspective, distinguishing between the effects of habitat amount and fragmentation is important, because management actions may differ in response to these factors. For example, if habitat loss, rather than fragmentation, is responsible for a species decline, establishing habitat corridors may be an inefficient conservation measure.

Despite this, few studies have been able to distinguish between the effects of habitat amount and fragmentation (McGarigal and Cushman 2002). It is difficult to explore independent effects of loss and fragmentation with correlational studies and mensurative experiments, because habitat fragmentation indices are usually strongly correlated with habitat amount (e.g., Trzcinski et al. 1999; Boulinier et al. 2001; Tischendorf 2001). For example, isolation increases and connectivity decreases as habitat amount decreases (Fortin et al. 2003). This correlation is unavoidable, because landscapes with large amounts of habitat are relatively unfragmented by definition. In addition, some indices of habitat fragmentation, such as the total amount of edge, have low values when there is either a lower high amount of habitat within a landscape, so correlation between habitat amount and fragmentation can be nonlinear (e.g., Tischendorf 2001; Fortin et al. 2003). Correlation between habitat amount and fragmentation is sometimes ignored if it is below some arbitrary value of $r$ (Linke et al. 2005). However, low and moderate $r$ values may still preclude distinguishing effects of habitat amount and fragmentation, and collinearity may dramatically increase variance estimates (Freckleton 2002). An alternative solution is to hold habitat amount constant while allowing fragmentation to vary (e.g., Tewksbury et al. 2002), but this design does not explore effects of habitat amount and fragmentation concurrently.

Most empirical studies that have attempted to distinguish between the effects of habitat amount and fragmentation have used statistical methods to separate these effects (Fahrig 2003). The most common statistical approach has been regression of residuals (e.g., McGarigal and McComb 1995; Trzcinski et al.1999; Villard et al. 1999; Bélisle et al. 2001; Westphal et al. 2003; Hamer et al. 2006; see also simulation studies, e.g., Flather and Bevers 2002; compare with Rosenberg et al. 1999; Langlois et al. 2001). This involves using regression to model the relationship between variables representing habitat fragmentation, always the response variable, and a variable representing habitat amount. The residuals of this relationship are then used as the fragmentation index, while the original index of habitat amount is retained unchanged (e.g., McGarigal and McComb 1995; Villard et al. 1999; Hamer et al. 2006). Although problems with using regression of residuals in ecology have been previously recognized (Freckleton 2002), several studies that applied this approach to the habitat loss versus fragmentation debate have been cited repeatedly (e.g., in Flather and Bevers 2002; Fahrig 2003; Turner 2005), and the use of this statistical approach has been encouraged (e.g., Fahrig 2003).

Results from empirical studies using this approach to examine habitat fragmentation and amount are inconsistent. For example, McGarigal and McComb (1995), Trzcinski et al. (1999), Bélisle et al. (2001), and Westphal et al. (2003) concluded that habitat amount had a greater impact on habitat use by species, whereas Villard et al. (1999) and Hamer et al. (2006) concluded that both habitat amount and fragmentation influenced habitat use. Cumulatively, results from such studies suggest that the effects of habitat amount exceed the effects of fragmentation (Fahrig 2003; Turner 2005). However, given that a number of ecological models suggest that habitat fragmentation influences movement, distribution and population persistence (e.g., With et al. 1997; With and King 1999; Urban and Keitt 2001), it is surprising that empirical studies do not indicate a stronger effect of habitat fragmentation. We suggest that the analytical approach used in empirical studies may bias their results towards finding effects of habitat amount over habitat fragmentation. Although residual regression is effective in making the habitat amount and fragmentation variables statistically independent to avoid collinearity, it may not be possible to distinguish statistically the biological effects of habitat amount and fragmentation (Koper and Schmiegelow 2006).

In this paper we use data describing grassland songbird relative abundances to demonstrate the effects of using residuals of habitat fragmentation variables regressed on habitat amount, and vice versa, to determine the relative importance of habitat amount and fragmentation. We also discuss statistical and study-design alternatives to using residuals to distinguish between the effects of habitat amount and fragmentation.

