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Fecundity determines the extinction threshold in a Canadian assemblage of longhorned beetles (Coleoptera: Cerambycidae)

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Abstract

Reproductive rate has been suggested to have a positive effect on the amount of habitat loss a species can tolerate while emigration from habitat patches has been suggested to have both positive and negative effects. Forest fragmentation has been suggested to have negative effects on forest species. We determined the extinction threshold for 12 species of saproxylic (dead wood dependent) longhorned beetles (Coleoptera: Cerambycidae) using trap catch data from Ontario, Canada. We also determined the maximum egg production of each species and whether they were likely to move outside of forest patches. We found a strong negative relationship between reproductive rate and the minimum habitat amount required for species presence. This relationship is obscured if the scale of investigation is not appropriate for the study organism. As well, species caught moving outside forest habitat had lower extinction thresholds than species not caught moving outside forest but this was not significant after accounting for reproductive rate. Fragmentation did not have an effect on the minimum habitat requirements. These relationships can inform predictions of which species will be most affected by habitat loss.

Introduction

Habitat loss due to human activities is the main reason for the current loss of species (Terborgh 1974; Ehrlich and Ehrlich 1981; Winchester 1997; Lande 1998). The conversion of natural areas to suit human activities such as urban development and agriculture (Leemans and Zuidema 1995) leaves less habitat for most other species (Walker 1992; Turner et al. 1994). This reduction in habitat results in smaller and more isolated populations which are at greater risk of extinction due to stochastic demographic and environmental variation (Pimm et al. 1988; Raup 1991; Lande 1998). Understanding how habitat loss affects the extinction risk of different species is therefore an important part of improving conservation efforts (Pimm et al. 1988; Pearson et al. 1999; With and King 1999; Fahrig 2001; Reed and Shine 2002).

An important aspect of a species' response to habitat loss is the possibility of a sudden increase in the probability of extinction at some critical amount of habitat (Lande 1987). This amount of habitat has been termed the extinction threshold (Lande 1987). This phenomenon has been found in spatially explicit models (Bascompte and Sole 1996; With and King 1999; Fahrig 2001), and there is some empirical evidence for it as well (eg: Carlson 2000). Determining the critical amount of habitat that must be preserved to prevent different species from reaching the extinction threshold should be a key part of conservation research. Moreover, if species characteristics, such as life history traits or behaviour, correlate with the threshold, we could predict which species will be at risk at a given level of habitat loss without having to resort to detailed studies on each species. One problem in conservation is that in many cases the necessary remedial actions must be informed by detailed, species-specific studies (Doncaster et al. 1996; Eriksson and Kiviniemi 1999). Easily obtained estimates of extinction risk could facilitate conservation efforts (Davies et al. 2000; Duncan and Lockwood 2001).

Species characteristics that are likely to influence the risk of extinction include the intrinsic rate of population growth (Ehrenfeld 1970; Bennet and Owens 1997; McKinney 1997) and the rate of movement between habitat patches (Terborgh 1974; Lande et al. 1998; Huxel and Hastings 1999). Species with higher reproductive rates should rebound from population declines more quickly (MacArthur and Wilson 1967). Small populations face a high risk of extinction (Pimm et al. 1988; Raup 1991; Boyce 1992; e.g: Hecnar and M'Closkey 1997) and increasing population numbers quickly will reduce the time that the population is more vulnerable to subsequent stochastic events. Therefore species with greater reproductive rates should tolerate more habitat loss and so have a lower extinction threshold. A simulation study of factors affecting the extinction threshold predicted that reproductive rate had a very strong effect on the threshold amount of habitat (Fahrig 2001). Species with higher reproductive rate were predicted to tolerate more habitat loss and so have a lower extinction threshold by this model. Vance et al. (2003) found evidence of this relationship in their study of forest breeding birds. They found a negative relationship between species reproductive rate and the amount of forest necessary for 50% probability of occurrence.

