

Positive effects of forest fragmentation, independent of forest amount, on bat abundance in eastern Ontario, Canada

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Abstract While studies have found that bat abundance is positively related to the amount of forest cover in a landscape, the effects of forest fragmentation (breaking apart of forest, independent of amount) are less certain, with some indirect evidence for positive effects of fragmentation. However, in most of these studies, the variables used to quantify fragmentation are confounded with forest amount, making it difficult to interpret the results. The purpose of this study was to examine how forest amount and forest fragmentation independently affect bat abundance. We conducted acoustic bat surveys at the centers of 22 landscapes throughout eastern Ontario, Canada, where landscapes were chosen to avoid a correlation between forest amount and forest fragmentation (number of patches) at multiple spatial scales, while simultaneously controlling for other variables that could affect bat activity. We found that the effects of forest amount on bat relative abundance were mixed across species (positive for *Lasiurus borealis*, negative for *Perimyotis subflavus* and

Lasionycteris noctivagans). When there was evidence for an effect of forest fragmentation, independent of forest amount, on bat relative abundance, the effect was positive (*Myotis septentrionalis*, *Myotis lucifugus* and *Lasiurus borealis*). We suggest that the mechanism driving the positive responses to fragmentation is higher landscape complementation in more fragmented landscapes; that is, increased access to both foraging and roosting sites for these bat species. We conclude that fragmented landscapes that maximize complementation between roosting and foraging sites should support a higher diversity and abundance of bats.

Keywords Landscape structure · Landscape composition · Landscape configuration · Spatial heterogeneity · Habitat loss · Habitat fragmentation · Resource proximity · Multi-scale analysis · Inter-patch movement · Chiroptera

Introduction

The conversion of forest to agriculture leads to both a reduction in the amount of forest cover and a change in the spatial configuration of the forest area that remains (Haila 2002). Of these processes, it is the loss of forest habitat that is often considered most detrimental to forest species, with negative effects of forest loss reported across many taxa, including bats (Gorresen and Willig 2004), birds (Trzcinski

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et al. 1999), small mammals (Nupp and Swihart 2000), and amphibians (Vallan 2000). The effects of forest fragmentation (the breaking apart of forest, independent of amount), on the other hand, are usually much weaker and as likely to be positive as negative (Fahrig 2003). For example, studies have shown that the effects of fragmentation on temperate birds can vary in both direction (positive, negative, or no effect) and magnitude across different species (McGarigal and McComb 1995; Trzcinski et al. 1999; Villard et al. 1999).

In North America, bats are generally associated with forest systems, which they rely on for roosting or foraging at least some of the time (Wunder and Carey 1996). Bats tend to be more specialized in their choice of roosting habitat with most species roosting either in the cavities of trees and snags (e.g., *Myotis septentrionalis*, *Myotis lucifugus*, *Lasionycteris noctivagans*, *Eptesicus fuscus*) or in the foliage of trees (e.g., *Perimyotis subflavus*, *Lasiurus borealis*, *Lasiurus cinereus*) (van Zyll de Jong 1985). In contrast, bats tend to be more opportunistic in their choice of foraging habitat, with many species foraging within forested areas, in forest gaps and open areas, and along forest edges, depending on variations in prey availability and spatial clutter (Furlonger et al. 1987; Grindal 1996; Wunder and Carey 1996; Patriquin and Barclay 2003; Morris et al. 2010). Since these resources are often separated by large distances, many bats commute several kilometres between roosting and foraging sites each night (e.g., Elmore et al. 2005; Broders et al. 2006). It is therefore reasonable to expect that changes in landscape structure would affect bat abundance and distribution (Law and Dickman 1998).

While a number of studies have examined the effects of landscape structure on bats in other regions (e.g., Law et al. 1999; Lumsden and Bennett 2005 in Australia; Estrada and Coates-Estrada 2002 in Mexico; Cosson et al. 1999; Gorresen and Willig 2004; Bernard and Fenton 2007 in South America), only a few have examined the question in a North American context (e.g., Erickson and West 2003; Duchamp and Swihart 2008). Overall, the results suggest that forest loss has a negative effect on bat abundance and distribution (Law et al. 1999; Duchamp and Swihart 2008). Some of these studies also suggest that forest fragmentation has a negative effect on bats (Cosson et al. 1999; Schulze et al. 2000), while others provide evidence of a weaker

but potentially positive effect of fragmentation (Estrada and Coates-Estrada 2002; Lumsden and Bennett 2005). While these studies provide valuable insight into the potential effects of landscapes structure on bats, the range of species, trophic groups and geographic regions examined across these studies make it difficult to generalize their results.

To further complicate matters, in most studies on the effects of landscape structure on bats, the variables used to quantify landscape configuration (or forest fragmentation) are confounded with measures of landscape composition (or forest amount). For example, a number of studies (e.g., Cosson et al. 1999; Estrada and Coates-Estrada 2002) have compared the abundance of bats between a large tract of continuous forest and several smaller forest patches, and concluded that a difference in the number of captures indicates an effect (either positive or negative) of fragmentation. However, in this situation the effects of forest loss and fragmentation are confounded, making it difficult to interpret the results. The purpose of this study is therefore to examine how forest amount and forest fragmentation independently affect bat abundance.