## Methods

### Avian surveys and analyses

We used previously published data for this study (see Koper and Schmiegelow 2006 for further detail). We conducted five-minute, 100-m fixed-radius point count plots between dawn and 10 AM, from May 24 to July 4, 2000–2002, to survey songbird relative abundance in southern Alberta grasslands. One hundred and sixty four point-count plots were clustered within 16 non-overlapping, 5-km-radius landscapes. We focus our analyses here on six species: brown-headed cowbird (*Molothrus ater*), chestnut-collared longspur (*Calcarius ornatus*), horned lark (*Eremophila alpestris*), Savannah sparrow (*Passerculus sandwichensis*), vesper sparrow (*Pooecetes gramineus*), and western meadowlark (*Sturnella neglecta*).

We modeled avian response using linear mixed-effects models within S-plus 6.2 (Insightful Corporation 2001), with landscape and year as random variables. The natural log of avian relative abundances was used in some cases to normalize species distributions. We used Wald-type tests to determine significance, as these produce reliable *P*-values regardless of sample size (Insightful Corporation 2001). We used $\alpha = 0.1$ to indicate significance, based on an *a priori* power analysis to ensure a power of 0.8 to detect a 20% change in relative abundance (Faul and Erdfelder 1992; Koper 2004).

We conducted analyses both with and without an interaction term between grassland amount and fragmentation, to control for different effects of habitat fragmentation when different habitat amounts are present in the landscape (Flather and Bevers 2002; but see Fahrig 2003).

### Landscape analysis

A vegetative cover map was derived from Landsat TM images collected from 1993–1995 (Prairie Farm Rehabilitation Administration 2002), at a resolution of 30 m. We created landscapes around our data points using ArcGIS 8.2, and used FRAGSTATS Version 3 (McGarigal et al. 2002) to quantify grassland amount (ha) and derive indices of fragmentation for each 5-km landscape. Amount of grassland ranged from 2,078 ha to 7,400 ha, out of a possible 7,854 ha (26–94% of each landscape).

The 16 research landscapes were too few to derive residuals using generalized additive models (GAMs, see below), so we randomly selected 84 non-overlapping landscapes from our mixed-grass prairie study region in southern Alberta to describe the regional distribution and fragmentation of grassland. These random landscapes were added to the 16 research landscapes, resulting in 100 landscapes. Scatter plots were used to compare the research landscapes with the 84 random landscapes, to ensure that the random landscapes were representative of the research landscapes. Research landscapes were well distributed among the random landscapes and had similar average amounts of habitat (random = 4,860 ha ± SD 2514, research = 4755 ha ± SD 1479). All 100 landscapes were used to determine the relationships between the fragmentation indices and grassland amount and derive residuals, while avian analyses were restricted to our 16 research landscapes. We avoided problems associated with the modifiable area unit problem, in which spatial patterns are influenced by data aggregation, by using the same extent and grain size for all landscapes, and by using the minimum grain size that could be mapped (Jelinski and Wu 1996; see also Koper and Schmiegelow 2006).

### Fragmentation and amount indices

We used three indices of fragmentation for this study, because even though fragmentation indices are often correlated (Fortin et al. 2003), we wanted to know whether the variation among the selected indices affected our results. We selected landscape shape index (LSI), number of grassland patches (NP), and total length of edge between grassland and any other cover type (TE). The LSI is the total length of grassland edge divided by the minimum length of edge that could surround that amount of grassland in a landscape if it were maximally clumped, and is unitless (McGarigal et al. 2002). The natural logs of LSI, NP, and TE were used as fragmentation indices, to minimize heteroscedasticity. These indices were chosen because they are related to the amount of habitat edge (McGarigal et al. 2002), and edge effects are one of the main causes of fragmentation effects (Fahrig 2003). We did not use common fragmentation indices related to patch isolation and size (e.g., mean patch size) as fragmentation indices, because these are more properly interpreted as indices of habitat amount; for example, patch isolation is an index of the lack of habitat around the patch (Fahrig 2003).

We used GAMs to describe relationships between fragmentation indices and grassland amount, due to their nonlinear form (Quinn and Keough 2002). To determine the effects of taking residuals of the fragmentation variable regressed on amount, we first regressed the fragmentation index on amount of grassland. We used the residuals as the fragmentation index, and amount of grassland as the amount index. We call this the *fragmentation-residual model*, adding an index name to identify which fragmentation measure was used (i.e., LSI-, NP-, or TE-fragmentation-residual model). We then regressed grassland amount on each unaltered fragmentation index [ln(LSI, NP, or TE)], and used the residuals as the index of amount of grassland, and the unaltered fragmentation index as the index of fragmentation. We call this the *amount-residual model*.