Emigration from habitat patches has also been predicted to affect the amount of habitat at the extinction threshold (Pagel and Payne 1996). Movement between habitat patches is needed for recolonization of patches in which local extinctions have occurred (Hanski et al. 1995; Britton et al. 2001). For example, Speight (1989) has suggested that many forest remnants in the United Kingdom lack many species of saproxylic beetles even 200–300 years after being isolated because the distance to any source of colonizers is too great compared to the movement distances of the beetles. Dispersing individuals may also prevent local extinctions through a rescue effect (Brown and Kodric-Brown 1977). Therefore, the ability of a species to move through non-habitat areas is predicted to restock or replenish declining populations, thereby lowering the amount of habitat necessary for persistence.

In contrast, in a simulation study Fahrig (2001) found that increasing the emigration rate leads to an increase in the amount of habitat needed for population persistence. This increase in the extinction threshold was due to the increased mortality associated with movement through non-habitat (matrix) areas (Fahrig 2001). The amount of habitat at the extinction threshold was further increased by emigration when the probability of mortality in the matrix was increased. Therefore this model predicts that species with a high probability of emigration from habitat patches will require more habitat in the landscape for persistence, or a higher extinction threshold, than species with a low probability of emigration. This difference will be greater in landscapes that contain a more hostile matrix. Because emigration has been predicted to have both negative and positive effects on population persistence, determining the effect size and direction for real species should be a conservation priority.

Habitat fragmentation within a landscape may also have an effect on the extinction threshold. Habitat fragmentation had a weak positive effect on the amount of habitat necessary for persistence in Fahrig's (2001) simulation study. Organisms that live in highly fragmented habitat may have a low probability of colonization and population rescue. In an extreme case, the patches in such a landscape may become completely isolated so that the individual patches are not colonized following local extinctions. Habitat fragmentation has probably been responsible for local extinctions of several species of ground beetles with low dispersal ability in heathland fragments (de Vries et al. 1996).

Studies of the effects of habitat fragmentation are usually confounded by the effects of habitat loss (Fahrig 1997; Trzcinski et al. 1999). In most studies, landscapes that are more fragmented also have less habitat. The isolation effects mentioned above are caused by the removal of the habitat between the remaining fragments, and not necessarily by fragmentation per se (Fahrig 1997). The correlation between habitat loss and habitat fragmentation may lead to misguided management if fragmentation is perceived to be an important determinant of species persistence after habitat loss is accounted for when this is not in fact correct. It is important to know whether the configuration of habitat resulting from habitat loss can help mitigate that loss (Fahrig 1997). We therefore looked for the effects of fragmentation after accounting for habitat amount.

Determining whether extinction thresholds are a real pattern in species response to habitat loss is important if conservation efforts are to be successful because this would indicate that additional incremental losses of habitat may lead to extinction rather than a small incremental reduction in a population with an associated small increase in the probability of extinction. As well, it is important that we understand how the characteristics of different species and landscapes affect the extinction threshold in order to predict the effects of habitat loss and to guide conservation efforts. The purpose of this study was to test the effects of reproductive rate, emigration, and fragmentation on extinction thresholds using abundance data on saproxylic longhorned beetles (Coleoptera: Cerambycidae). We predicted that the effect sizes would be ordered reproductive rate > emigration > fragmentation, following the simulation study results (Fahrig 2001). Because different species respond to habitat at different spatial scales (e.g.: Roland and Taylor 1997; Steffan-Dewenter et al. 2002; Holland et al. 2004) studies must be scaled appropriately for the study organisms (Addicott et al. 1987). We therefore looked for these relationships using the spatial scales of response of each species by measuring forest habitat at these scales.

Methods

The field work for this study was carried out in Ontario, Canada within 19 sampling areas located in the rural area to the west, south, and east of the city of Ottawa. Each 1 km^2 sampling area had 10 randomly located beetle trapping locations with a baited Lindgren funnel trap that ran for 4–5 months during the summers of 1999 and 2000. The data used in this study then is based on trap catches for approximately 1700 trap-months. Details of the sampling and the location of traps within the sampling areas can be found in Holland et al. (2004). We found the amount of habitat at the extinction threshold for 12 species of saproxylic (dead wood dependent) longhorned beetles using abundance data from Holland et al. (2004). The extinction threshold was defined as the lowest proportion of forest for which the species was present. The forest measurements were collected using digital topographical maps (National Capital Commission 1999) within ArcView GIS (ESRI Corp., Redlands, California, USA).