During the summer residency period, bats have two basic habitat requirements: roosting and foraging habitat (Brigham 2007). Of these required habitat types, it is the availability of potential roosting sites that is generally considered to be the strongest limiting factor for temperate bat species (Humphrey 1975). Since most North American bats roost in forest structures (tree and snag cavities or tree foliage), we would expect more bats in landscapes with more forest (Wunder and Carey 1996). Accordingly, studies have found that landscapes with more forest (and more potential roosting sites) have higher bat abundance and diversity (Humphrey 1975; Gehrt and Chelsvig 2003; Duchamp and Swihart 2008).

Since bats require two types of habitat (foraging and roosting), we would also expect a greater abundance of bats in landscapes where those resources are in close proximity than in landscapes where they are separated by large distances (Law and Dickman 1998). Dunning et al. (1992) used the term 'landscape complementation' to describe the extent to which landscape structure facilitates movement between (or access to) different types of required habitat. In general, an increase in the level of habitat fragmentation (holding habitat amount constant) will lead to higher

complementation between habitat types, which should have a positive effect on species with complementary resource needs (Law and Dickman 1998). For example, consider a hypothetical bat species that roosts in forests and forages opportunistically along forest edges and in open areas (Fig. 1a to b). If we increase the number of forest patches (i.e., fragmentation) while holding forest amount constant, we will also increase the level of interdigitation of roosting and foraging sites. As a result, individuals can obtain resources more efficiently and spend less time commuting between habitat types (Dunning et al. 1992).

While the amount of potential roosting habitat is largely a function of forest amount, the spatial configuration of different resources in a landscape is also important in determining whether a potential roosting site will actually be occupied (Wunder and Carey 1996). Many bat species will preferentially select roosting sites that are within close proximity to other resources, such as foraging sites (Wunder and Carey 1996). In fact, O’Keefe et al. (2009) found that some bats select roosting sites close to forest edges and open areas in an apparent attempt to reduce commuting flight costs. Accordingly, several studies have found that bat abundance can be higher in landscapes where forest and non-forest cover (i.e., agriculture) are

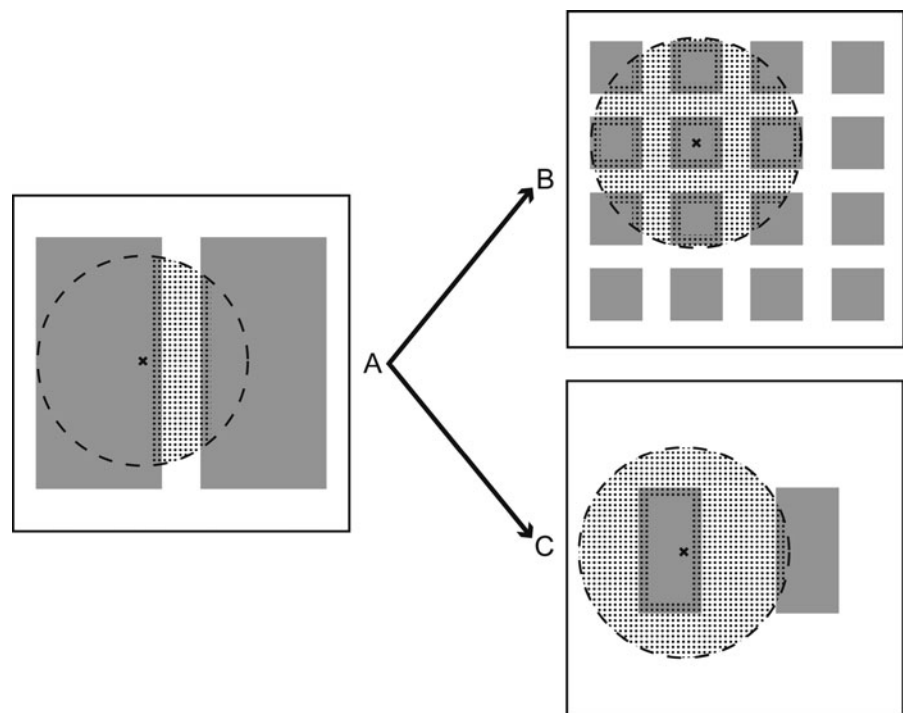
mixed, presumably due to the increased availability and proximity of required resources (Gehrt and Chelstvig 2003; Loeb and O’Keefe 2006; Yates and Muzika 2006; Duchamp and Swihart 2008). For such species, increasing the fragmentation of forest (for a constant amount of forest) should increase accessibility of foraging habitat from roosting habitat, resulting in a positive overall effect of forest fragmentation.

Our objective was to measure the relative abundance of bats in a set of landscapes selected such that the amount of forest cover and the degree of forest fragmentation (or number of forest patches) varied independently, to test the predictions that: (1) bat abundance will be positively correlated with forest amount; and (2) bat abundance will be positively correlated with forest fragmentation.