To determine the effect of collinearity on the standard error of parameter estimates, we compared the percent increase of standard errors of habitat amount and LSI parameter estimates between models where only the raw indices of habitat amount and ln(LSI) were used (in which collinearity was present because of the correlation between habitat amount and ln(LSI), and the fragmentation-residual and amount-residual models, which were not collinear.

## Results

The LSI, TE and NP indices were correlated (Fig. 1). All fragmentation indices were also correlated nonlinearly with habitat amount, and had their highest values when amount of grassland was lowest (Fig. 2).

Our models produced very similar results when using LSI, NP and TE fragmentation indices. Accordingly, and because ln(LSI) was correlated with both ln(NP) and ln(TE) (Fig. 1), we summarize results from the latter indices but do not present the full models. Further, as interactions were not significant ($P > 0.16$) and model results did not differ with and without inclusion of the interaction term (possibly because we only used landscapes with at least 26% grassland), we report results without the interaction term.

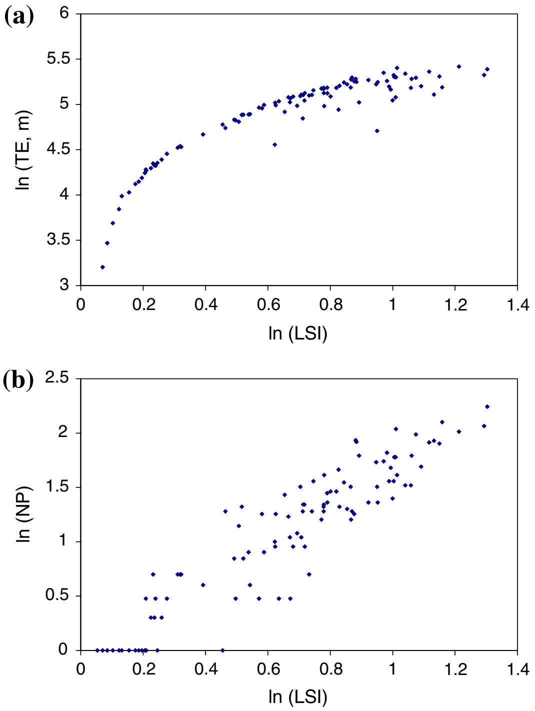

**Fig. 1** Relationships between (**a**) the natural log of the total amount of edge between grassland and other habitat types [ln(TE)], in metres (m), and the natural log of the unitless landscape shape index [ln(LSI)], and (**b**) the natural log of the number of grassland patches [ln(NP)] and ln(LSI), in 100 5-km-radii landscapes in southern Alberta, 1993–1995