The larvae of longhorned beetles mine galleries within either live or dead wood (Linsley 1954) and are confined to a single tree or piece of dead wood (Hanks 1999). The adult stage is brief in comparison to the larval stage, usually lasting only a few weeks (Safranyik and Moeck 1995). We only used species that have larvae that can develop within many different species of dead wood to ensure that the amount of forest was a good measure of the amount of habitat available to these species. Using only these species also avoided the possible confounding effect of more specialized species being more prone to extinction (McKinney 1997; Kotze and O'Hara 2003).

A previous study demonstrated that each beetle species responds to forest habitat at a different characteristic scale (Holland et al. 2004). The characteristic scale of response refers to the scale (radius of circular area around a sampling site) at which the species responds most strongly to some aspect of its environment. In this study, it refers to the scale of forest measurement at which the relationship between the amount of forest habitat and the abundance of the species is strongest. Therefore, in this study the amount of forest that is available around each trapping site was measured at the scale appropriate for that species, as determined in Holland et al. (in review).

The reproductive rate for each species was determined by dissecting 20 female beetles of each species and counting the number of developed eggs. Specimens from the Holland et al. (2004) study had been stored in 70% ethanol in the summers of 1999 and 2000. The eggs were in excellent condition and easily counted when the specimens were dissected in autumn of 2002. We used the maximum number of eggs rather than the mean because some beetles would have already oviposited some eggs when caught and this was not possible to determine from the dissections. Reproductive output should also include generation time (or number of clutches per year for some taxa). For the three species for which we were able to find this information in the literature the generation time was 1 year. We assumed a generation time of 1 year for the remaining nine species and used the natural logarithm of the maximum egg production as a relative index (hereafter called reproductive rate) of population growth rate.

Cerambycidae species were classified as emigrating outside forest habitat patches or remaining within forest habitat in an earlier study (Holland et al. in review). In this earlier study we used Lindgren multiple funnel traps and flight intercept traps, both placed outside forest patches, to catch individuals emigrating from forest. This was done in areas where we were trapping within the forest patches as well and therefore knew which species were present. This allowed us to categorize 9 of the 12 species used here as emigrating or not emigrating. The other three species were not caught in the forest or matrix in areas with non-forest traps, and so these species could not be classified.

Each species was used as a data point in our analyses with extinction threshold as the response variable. To test the prediction of the effect of reproductive rate on extinction threshold we used linear regression analysis. To test the effect of emigration from forest on the extinction threshold we used a *t*-test (assuming unequal variance) to compare the proportion of forest at the extinction threshold for species caught moving outside forest habitat and those caught only within forest. We tested the effects of these two variables separately because the lack of movement data for three of the species meant these could not be included in a multiple linear regression. Using a multiple linear regression with the remaining nine species would have resulted in very low power to detect an effect of reproductive rate, but we did use multiple regression analysis to check the emigration results after taking reproductive rate into account.

A possible confounding factor in the analysis of the effect of emigration is the difference in commonness among the different species. If all species are caught moving outside forest in direct proportion to their relative numbers and not because there is a real difference in movement, this would lead to the more common species being assigned to the "species moving" category despite the lack of a difference. To see if this was occurring we conducted a *t*-test (assuming unequal variance) to compare the mean total number of individuals caught in the moving and not moving categories.

We used the Effective Number of Habitat Patches (ENHP) to measure forest fragmentation (Jaeger et al. in review). The formula for this is ENHP $= 1/(\sum(A_i/A_t)^2)$, where A_i is the area of habitat patch i, and A_t is the total area of the study region. In our case, A_t is the area encompassed by a circle with radius equal to the characteristic scale of response of the species to forest. The ENHP is the reciprocal of the degree of coherence (C); conceptually, C measures the probability that any two points randomly placed in the region will occur in the same habitat patch (Jaeger 2000). We wanted to include small treed patches and fencerows when measuring fragmentation, so digital 1:15000 colour air photographs (City of Ottawa 2000) were used to digitize all treed patches that were not included in the original digital topographical maps (National Capital Commission 1999). M. Burrell digitized these features using ArcView. Fencerows were digitized as continuous features whenever the canopy gaps were less wide than twice the canopy width at the gap. All treed fencerows and small treed patches within 2 km of the trapping sites were digitized. We then created two separate forest habitat themes with which to measure fragmentation: one with all originally mapped forest patches plus the smaller patches that we digitized, and one that further included all treed fencerows. Within each theme we merged all contiguous and overlapping patches and fencerows. Therefore two patches joined by a fencerow were considered a single patch. Patches that appeared separate within the 2 km radius, but that were actually joined by some connection beyond the 2 km line, were treated as a single patch. The ENHP was then calculated by measuring the proportion of the region that each forest patch represented within a given radius of each of the trapping sites using a custom ArcView script. The fragmentation with and without fencerows was calculated at spatial scales of 20–200 m in 20 m increments, and 400 m to 2 km in 200 m increments. We compared the range of values of the fragmentation values across all scales both with and without fencerows included. Both these measures of fragmentation had a relatively large range of values at 1400 m so we used this as the scale at which to compare the effects of habitat amount and fragmentation.