Methods

To examine the independent effects of forest amount and forest fragmentation on bat abundance, we used a mensurative experimental approach (McGarigal and Cushman 2002). We selected forest patches centred on landscapes, where the landscapes were chosen to avoid a correlation between forest amount and forest

Fig. 1 An example of landscape complementation for a hypothetical bat species that roosts in forest (*grey*) and forages (*dotted*) opportunistically along forest edges and in open areas within a given distance (*circle*) of a roosting site (*x*). As we move from landscape **a** to **b**, the number of forest patches (fragmentation) increases while holding forest amount (potential roosting habitat) constant. As we move from **a** to **c**, forest amount decreases while holding the number of forest patches constant. In both landscapes **b** and **c**, the two types of required habitat (roosting and foraging) are more accessible from each other, resulting in higher landscape complementation



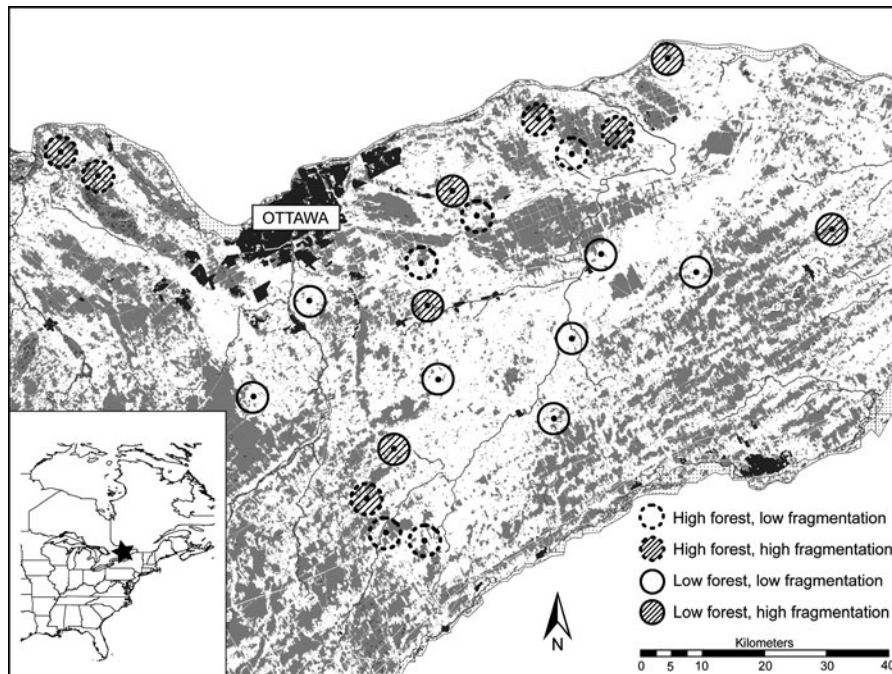


Fig. 2 Map of eastern Ontario, Canada showing the 22 surveyed landscapes, where landscapes are defined as the area within a 2.5 km radius (*circle*) of a focal forest patch where bats were surveyed (*black dot*). The *light grey* areas represent forest cover, *dark grey* areas represent urban development, and

fragmentation, while simultaneously controlling for other variables that could affect bat activity. We avoided a correlation between forest amount and fragmentation by ensuring that our sample landscapes included not only the common combinations of high forest amount with low fragmentation and low forest amount with high fragmentation, but also the poorly represented combinations of low forest amount with low fragmentation and high forest amount with high fragmentation (Trzcinski et al. 1999). We used the number of forest patches in a landscape as a measure of fragmentation (the breaking apart of forest, independent of forest amount).

Site selection

We conducted our study in the rural areas of eastern Ontario, near Ottawa, Canada (Fig. 2). The region is dominated by agricultural land use and interspersed with remnant forests, mainly mixed-woods and deciduous stands (Thompson 2000).

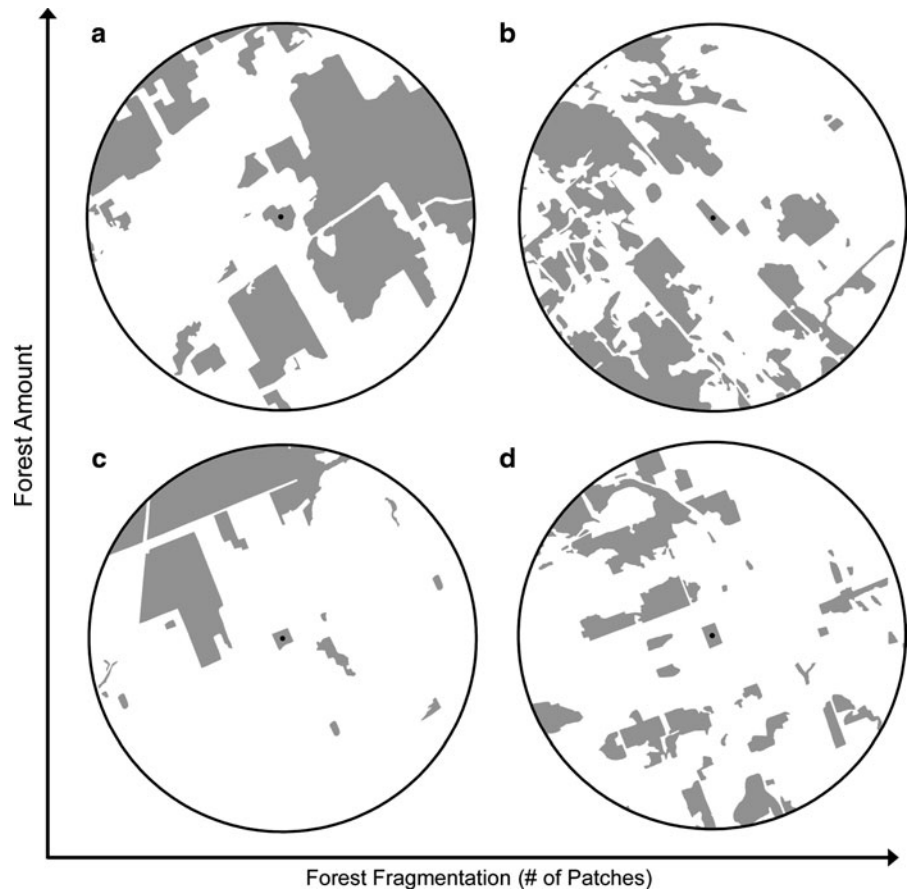
We selected 22 non-overlapping landscapes from across eastern Ontario (Fig. 2). First, we identified