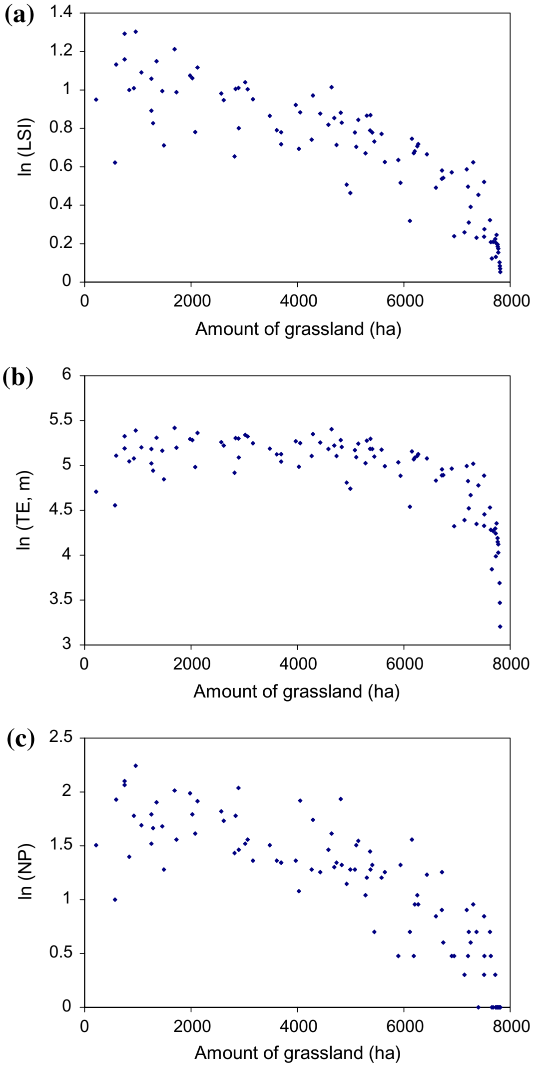

**Fig. 2** Relationships between (**a**) the natural log of the unitless landscape shape index [ln(LSI)] and amount of grassland in ha, (**b**) the natural log of the total amount of edge between grassland and other habitat types [ln(TE)], in ln(metres, m) and amount of grassland in ha, and (**c**) the natural log of the number of grassland patches [ln(NP)] and amount of grassland in ha, in 100 5-km-radii landscapes in southern Alberta, 1993–1995

The LSI-fragmentation-residual model suggested that 3 of 6 species had relative abundances influenced by habitat amount but not fragmentation, while 2 of 6 species had relative abundances marginally influenced by habitat fragmentation but not amount (Table 1). In contrast, the LSI-amount-residual model indicated that 5 of 6 species had relative abundances influenced by habitat fragmentation, while no species were influenced by habitat amount. Savannah sparrow relative abundances were independent of habitat amount or fragmentation.

For all three species responding to habitat amount in the fragmentation-residual model, habitat fragmentation appeared influential in the amount-residual model. In the two species consistently influenced by habitat fragmentation (horned lark, HOLA, and western meadowlark, WEME), the LSI-fragmentation-residual model suggested only a marginally significant response ($P > 0.096$, $\mathrm{SE_{HOLA}} = 1.006$, $\mathrm{SE_{WEME}} = 0.378$), while the LSI-amount-residual model suggested a stronger effect ($P < 0.028$, $\mathrm{SE_{HOLA}} = 0.609$, $\mathrm{SE_{WEME}} = 0.196$). In general, parameter estimates for fragmentation and amount variables often differed substantially between the amount-residual and fragmentation-residual models (Table 1).

We found very similar results when using the NP and TE fragmentation indices. Both the TE- and NP-fragmentation-residual models suggested that 3 of 6 species responded significantly to habitat amount, while no species responded significantly to fragmentation. The TE-amount-residual model suggested that 1 of 6 species responded to habitat amount, while 3 of 6 species responded to fragmentation; the NP-amount-residual model suggested that no species responded to habitat amount, while 4 of 6 species responded to fragmentation.

Collinearity influenced the standard error of the fragmentation variable more strongly than the habitat amount variable. The standard error of habitat amount was on average 10.8% (range –1.80–16.25%) higher in the presence of collinearity, while the standard error of ln(LSI) was on average 38.3% (range 35.4–40.6%) higher in the presence of collinearity.

## Discussion

Emerging consensus within the field of landscape ecology suggests that habitat amount exerts a stronger influence on biotic response than habitat fragmentation (Fahrig 2003; Turner 2005). We demonstrated that including the residuals from

**Table 1** The effects of using residuals as indices of grassland amount or fragmentation, represented by the natural log of the landscape shape index, on apparent effects of grassland amount and fragmentation on prairie songbirds in southern Alberta, Canada, 2000–2002

| Species | Transformation of response variable | Model | Grassland amount (ha) × 1000 | | Grassland fragmentation | |
|---|---|---|---|---|---|---|
| | | | $\beta$ | $P$ | $\beta$ | $P$ |
| Brown-headed cowbird | Ln | Fragmentation-residual | –0.394 | 0.057 | 2.525 | 0.260 |
| | | Amount-residual | –0.162 | 0.498 | 2.727 | 0.062 |
| Chestnut-collared longspur | None | Fragmentation-residual | 0.514 | 0.002 | –2.703 | 0.104 |
| | | Amount-residual | 0.244 | 0.221 | –3.809 | 0.003 |
| Horned lark | None | Fragmentation-residual | 0.190 | 0.105 | –1.796 | 0.098 |
| | | Amount-residual | 0.000 | 0.783 | –1.509 | 0.028 |
| Savannah sparrow | None | Fragmentation-residual | –0.082 | 0.932 | 1.647 | 0.121 |
| | | Amount-residual | 0.087 | 0.269 | 0.635 | 0.328 |
| Vesper sparrow | Ln | Fragmentation-residual | –0.320 | 0.066 | 1.619 | 0.429 |
| | | Amount-residual | –0.142 | 0.512 | 2.474 | 0.058 |
| Western meadowlark | None | Fragmentation-residual | –0.057 | 0.297 | 0.680 | 0.096 |
| | | Amount-residual | 0.018 | 0.416 | 0.492 | 0.027 |