To test for effects of habitat amount and fragmentation we used multiple logistic regression with occurrence as the response variable and habitat amount and fragmentation at 1400 m as predictor variables. We included species as a class variable. The measures of fragmentation with and without fencerows were highly correlated (Pearson $r = 0.8657$) so we used 2 models, each including one of these. These tests had inflated power because they used data from all 190 plots despite the fact that the measured predictor variables are not from spatially independent areas at the 1400 m scale. We adjusted the results for this by applying a correction factor to the standard error of the estimates before calculating the Wald statistic and testing for significance. At 1400 m, randomly sampling spatially independent sites (separated by at least 2800 m) yields an average of 18 sites possible (Figure 1). We therefore multiplied the standard error values by $(190/18)^{1/2} = 3.249$. We also checked the significance of habitat amount-fragmentation interaction terms.

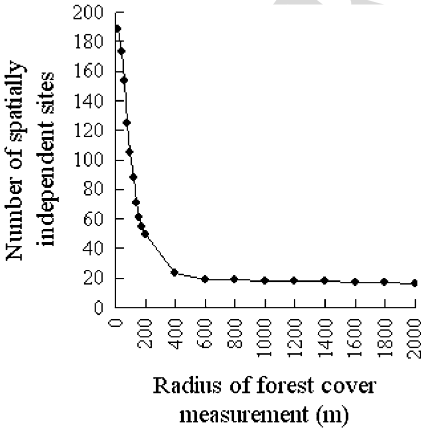

Figure 1. The relationship between the spatial scale at which we measured habitat and the number of sites that remained spatially independent, or did not have overlapping areas of forest cover measurement.

Results

Figure 2 shows the abundance of each species across the range of forest habitat proportions, with this proportion measured at the characteristic scale of response to forest habitat for each species (Holland et al. 2004). The proportion of forest at the extinction thresholds for the 12 species ranged from 0.0476 to 0.9897 (Table 1) forest cover. The maximum number of eggs per female within a species ranged from 9 to 236, corresponding to reproductive rates of 2.20 to 5.46 (Table 1). Larger beetle species tended to have greater egg counts. To test this we performed a linear regression between mean body length data from Holland et al. (in review) and the maximum egg count with the latter as the response variable. There was a significant positive relationship between maximum egg count and body size ($R^2 = 0.555$, $F = 12.5$, df $= 11$, $p = 0.0054$). There was a significant negative effect of reproductive rate on the extinction threshold (Figure 3a, $R^2 = 0.617$, $F = 16.1$, df $= 11$, $p = 0.0025$). Species with higher reproductive output were able to persist in areas with less forest habitat, as predicted. This relationship explained 61.7% of the variance in the extinction threshold values.

The mean number caught and associated standard errors of the emigrating and not emigrating categories were 40.0 ± 11.0 and 46.1 ± 13.8 respectively. This test clearly showed that the species assigned to the moving category were not more common than those we didn't catch moving ($t = 0.371$, df $= 5$, $p > 0.3$), so that there is a real difference in the probability of emigration from forest between the two groups. The *t*-test revealed a significant difference ($t = 3.935$, df $= 7$, $p < 0.01$) in the extinction thresholds between the species we caught moving and those not caught moving outside forest habitat (Figure 4). The species that were caught moving had lower extinction thresholds. To ensure that this result held after accounting for reproductive rate we used a multiple linear regression with emigration and reproductive rate as predictors of the extinction threshold. Despite the lowered power of this analysis reproductive rate remained a strong predictor of the extinction threshold amount of habitat, but emigration was no longer significant.