the remaining areas represent agriculture. Landscapes are shown as categorized into four classes based on the amount of forest cover and degree of fragmentation (number of patches), although these were analyzed as continuous variables

all patches of mixed deciduous forest (focal patches) within the size range 4.0–10.0 ha across our study area; the narrow size range was chosen to control for potential effects of local patch size on bat activity. This resulted in 4,678 candidate patches. We then defined a ‘landscape’ as the area within a 2.5 km radius around each of these focal patches. We chose this scale based on distances our bat species commute between roosting and foraging sites (about 1–2 km). To account for the possibility that different species respond to the landscape at different spatial scales, we also quantified landscape structure within 1, 1.5, 2, 3, 4, and 5 km radii of each focal patch.

To eliminate possible landscape-scale confounding variables, we further reduced the candidate set of patches by taking the set whose associated landscapes had small ranges in: amount of wetlands (0.0–3.0% of a possible 0.0–80.0%); open water (0.0–1.1% of a possible 0.0–96.2%); road density (8.0–30.9 m/ha of a possible 0.0–36.9 m/ha); and building density (0.05–0.19 buildings/ha of a possible 0.00–0.42 buildings/ha). In addition, we selected

Fig. 3 Sample landscapes showing independent variation in forest amount and forest fragmentation (number of forest patches): (a) high forest amount, low fragmentation; (b) high forest amount, high fragmentation; (c) low forest amount, low fragmentation; and (d) low forest amount, high fragmentation



only candidate landscapes where the dominant non-forest land cover was agricultural (row crops and pasture). These criteria reduced the set of candidate landscapes to 110.

After controlling for these potential confounding variables, the final step in site selection was to find a subset of these landscapes that minimized the correlation between forest amount and the number of forest patches at all spatial scales, while maintaining as much variation as possible in each of the two variables (Trzcinski et al. 1999). In our final set of 22 landscapes, forest amount ranged from 4.2 to 42.4% (of a possible 0.4–73.9%), the number of forest patches ranged from 15 to 84 (of a possible 7–192), and the correlation between the two ranged from 0.061 to 0.392, and decreased with increasing landscape size (see Supplementary Materials).

All landscape variables were based on land cover data from the Ontario Fundamental Dataset (OMNR 2003) and quantified using ArcGIS 9.3 (ESRI 2006).

Field surveys

We conducted acoustic bat surveys at each of the 22 landscapes for one session each, between May 26th and July 27th 2009. To limit seasonal variation in activity, we restricted acoustic surveys to the summer residency period for bat species in eastern Ontario (van Zyll de Jong 1985). We also avoided correlations between our predictor variables of interest (forest amount and fragmentation) and time of survey during the season. We did this by first classifying landscapes into one of four categories (Fig. 3): (a) high forest amount, low fragmentation ($n = 5$); (b) high forest amount, high fragmentation ($n = 5$); (c) low forest amount, low fragmentation ($n = 7$); and (d) low forest amount, high fragmentation ($n = 5$). We then surveyed one randomly selected landscape from each of the four classes within each four-day sampling period.

We recorded full-spectrum echolocation calls directly to a laptop computer using calibrated

AR125 ultrasonic receivers and SPECT'R 3.0 software (Binary Acoustic Technology). Using the Snapshot Mode, we recorded all signals that were more than 10 db above the level of background noise with a frequency between 15 and 120 kHz, which includes the frequency range of all seven species we expected to encounter in our study area (van Zyll de Jong 1985).

We deployed two receivers per focal patch. We placed the first receiver 2 m into the adjacent agricultural matrix so that it would record bat activity along the forest edge, and the second receiver 50 m into the focal patch within a partial clearing with the microphone pointed in the same direction as the first receiver (Patriquin and Barclay 2003). We mounted both receivers atop tripods (1.2 m high) and pointed them at 45-degrees from the horizon. Surveys began 30 min before dusk and lasted 3 h to coincide with the peak foraging period of local species (van Zyll de Jong 1985). We did not conduct surveys on nights with rain since it has been found to substantially reduce bat activity (Erickson and West 2002).

At each focal patch, we also measured local habitat variables to statistically control for any effects on bat activity. During the acoustic surveys, we recorded temperature (thermometer) and wind speed (Beaufort Wind Scale) every 30 min. We later excluded wind speed from the analysis since there was little variation across sampling days (average of 0.0–1.5 on the Beaufort Wind Scale). We also measured the mean density of trees and snags (standing dead trees) across six 10 × 10 m quadrats at each focal patch. Finally, to control for any effects of prey availability on bat activity, we used two black-light traps per site to capture nocturnal flying insects in conjunction with our bat surveys. We placed each light trap at least 50 m from the nearest acoustic receiver (Tibbels and Kurta 2003). We used the dry weight (biomass) of insects as a measure of prey availability at each site. Refer to Supplementary Materials for further information on the local variables.