regression of fragmentation on grassland amount as an index of habitat fragmentation biased our conclusions towards finding an effect of habitat amount on species densities, and against finding an effect of habitat fragmentation. In contrast, the amount-residual models suggested that habitat fragmentation had a strong effect on species response, while habitat amount had little or no effect. This result is particularly significant because we detected effects of fragmentation in landscapes with relatively high amounts of habitat, where such effects are less expected (e.g., Flather and Bevers 2002). Several theoretical models also suggest the importance of habitat fragmentation on mediating biotic response (e.g., With et al. 1997; With and King 1999; Urban and Keitt 2001), but this importance has not received strong empirical support (Fahrig 2003). However, using residuals as indices of fragmentation may have biased the results of earlier empirical studies.

Estimating effect sizes is often more biologically relevant than reporting statistical significance (Guthery et al. 2005). When residual regression is used, parameter estimates for the residual variables must be interpreted differently from the unmanipulated variables. The size of the parameter estimate for the residual variable indicates the additive effect of that variable to the effect of the variable with which it is correlated. The parameter estimate for the same variable, if not manipulated using residuals, is interpreted as the effect of that variable on the response variable. Regression of residuals may bias parameter estimates (Freckleton 2002), and interpretation is not intuitive. It is therefore not surprising that parameter estimates differed between the amount-residual and fragmentation-residual models, and care must be taken to interpret each parameter estimate correctly.

Although regression of residuals eliminates statistical collinearity between the habitat fragmentation and amount variables, it does not follow that the resulting fragmentation index represents a comprehensive measure of all of the ecological outcomes of habitat fragmentation. Moreover, the unaltered habitat amount index does not represent the ecological outcomes of habitat amount to the exclusion of habitat fragmentation. Rather, our results suggest that, in conventional analyses, while the fragmentation index indeed represents only the effects of habitat fragmentation (a subset of these effects, in fact), the habitat amount index represents both the effects of habitat amount and the effects of habitat fragmentation not modeled by the residuals of the fragmentation index. This is because the joint variance explained by both variables is entirely aligned with the habitat amount variable. When independent variables are correlated, $v_1$ represents the variance explained only by variable $x_1$, $v_2$ represents the variance explained only by $x_2$, and $v_{12}$ represents the joint variance explained by both variables (Freckleton 2002). When fragmentation ($x_1$) is regressed on habitat amount ($x_2$) to produce residuals as an index of fragmentation, the fragmentation index represents only the variance explained by $v_1$, while the habitat amount index represents the variance explained by both $v_2$ and $v_{12}$. Furthermore, as the correlation between the two covariates increases, $v_1$ decreases (Freckleton 2002); the apparent effect of habitat fragmentation therefore decreases, while the apparent effect of amount ($v_2$ + $v_{12}$) increases.

Given that the habitat amount index actually represents the influence of more than just habitat amount, a stronger observed effect of the unaltered habitat amount index, compared to the residuals of the habitat fragmentation index, is not surprising. However, it does not indicate that habitat amount genuinely has a stronger effect on species than habitat fragmentation. Indeed, the approach itself presupposes that one variable (amount) takes precedence over another (Freckleton 2002).

Statistically separating the covariation between habitat amount and fragmentation is problematic, because the independent effects of fragmentation and amount are not observable to the researcher. We can observe the combined ecological outcomes of habitat amount and fragmentation ($v_{12}$), but have no way to determine how amount and fragmentation independently affect species. *A priori* selection of landscapes cannot fully control for covariance between habitat fragmentation and amount metrics because of the intrinsic covariation between these variables in field situations (e.g., McGarigal and McComb 1995). Amount and fragmentation even covary in simulated landscapes (e.g., Flather and Bevers 2002), because for any particular amount of habitat within a landscape, a restricted range of fragmentation values is possible.