The logistic regression with fragmentation measured including fencerows was not significant

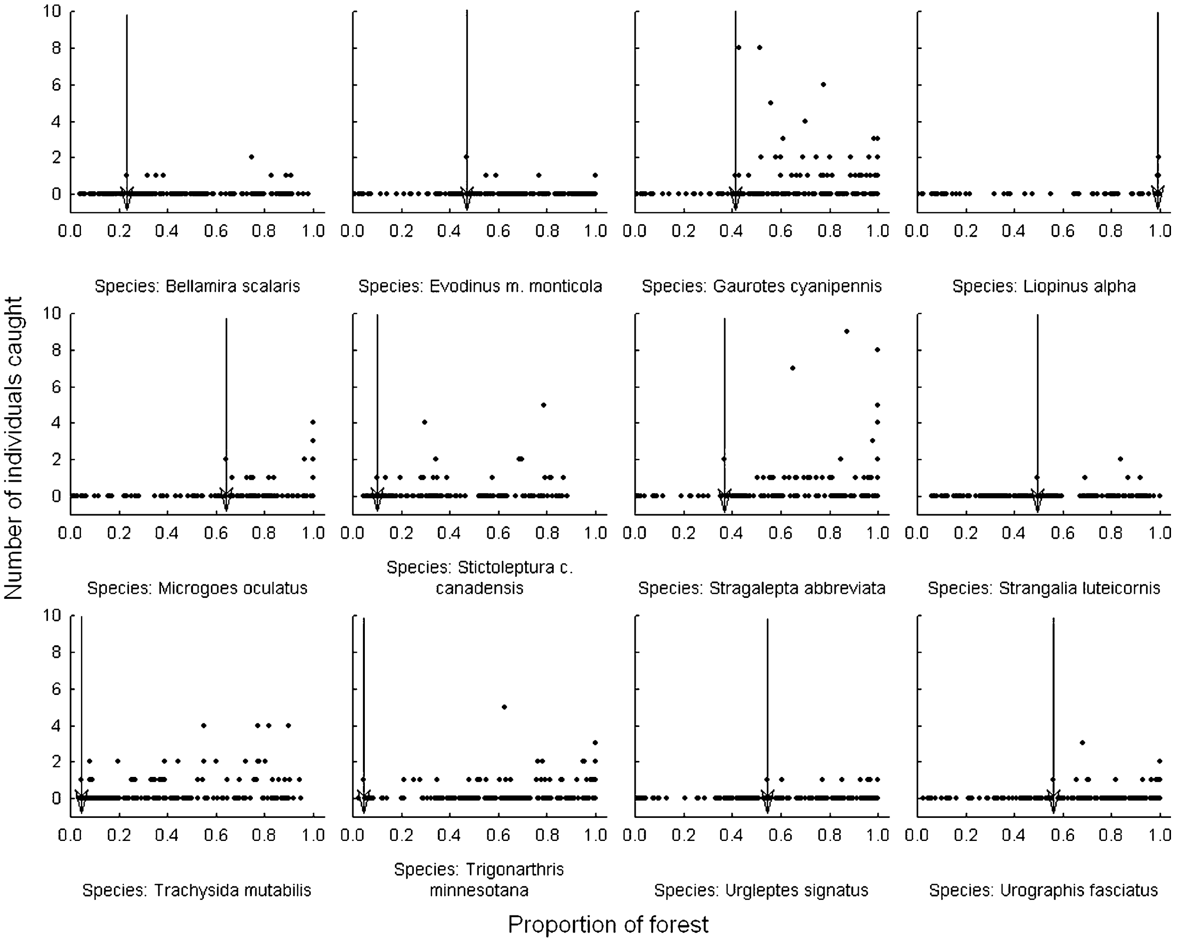

Figure 2. Determining the extinction threshold for the Cerambycidae species. The number of individuals caught at our sampling sites was plotted against the proportion of forest cover around the sites. The forest cover was measured at the characteristic scale of response for each species (Table 1). The arrows indicate the extinction threshold amount of habitat for each species.

Table 1. Values of the predictor variables and the extinction thresholds.