Bat species identification

Seven bat species were expected to occur in the study area during the summer months: eastern pipistrelle (*Perimyotis subflavus*), northern long-eared bat (*Myotis septentrionalis*), little brown bat (*Myotis lucifugus*), silver-haired bat (*Lasionycteris noctivagans*), big

brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), and hoary bat (*Lasiurus cinereus*).

We used quadratic discriminant function analysis (DFA) to classify our recordings to species by comparing the parameters of our recorded calls to a library of validated reference calls (Russo and Jones 2002). The library consisted of 269 full-spectrum recordings from free-flying bats (all seven species) at various locations in Ontario (Hooton and Adams, unpublished data). The quadratic DFA model correctly classified 88.8% (239 of 269) of all reference calls to species. Correct classification rates for each species were: *P. subflavus* 87.9%; *M. septentrionalis* 95.2%; *M. lucifugus* 79.4%; *L. noctivagans* 92.9%; *E. fuscus* 90.2%; *L. borealis* 93.1%; and *L. cinereus* 94.9%. A MANOVA test also showed that the DFA model provided significant species discrimination (Wilk's $\lambda = 0.664$, $F = 18.844$, d.f. = 7, $P < 0.001$).

To identify our recordings to species, we queried the quadratic DFA model using the same call parameters that were used to build the identification model. If there was uncertainty or inconsistency in the classification, that recording was considered unidentifiable and labelled as 'unknown'. We used Minitab 15 (2006) for the quadratic DFA and species classifications. Refer to Supplementary Materials for further information on the species identification process.

Statistical analysis

Walsh et al. (2004) suggested that bat activity (number of bat passes per species at a site) may be used to quantify bat relative abundance provided: (a) there is no change in equipment sensitivity over time; (b) there is no trend in species detectability across time or sites; (c) passes can be reliably and consistently identified to species; and (d) survey points are consistent from site-to-site. Since our sampling protocol meets these assumptions, we used bat activity as a measure of relative abundance. When quantifying bat activity per site, we combined the number of bat passes recorded using both receivers (forest edge and interior) since almost all passes (97.5%) were recorded along the forest edges and the results of the analysis did not change if we used only passes recorded along the forest edges. To ensure that bat activity was not spatially autocorrelated across the region, we used Moran's *I* tests for each species.

To identify redundant predictor variables, we examined pairwise correlations between sample date, temperature, tree density, snag density, insect biomass, forest amount, and number of forest patches. We removed temperature from the analysis since it was strongly correlated with both date ($r = 0.650$) and insect biomass ($r = 0.550$). We also excluded landscape variables that were explicitly controlled for in the site selection process (see “Site selection”) because they represented only a narrow range of possible values and had weak correlations with our landscape predictors of interest. We tested all variables for normality using Q–Q plots and Shapiro–Wilk tests and applied a logarithmic (log 10) transformation where appropriate.

Since we could not control for local variables (date, insect biomass, tree density, snag density) in the site selection process, we controlled for their potential effects on bat activity by including them in the landscape models. To identify which local variables significantly affected bat activity, we used backward stepwise (P -to-remove > 0.05) generalized linear models (GLM) with negative binomial link functions for each species, since activity (count) data for each species showed evidence of over-dispersion. In each model, we used the number of passes per species per site as the response variable and included as predictors all local variables (date, insect biomass, tree density, snag density). For each species, we retained only those local variables with a significant ($\alpha = 0.05$) effect on activity for inclusion in the landscape models (Table 1).

To examine the effects of landscape structure (forest amount and forest fragmentation) on bat activity, we used generalized linear models with negative binomial link functions for each species at each spatial scale. In each statistical model, we included the amount of forest cover and the number of forest patches as our predictor variables of interest and we included any local variable that was significant ($\alpha = 0.05$) in the final step of the stepwise GLM for each species (see above), allowing us to statistically control for their effects while testing for the effects of the landscape variables on bat relative abundance.

We assessed statistical significance in all models using Wald χ^2 tests. We measured the proportion of the deviance explained by each predictor of interest (forest amount and number of forest patches) at each

Table 1 Results of backward stepwise (P -to-remove > 0.05) generalized linear models (GLM) examining the effects of local variables (date, insect biomass, tree density, snag density) on bat activity per species

| Species | Local variables | DE | β | P |
|---------------------------|-----------------|-------|---------|--------|
| <i>P. subflavus</i> | – | – | – | – |
| <i>M. septentrionalis</i> | Date | 0.275 | 1.102 | <0.001 |
| | Tree density | 0.149 | 0.981 | 0.012 |
| <i>M. lucifugus</i> | Date | 0.258 | 0.757 | 0.001 |
| | Tree density | 0.192 | 0.642 | 0.006 |
| <i>L. noctivagans</i> | Date | 0.259 | 2.732 | <0.001 |
| | Snag density | 0.429 | 2.541 | <0.001 |
| <i>E. fuscus</i> | Snag density | 0.111 | 0.588 | 0.016 |
| <i>L. borealis</i> | Date | 0.329 | 1.432 | <0.001 |
| | Snag density | 0.273 | −0.915 | <0.001 |
| <i>L. cinereus</i> | Date | 0.211 | 0.673 | 0.001 |

Only local predictors that were statistically significant in the last step of the stepwise GLM were included in the landscape model (DE [is the] Proportion of deviance explained by the predictor; β_i [is the] standardized regression coefficient; P -values based on Wald χ^2 -tests)

spatial scale, where the deviance explained = $1 -$ (the deviance in each fitted term/the deviance in the null or intercept-only model) (Crawley 1993). Statistical analyses were performed using SPSS 16.0 (2008), except the Moran’s I tests for spatial autocorrelation, which were performed using ArcMap 9.3 (ESRI 2006).