Other statistical methods for dealing with collinear variables have been developed. Principal components analysis (PCA) may be useful for the analysis of collinear data (Quinn and Keough 2002). However, while PCA has been used for separating the effects of habitat amount and fragmentation (Trzcinski et al. 1999), it does not result in a clean separation with all data sets (M.K. Trzcinski, pers. comm., 12 Jan, 2007). Further, in Trzcinski et al. (1999), the principal components that described habitat amount and fragmentation remained weakly correlated with each other, so the authors still used the residuals of the fragmentation principal component regressed on the habitat amount principal component as an index of fragmentation. Application of PCA may be problematic because it is not as effective when independent variables are nonlinearly correlated (Quinn and Keough 2002). Transforming fragmentation or amount variables to linearize their correlation may help address this problem (Quinn and Keough 2002), but many fragmentation indices are nonlinearly correlated with habitat amount in such a way that they cannot easily be transformed to linearize the relationship (Fahrig 2003). We therefore conclude that PCA might help distinguish between the effects of habitat amount and fragmentation in some cases, but cannot be depended on to do so.

A second approach to analyzing collinear data is ridge regression, a biased estimation technique (Quinn and Keough 2002) that shrinks parameter estimates in proportion to their variance. Collinearity among variables greatly increases their variance (Pagel and Lunneborg 1985). While several studies have outlined the potential benefits of analyzing collinear data using ridge regression (e.g., Marquardt and Snee 1975; Schoeman et al. 2002), the approach remains controversial (Quinn and Keough 2002). We are unaware of any studies that have used this approach to analyze the effects of habitat amount and fragmentation.

Heuristically, collinear variables have high variances because of uncertainty regarding which of the collinear variables influences the response variable, not because they necessarily have little influence on the response variable. Ridge regression does not always improve accuracy or predictive ability of models with collinear variables, particularly when collinear variables have a large effect on response variables (Pagel and Lunneborg 1985). It is only appropriate if the true population value estimated by a parameter is inversely correlated with the parameter variance (Pagel and Lunneborg 1985). From a landscape ecology perspective, apparently small effects of either fragmentation or habitat amount in a ridge-regression model might result from the high parameter variance caused by the collinearity, and not from a small effect of these variables *per se*. Furthermore, it is recognized that ridge regression reduces bias more effectively for some variables than others (Pagel and Lunneborg 1985). If variance of fragmentation variables is more strongly influenced by collinearity than is variance of habitat amount, as in our data, ridge regression would negatively bias fragmentation more than habitat amount. Nonetheless, statistical methods that we have not applied to our data, such as ridge regression and PCA, may offer better solutions to separating the effects of habitat amount and fragmentation than using residuals.

Beyond the issue of collinearity, we believe there have been additional analytical problems that also bias the landscape ecology literature towards finding effects of habitat amount that may, in fact, be driven by fragmentation. For example, statistical models that included local distance-to-edge variables indicated fewer significant effects of habitat amount compared to similar models that included only landscape-level variables (Koper and Schmiegelow 2006). This suggests that studies conducted at only the landscape scale may find apparent effects of habitat amount that are in fact driven by edge effects (Koper and Schmiegelow 2006). Edge effects are usually associated with habitat fragmentation (Fahrig 2003). In light of these and our present findings, we suggest that conclusions drawn by some previous empirical landscape ecology studies, regarding the overwhelming influence of habitat amount, may have been biased.

Ultimately, habitat amount and fragmentation covary so closely that in most cases, alteration of habitat amount will concurrently influence habitat fragmentation, so predicting the effects of either habitat amount or fragmentation using pattern-based statistical models will ultimately lead to the same results. However, these results must be interpreted in the context that it is unclear whether the mechanism behind the observed effect resulted from habitat amount or fragmentation.

We highlight two distinct exceptions where it is important and possible to distinguish between the effects of habitat amount and fragmentation. The first is when research focuses on mechanisms. For example, predator distributions may explain some of the effects of habitat edges that result from habitat fragmentation (Bergin et al. 2000; Johnson and Igl 2001). If we want to understand the mechanisms behind the effects of habitat amount and fragmentation, this can be achieved only through research that focuses on these mechanisms directly, rather than on structural patterns of habitat amount and fragmentation (Schneider 2001). Similarly, if management actions are focused on manipulating mechanisms behind observed patterns, then understanding these mechanisms is critical. Predator management may have entirely different effects if prey species are declining because of habitat loss, versus declining because of a reduction in productivity resulting from higher predation rates near habitat edges. In this case the mechanism, rather than the pattern of habitat on the landscape, is the focus of management, and direct manipulation of the predator population is warranted.