Species	Max. eggs	Repr. rate	Emigrate?	Extinction threshold	Scale of response (m)
Bellamira scalaris (Say)	236	5.46	N	0.231	1000
Evodinus m. monticola (Rand.)	37	3.61		0.471	160
Gaurotes cyanipennis (Say)	101	4.62	N	0.413	160
Liopinus alpha (Say)	10	2.30		0.990	20
Microgoes oculatus (LeC.)	20	3.00	N	0.641	60
Stictoleptura c. canadensis (Oliv.)	160	5.08	Y	0.101	1600
Strangalepta abbreviata (Germ.)	40	3.69	N	0.369	120
Strangalia luteicornus (F.)	9	2.20		0.497	800
Trachysida mutabilis (Newm.)	80	4.38	N	0.048	1200
Trigonarthris minnesotana (Csy.)	152	5.02	Y	0.048	200
Urgleptes signatus (LeC.)	14	2.64	N	0.546	140
Urographis fasciatus (DeG.)	58	4.06	N	0.559	180

The extinction thresholds were determined as per Figure 2, with the amount of forest cover measured at the characteristic scale of response of each species.

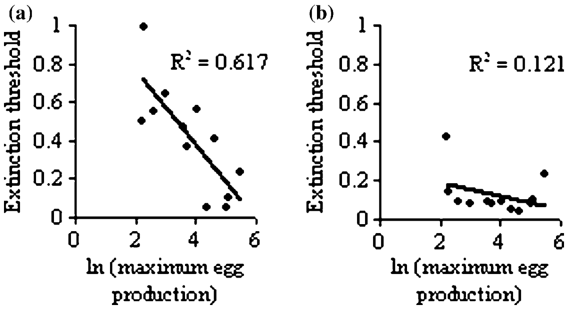

Figure 3. Relationship between reproductive rate and the extinction threshold. In a, each of the twelve species had the extinction threshold determined at the spatial scale that it responds most strongly to forest habitat, or the characteristic scale of response to forest habitat. The equation of the best fit line was ext.thresh. = −0.1929(ln(max. egg. prod.)) + 1.1499. In b, each of the 12 species had the extinction threshold determined by plotting the abundance against the proportion of forest within 1 km of the sampling site for each species. This relationship is no longer significant when done at this scale.

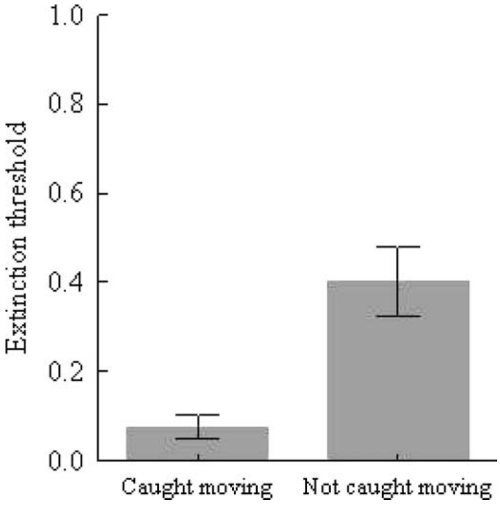

Figure 4. Comparison of extinction thresholds of species caught outside forest habitat ($N = 2$) and species not caught outside of forest habitat ($N = 7$). The species caught outside forest habitat had a lower mean habitat amount at the extinction threshold. Emigration was not significant when included in a multiple linear regression with reproductive rate as a second predictor variable.

even before correcting for the number of spatially independent trapping locations so we assumed that the fragmentation measured without these features was a better predictor of occurrence. The habitat amount-fragmentation interaction terms were not significant in either model. After adjusting the Wald statistics for the possible number of spatially independent sites, fragmentation measured without fencerows was not significant (Wald = 1.0566, df = 1, $p > 0.3$) while habitat amount was still a marginally significant positive predictor of occurrence (Wald = 3.8075, df = 1, $p = 0.051$).

Discussion

The results support the prediction that reproductive rate has a strong negative effect on the extinction threshold amount of habitat. Species with low reproductive rates were only found in landscapes with a large proportion of forest remaining, whereas species with higher reproductive rates were found in landscapes with less forest habitat remaining. This result implies that, as habitat is lost in a landscape, species with lower reproductive rates experience local extinctions before species with higher reproductive rates. This agrees with the empirical study of forest breeding birds by Vance et al. (2003). Similar to our study, their results imply that species with lower reproductive rates will become locally extinct first as habitat is lost.