Results

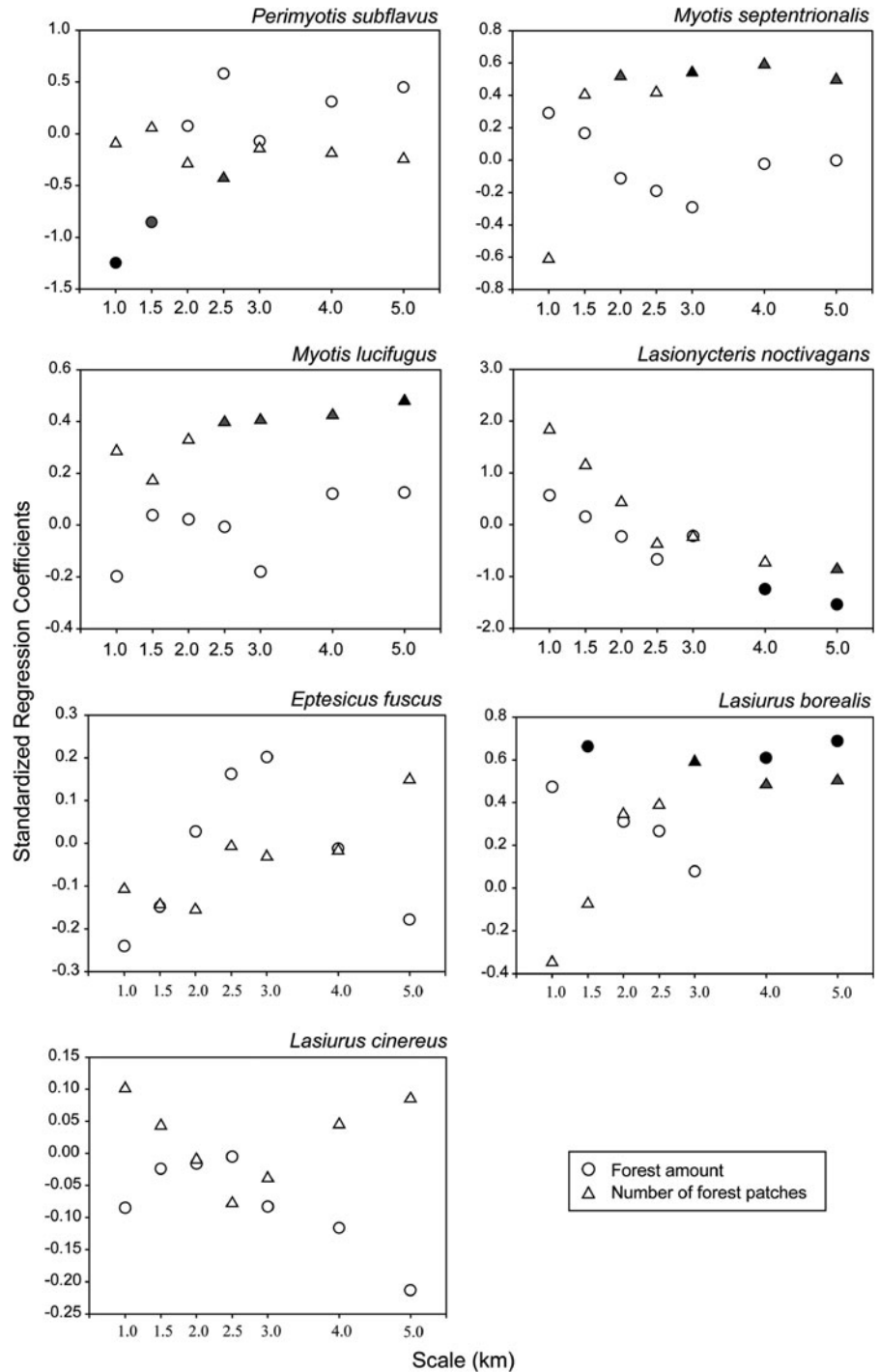
Overall, 6,652 bat passes were recorded, representing all seven local species. The most commonly encountered bat species across all landscapes was *L. cinereus* (present at 21/22 sites), followed by *E. fuscus* (20/22), *M. lucifugus* (17/22), *L. borealis* (17/22), *M. septentrionalis* (12/22), *L. noctivagans* (6/22), and *P. subflavus* (4/22). Of the 6,652 passes, 147 could not be identified to species. Bat activity was not significantly spatially autocorrelated for any species (Moran’s I from -0.157 to 0.201 , $P > 0.05$).

The effects of forest amount on bat activity were mixed across species (Fig. 4), with a significant positive effect on the relative abundance of *L. borealis* (deviance explained = 11.2%, Wald $\chi^2 = 5.626$, d.f. = 1, $P = 0.018$ at 5 km), but a significant

negative effect on *P. subflavus* (deviance explained = 16.6%, Wald $\chi^2 = 7.003$, d.f. = 1, $P = 0.008$ at 1 km) and *L. noctivagans* (deviance explained = 22.2%, Wald $\chi^2 = 4.771$, d.f. = 1, $P = 0.029$ at 5 km).