The second exception is in studies where there is little range in habitat amount, but a large range in habitat fragmentation. This approach is demonstrated in studies that hold amount constant while manipulating fragmentation (e.g., Tewksbury et al. 2002). We emphasize that in this case the researcher cannot study the effects of both habitat fragmentation and habitat amount concurrently; nonetheless, they can determine effects of habitat fragmentation in the absence of changes in habitat amount. This may be particularly important in regions where there is little habitat (Fahrig 1998; Flather and Bevers 2002; but see Fahrig 2003). The management correlate to this is that some management activities, such as constructing corridors or road underpasses, might have a large impact on fragmentation while resulting in little change in habitat amount. Theoretical studies that suggest that both habitat amount and fragmentation are important provide a justification for manipulative experiments that can address the significance of either habitat amount or fragmentation.

Exploring mechanisms is possible through inclusion of biologically relevant variables in landscape models. For example, including distance-to-edge metrics in landscape models (e.g., Koper and Schmiegelow 2006) does not directly address mechanisms, but it narrows down the list of possibilities that become candidates for experimentation. Thus, we echo earlier calls for an increased emphasis on mechanisms in fragmentation research (Debinski and Holt 2000), recognizing that our ability to attribute causal relationships of habitat variables *post hoc* is much weaker than by designing studies to address them explicitly. Directly exploring mechanisms, and manipulating fragmentation while holding habitat amount constant, are alternative study designs that provide an opportunity to distinguish the effects of fragmentation from habitat amount. However, we suspect that the relative ease with which correlative studies are conducted will continue to make them prevalent in the literature. Therefore, there is a clear need for future research that critically evaluates the potential biases of alternative statistical approaches such as PCA (e.g., Trzcinski et al. 1999) and ridge regression in analyzing landscape data. We also cannot predict the extent to which the problem we have identified with residual analysis has influenced previous studies, but we believe that reexamining their results in light of this discussion would be very informative, and may reopen the debate about habitat loss and fragmentation in an instructive manner.

Despite methodological issues, important take-home messages from the literature remain. First, habitat loss and fragmentation in combination have critical negative effects on most species, and habitat loss generally causes additional habitat fragmentation; management to conserve habitat must therefore remain a priority. Second, theoretical models suggest that both habitat amount (e.g., Fahrig 1998) and fragmentation (e.g., With and King 1999; Urban and Keitt 2001) may influence species. Third, it seems logical that habitat amount would have a greater effect on populations than habitat fragmentation, at least when amounts of habitat are relatively high; we simply point out that the empirical evidence in support of this logic is less strong than previously assumed.

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## References

Bergin TM, Best LB, Freemark KE, Koehler KJ (2000) Effects of landscape structure on nest predation in roadsides of a Midwestern agroecosystem: a multiscale analysis. Landscape Ecol 15:131–143

Bélisle M, Desrochers A, Fortin M-J (2001) Influence of forest cover on the movements of forest birds: a homing experiment. Ecology 82:1893–1904

Boulinier T, Nichols JD, Hines JE, Sauer JR, Flather CH, Pollock KH (2001) Forest fragmentation and bird community dynamics: inference at regional scales. Ecology 82:1159–1169

Debinski DM, Holt RD (2000) A survey and overview of fragmentation experiments. Conserv Biol 14:342–355

Fahrig L (1998) When does fragmentation of breeding habitat affect population survival? Ecol Modell 105:273–292

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Ann Rev Ecol, Evol Syst 34:487–515

Faul F, Erdfelder E (1992) GPower: *a-priori*, post-hoc, and compromise power analyses for MS-DOS (computer program). Bonn University, Bonn

Flather CH, Bevers M (2002) Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. Am Nat 159:40–56

Fortin M-J, Boots B, Csillag F, Remmel TK (2003) On the role of spatial stochastic models in understanding landscape indices in ecology. Oikos 102:203–212