Using an arbitrary scale to determine the extinction threshold may have caused us to miss the reproductive rate-extinction threshold relationship. To test this idea we used an arbitrary 1 km scale (radius around each trapping site) to measure forest and plotted the abundance of each species against the proportion of forest within a 1 km radius. We again considered the extinction threshold to be the minimum proportion of forest at which a species occurred. A regression of the extinction thresholds against the reproductive rate of the species reveals a much weaker trend (Figure 3b) that is not statistically significant ($R^2 = 0.121$, $F = 1.378$, df = 11, $p > 0.2$). The variance explained by this regression is about one-fifth that explained by the relationship that we found by using the characteristic scale of response for each species. The non-significance of the results obtained using the same arbitrary 1 km scale for all species would have led to the conclusion that reproductive rate does not have an effect on the extinction threshold. The difference between this result and that found using the characteristic scale of response for each species underscores the importance of conducting studies at an appropriate spatial scale (compare Figure 3a and b).

Vance et al. (2003) used the same spatial scale for all species in their study of forest breeding birds. Interestingly, the variance explained by the reproductive rate-habitat necessary regression in their study ($R^2 = 16$) is very close to the value we obtained when using a constant scale for all species ($R^2 = 0.121$). This suggests that the magnitude of the reproductive rate effect on the extinction threshold amount of habitat may be similar in different taxa. It seems likely that they would have found an even stronger effect if the habitat necessary for 50% probability of persistence had been measured at the characteristic scale of response for each species. Although the variance explained in their study is only slightly higher than in our results with a constant scale, they did find a significant effect of reproductive rate this way, probably because they had a larger number of species ($n = 41$).

Larger beetles tended to have a greater maximum egg count. This raises the possibility that the mean size of the species is largely responsible for determining the extinction threshold rather than fecundity. We did not have any *a priori* reason to suspect that body size would influence the extinction threshold and so did not include this as a predictor. In fact, studies that do use body size as a predictor of proneness to extinction tend to use this as a composite indicator of other variables such as fecundity. In our study, the size-reproductive rate is positive, opposite to most studies of other taxa. We conclude that larger beetles tended to have greater reproductive and therefore lower extinction thresholds; the threshold amount of habitat is determined by reproductive rate, not body size.

Our results indicate that species prone to emigration out of forest habitat may have a lower extinction threshold than species that do not move out of forest habitat. However this result did not hold in the (admittedly low power) multiple regression with reproductive rate. It is possible that the increase in non-forest area does not lead to an increase in mortality during movement for the species that move out of forest. The idea that non-habitat matrix is completely hostile is an ideological artifact of island biogeography (D'Eon 2002) and does not always apply to species moving between terrestrial habitat patches (Huxel and Hastings 1999). As adults, many species of longhorned beetles eat pollen and nectar (Yanega 1996) and are commonly found on flowers of shrubs and herbaceous vegetation in fencerows (Samways 1994) and other non-forest habitats. For species that are commonly found feeding as adults within non-forest habitat, movement into non-forest areas may actually increase survival of these species. Some species have evolved either mimicry or cryptic colouration (Yanega 1996), suggesting that they are at least partially adapted to predators. Laurance (1991) found that the extinction proneness of 66 species of rainforest mammals was negatively related to their tolerance of the matrix.

It is also likely that the species that move outside forest to obtain floral resources are more likely to recolonize forest patches that experience local extinctions than species that do not readily move through non-forest areas. Females of the species that move outside forest must locate suitable larval habitat for laying eggs. Shibata (1987) has found evidence to suggest that species of longhorned beetles that must move to find food and then oviposition sites disperse farther than species that are not required to do so. It is very likely that in these species, females lay eggs in a forest patch other than the one they are from. Therefore, the species that leave forest habitat likely have higher rates of patch recolonization and higher rates of rescue from low numbers than species that do not move outside forest habitat. Unfortunately, we were not able to reliably separate the effects of reproductive rate and emigration to test the effect of emigration.