When there was evidence for an effect of forest fragmentation (number of forest patches), independent of amount, on bat activity, the effect of fragmentation was positive (Fig. 4). Specifically, forest fragmentation had a significant positive effect on the relative abundance of

Fig. 4 Scatterplots of standardized regression coefficients from generalized linear models examining the effects of forest amount and fragmentation on bat activity per species at multiple spatial scales. The filled-in symbols indicate statistical significance levels, where black is significant at the 0.05 level and grey is significant at the 0.10 level



M. septentrionalis (deviance explained = 11.9%, Wald $\chi^2 = 4.980$, d.f. = 1, $P = 0.026$ at 3 km), *M. lucifugus* (deviance explained = 12.1%, Wald $\chi^2 = 3.862$, d.f. = 1, $P = 0.049$ at 5 km) and *L. borealis* (deviance explained = 13.5%, Wald $\chi^2 = 5.839$, d.f. = 1, $P = 0.016$ at 3 km).

Discussion

We predicted that the relative abundances of all seven bat species would be higher in landscapes with more forest. This prediction was based on the assumptions that landscapes with more forest provide more potential roosting sites and that roosting site availability is the main factor limiting bat abundance in our area. Instead, we found that, when significant, the effects of forest amount were mixed across species: as the amount of forest cover increased, the relative abundance of *L. borealis* increased, while the relative abundances of *P. subflavus* and *L. noctivagans* decreased. These results support the assumption that abundance of *L. borealis* is limited by the availability of potential roosting sites (Hutchinson and Lacki 2000; Elmore et al. 2005), but do not support this assumption for *P. subflavus* and *L. noctivagans*. Carter et al. (1999) found that *P. subflavus* prefers to forage in open areas or among sparse vegetation, and Patriquin and Barclay (2003) found that *L. noctivagans* foraged almost exclusively in large forest gaps (clear-cut areas), avoiding intact forest altogether. It is therefore possible that the availability of open areas for foraging, and not the availability of potential roosting sites, may be driving the observed negative relationship of *P. subflavus* and *L. noctivagans* with forest amount.

In addition to the effects of forest amount, we also predicted a higher relative abundance of all seven bat species in landscapes with higher forest fragmentation (more forest patches), based on the assumption that landscapes with more forest patches (but the same amount of forest) would result in higher complementation between (or access to) required foraging and roosting habitat (Fig. 1a to b). Access to different types of required habitat is expected to increase the abundance and distribution of species with complementary resource needs (Dunning et al. 1992; Law and Dickman 1998). Consistent with this prediction, we found that when there was evidence for an effect of forest fragmentation, independent of forest amount, on

bat activity, the effect was positive: as the number of forest patches increased, the relative abundances of *M. septentrionalis*, *M. lucifugus*, and *L. borealis* increased. Also, consistent with the landscape complementation hypothesis, Yates and Muzika (2006) found that the probability of occurrence of *M. septentrionalis* increased when cover type interspersion increased. We therefore suggest that access to foraging sites from roosting sites (landscape complementation) is driving our observed positive responses to fragmentation. While the number of potential roosting sites is largely a function of forest amount, the spatial configuration of resources in a landscape will determine whether potential roosting sites can be used (Wunder and Carey 1996). The distance that bats travel from roosting to foraging sites may be particularly important for females due to higher energy demands during pregnancy and the effects of commuting distance on reproductive success (Tuttle 1976). As a result, *M. septentrionalis*, *M. lucifugus* and *L. borealis* select roosting sites that are close to foraging sites in an attempt to reduce commuting flight costs (Grindal 1999; O'Keefe et al. 2009). Consequently, bats may be more likely to occupy landscapes in which landscape structure facilitates access to different required resources (Humphrey 1975).

It is also possible that landscape complementation is driving the observed negative responses of *P. subflavus* and *L. noctivagans* to forest amount. As discussed, these species seem to prefer to forage in open areas. If we decrease the amount of forest cover while holding the number of forest patches constant (Fig. 1a to c), we should see an increase in the proximity of foraging and roosting sites (or higher landscape complementation). While the loss of forest cover will reduce the overall number of potential roosting sites, the quality of the roosting sites that remain may be increased due to their proximity to potential foraging habitat. If access to foraging sites from roosting sites (rather than the availability of roosting sites) is limiting the abundance of these species, the increase in landscape complementation may more than offset the loss of forest cover, resulting in an apparent positive effect of forest loss on the abundance of these species.