Freckleton RP (2002) On the misuse of residuals in ecology: regression of residuals vs. multiple regression. J Anim Ecol 71:542–545

Guthery FS, Brennan LA, Peterson MJ, Lusk JJ (2005) Information theory in wildlife science: critique and viewpoint. J Wildlife Biol 69:457–465

Hamer TL, Flather CH, Noon BR (2006) Factors associated with grassland bird species richness: the relative roles of grassland area, landscape structure, and prey. Landscape Ecol 21:569–583

Insightful Corporation (2001) S-plus 6 for windows guide to statistics, vol 1. Seattle

Jelinski DE, Wu J (1996) The modifiable areal unit problem and implications for landscape ecology. Landscape Ecol 11:129–140

Johnson DH, Igl LD (2001) Area requirements of grassland songbirds: a regional perspective. The Auk 118:24–34

Koper N (2004) Upland-nesting Ducks as Surrogate Species for Avian Conservation in the Dry Mixed-Grass Prairie. Dissertation, University of Alberta

Koper N, Schmiegelow FKA (2006) A multi-scaled analysis of avian response to habitat amount and fragmentation in the Canadian dry mixed-grass prairie. Landscape Ecol 21:1045–1059

Langlois JP, Fahrig L, Merriam G, Artsob H (2001) Landscape structure influences continental distribution of hantavirus in deer mice. Landscape Ecol 16:255–266

Linke J, Franklin SE, Huettmann F, Stenhouse GB (2005) Seismic cutlines, changing landscape metrics and grizzly bear landscape use in Alberta. Landscape Ecol 20:811–826

Marquardt DW, Snee RD (1975) Ridge regression in practice. Am Stat 29:3–20

McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecol Appl 12:335–345

McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps (computer program) University of Massachusetts http://www.umass.edu/landeco/research/fragstats/fragstats.html. Cited 20 Jun 2006

McGarigal K, McComb WC (1995) Relationships between landscape structure and breeding birds in the Oregon coast range. Ecol Monogr 65:235–260

Pagel MD, Lunneborg CE (1985) Empirical evaluation of ridge regression. Psychol Bull 97:342–355

Prairie Farm Rehabilitation Administration—Agriculture Agri-Food Canada. 2002. PFRA Ungeneralized Landcover for the Canadian Prairies. Regina.

Quinn GP, Keough MJ (2002) Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK

Rosenberg KV, Lowe JD, Dhondt AA (1999) Effects of forest fragmentation on breeding tanagers: a continental perspective. Conserv Biol 13:568–583

Schmiegelow FKA, Mönkkönen M (2002) Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. Ecol Appl 12:375–389

Schneider MF (2001) Habitat loss, fragmentation and predator impact: spatial implications for predator management. J Appl Ecol 38:720–735

Schoeman SJ, Aziz MA, Jordann GF (2002) The influence of multicollinearity on crossbreeding parameter estimates for weaning weight in beef cattle. S Afr J Anim Sci 32:239–246

Tewksbury JJ, Levey DJ, Haddad NM, Sargent S, Orrock JL, Weldon A, Danielson BJ, Brinkerhoff J, Damschen EI, Townsend P (2002) Corridors affect plants, animals, and their interactions in fragmented landscapes. Proc Natl Acad Sci 99:12923–12926

Tischendorf L (2001) Can landscape indices predict ecological processes consistently? Landscape Ecol 16:235–254

Trzcinski MK, Fahrig L, Merriam G (1999) Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecol Appli 9:586–593

Turner MG (2005) Landscape ecology: what is the state of the science? Ann Rev Ecol, Evol Syst 36:319–344

Urban D, Keitt T (2001) Landscape connectivity: a graph-theoretic perspective. Ecology 82:1205–1218

Villard M-A, Trzcinski MK, Merriam G (1999) Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conserv Biol 13:774–783

Westphal MI, Field SA, Tyre AJ, Paton D, Possingham HP (2003) Effects of landscape pattern on bird species distribution in the Mt. Lofty ranges, south Australia. Landscape Ecol 18:413–426

With KA (1997) The application of neutral landscape models in conservation biology. Conserv Biol 11:1069–1080

With KA, King AW (1999) Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. Landscape Ecol 14:73–82

With KA, Gardner RH, Turner MG (1997) Landscape connectivity and population distributions in heterogeneous environments. Oikos 78:151–169