Our coarse classification of movement propensity may mask more complex trends in the effect of dispersal on the extinction threshold. Thomas (2000) used data on butterflies grouped into three movement classes and found that species of intermediate mobility have shown the greatest recent declines, probably because these species tended to move out of habitat but not locate another suitable habitat location. The movement classes that Thomas (2000) made use of were based on actual movement distances. There is no information on movement for most species of cerambycids, and our flight intercept trapping in non-forest was an attempt to gain some of this knowledge. Improvements in dispersal monitoring techniques may yet allow for the collection of detailed movement data on cerambycids. There are at least two ways that we could reconcile our classification with the results of Thomas (2000). One possibility is that our binary emigrate/don't emigrate classification is appropriate and that the species we caught moving are comparable to lumping Thomas's long and medium range dispersers. If this scheme is appropriate then our results may not coincide with those for the butterflies. A second possibility is that there are some species that move so little that they were present but not caught even by our traps located within forest habitat. We could then classify species into three classes: species caught moving outside forest (long-distance dispersers), species caught only within forest (medium-range dispersers), and species present but not caught at all (non-dispersers). The non-dispersers may be unaffected by processes outside a very small area around their host log and so not face extirpation from habitat loss. If it is accurate then it is possible that our species are reacting to habitat loss in a manner similar to Thomas's butterflies if the unobserved non-dispersers have a low extinction threshold. Of course this idea is impossible to test with our current data since it relies on an unobserved class of species.

Our results show that fragmentation is not important in determining the occurrence of these species. In this test we gave considerable weight to the fragmentation variable by conducting the multiple logistic regression at a spatial scale where the range of fragmentation values was greatest. In fact they had a much greater range than the forest habitat amount values at this scale, but habitat amount was still a marginally significant predictor of occurrence while fragmentation was not. This result agrees with other studies that have found that habitat amount is much more important than habitat fragmentation (McGarigal and McComb 1995; Trzcinski et al. 1999). Conservation efforts directed at these species should focus on forest habitat retention, and should not be misguided by the idea that configuration can ameliorate habitat loss (Fahrig 1997).

If the distance that edge effects extend into the forest is large relative to the characteristic scale of response, taxa that respond to habitat at relatively small scales may seem to have very high extinction thresholds only because they are 'interior species'. This would cause the species to only occur in areas that are surrounded by close to 100% forest 'habitat', but only because the edge is not properly included in the measurement of the amount of habitat. Researchers studying interior species should be aware of the possibility of such false extinction thresholds. While such responses are more correctly viewed as a response to habitat type, they could still provide information on suitable conditions for the species of concern. This was probably not a problem in the present study, as none of the longhorned beetles in this study have been described as interior species to our knowledge. Eight species considered here responded at small scales of up to 200 m, but within these species the observed extinction thresholds ranged from 0.0478 to 0.9897. The only species with a small characteristic scale of response and a high extinction threshold was *Liopinus alpha*.

We know that the location and size of forest patches in our 29 study areas has been relatively constant during the past 25–30 years (Contreras 2002). However, much of the forest cover in the study region around Ottawa, Ontario was removed during intensive logging during the early and mid-1800's (Keddy 1993). It is possible that the intervening period has not been long enough for the cerambycid species in the area to come to equilibrium with the resulting habitat composition. If there is an extintion debt (sensu Tilman et al. 1994) this could affect our determinations of the extinction threshold amount of habitat. The affected species could be extant but lost from some areas in the future even without further addition loss of forest habitat. In such a scenario our estimates of the extinction threshold amount of habitat would be low; species would actually require more habitat than is suggested. Further, we do not know if the extinction thresholds should all be shifted by the same amount for the different species. Using insects can help to minimize the possibility of a time lag in response to habitat loss if species with short generation times are used. Given additional data to make comparisons, we could check for the possibility of an extinction debt by looking for a shift within the assemblages towards more rare species (Hanski and Ovaskainen 2002).

Our findings show that the minimum amount of habitat required for occurence depends on life history attributes of the species. Species with greater reproductive rate were able to persist in areas containing less forest habitat than species with lower reproductive rates. Relationships between species and their environment are obscured if the scale of investigation is not relevant to the species being studied. We suggest that the first step in such studies should be careful consideration of the research questions and the determination of the spatial scale at which the studied relationship is relevant.

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