Could a positive response to edge habitat be a simpler explanation than landscape complementation for the positive effects of fragmentation that we observed? This seems like a reasonable suggestion

since many bat species forage along forest edges (Morris et al. 2010). This would appear to be supported in our study since the majority (97.5%) of bat passes were recorded along forest edges. However, our study was not designed to identify foraging habitat preferences in bats, and it would be inappropriate to use our data to make such inferences, for two reasons: (i) the detectability of bats sampled along forest edges is likely much higher than the detectability of bats sampled within forest patches (Walsh et al. 2004), and (ii) since we did not sample bat activity in the agricultural matrix surrounding forest patches (mainly corn and soybean production) we do not know whether bats prefer edges over these areas for foraging. Furthermore, across our landscapes there were strong positive correlations between forest edge length and both forest amount (r from 0.674 to 0.834) and number of forest patches (r from 0.641 to 0.728) at all spatial scales. If the positive effects of fragmentation were driven by a response to forest edge, we would have expected species to respond similarly (same direction and magnitude) to both forest amount and fragmentation. For *M. septentrionalis* and *M. lucifugus*, we found positive effects of fragmentation but no significant effect of forest amount on relative abundance, indicating that the responses to fragmentation are probably not driven by positive edge effects for these species. On the other hand, we did find positive effects of both forest amount and fragmentation on *L. borealis*, suggesting that the response to fragmentation by this species could be a positive response to forest edge. An analysis of the relationship between bat activity and forest edge length confirmed these assumptions, where we found a significant ($\alpha = 0.05$) positive effect of forest edge on the relative abundance of *L. borealis* but not for the other two species. However, the fact that *L. borealis* responded to forest amount and fragmentation most strongly (highest deviance explained) at different spatial scales (5 and 3 km, respectively) suggests that different mechanisms, and not a common response to edge, may be driving the observed responses. Therefore, we suggest that our fragmentation results are more consistent with the landscape complementation hypothesis than a positive edge response hypothesis.

Our initially-assumed scale of effect of landscape structure on bat abundance (1–2 km) was based on past radio-tracking studies that measured the average

distance travelled between roosting and foraging sites. However, we found that all species (except *P. subflavus*) were affected most strongly by forest amount and/or forest fragmentation at larger spatial scales than expected (3–5 km). We offer two possible explanations for this. First, there are few studies examining the scale of movement for the seven species in this study. Since estimates of movement range are strongly influenced by sample size (Worton 1987; Harris et al. 1990), the previously estimated movement distances may be under-estimates. Secondly, the studies that do exist were conducted in other regions in mostly continuous forest (as opposed to a mix of forest and agriculture, as in this study). As such, their results may simply not apply to our region.

Two of the seven bat species (*E. fuscus* and *L. cinereus*) in our study showed no significant responses to either forest amount or fragmentation at any spatial scale, despite the fact that they were present at nearly all sites. These species are among the most widespread mammals in North America, with generalist habitat associations (Shump and Shump 1982; Furlonger et al. 1987; Kurta and Baker 1990; Agosta 2002). We suggest that the generalist nature of these species resulted in a lack of association with forest amount or forest fragmentation.

Although this is a correlational study, we carefully designed it to maximize our level of confidence that any observed effects of forest loss and fragmentation are actually due to these landscape structure variables. We selected landscapes to decouple the expected correlation between forest amount and forest fragmentation (number of forest patches), allowing us to examine their independent (unconfounded) effects on the relative abundance of bats. We also simultaneously controlled, to the extent possible, any confounding variables that could affect our measures of bat activity. As a result, we can eliminate the amount of wetlands and water, road density, and building density as possible confounding variables. In addition, we statistically controlled for effects of date, prey availability and tree and snag density. We also concluded that the response of bats to landscape structure was not likely attributed to a positive response to forest edge (with the possible exception of *L. borealis*; see above).

In addition, it is likely that our sampling method actually under-estimated the positive effect of forest fragmentation, because the probability of recording a bat that was present likely decreased with increasing

fragmentation. In landscapes with higher complementation (roosting and foraging habitats intermixed), we would expect bats to move shorter distances between roosting and foraging sites due to the spatial proximity of those resources. As a result, the amount of movement per bat would be lower in a more fragmented landscape, so that the number of bats detected at a given point in the landscape (where sampling occurred) should be lower. The fact that we found relatively strong evidence for a positive effect of fragmentation on bat activity despite this sampling bias suggests that our results may be somewhat conservative.

In most studies on the effects of landscape structure on bats, the variables used to measure forest fragmentation are confounded with forest amount, making it difficult to interpret the results. However, studies have suggested that increasing the level of heterogeneity [the spatial complexity and variability of different land cover types (Li and Reynolds 1995)] in agricultural landscapes should have a positive effect on bat abundance and distribution (Loeb and O’Keefe 2006; Yates and Muzika 2006; Duchamp and Swihart 2008). Since heterogeneous landscapes consist of various interspersed land cover types, we would expect movement between required resources to be facilitated in more heterogeneous landscapes, resulting in higher landscape complementation. In our study, we focused specifically on the effects of forest loss and fragmentation since most temperate bats are considered forest species. However, increasing forest fragmentation (holding amount constant) would also likely increase landscape heterogeneity. We would therefore expect forest fragmentation and landscape heterogeneity to be highly correlated, and both measures to show positive effects on bat abundance due to the associated increase in landscape complementation.

To our knowledge, this is the first study to examine the effects of forest fragmentation independent of forest amount on bats, providing direct evidence for positive effects of fragmentation. We postulate that the mechanism driving this positive response to fragmentation is an increase in landscape complementation; that is, increased access to (and not simply amount of) foraging and roosting habitat for bats. This study was specifically designed to examine the independent effects of forest loss and fragmentation. It was not designed to compare the relative effects of these variables to other local and landscape variables

(e.g., habitat structure, amount of water), which were omitted from, or controlled for, in this study. It is possible that some of these other variables are as (or more) important to bats as forest amount and fragmentation. However, our results do imply that moderately fragmented landscapes with a diversity of land cover types (providing suitable roosting and foraging habitat for most species) should support a higher diversity and abundance of temperate bats.

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