EXTINCTION DEBT OF FOREST PLANTS PERSISTS FOR MORE THAN A CENTURY FOLLOWING HABITAT FRAGMENTATION

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Abstract. Following habitat fragmentation individual habitat patches may lose species over time as they pay off their ''extinction debt.'' Species with relatively low rates of population extinction and colonization (''slow'' species) may maintain extinction debts for particularly prolonged periods, but few data are available to test this prediction. We analyzed two unusually detailed data sets on forest plant distributions and land-use history from Lincolnshire, United Kingdom, and Vlaams-Brabant, Belgium, to test for an extinction debt in relation to species-specific extinction and colonization rates. Logistic regression models predicting the presence–absence of 36 plant species were first parameterized using data from Lincolnshire, where forest cover has been relatively low (~5–8%) for the past 1000 years. Consistent with extinction debt theory, for relatively slow species (but not fast species) these models systematically underpredicted levels of patch occupancy in Vlaams-Brabant, where forest cover was reduced from ~25% to <10% between 1775 and 1900 (it is presently 6.5%). As a consequence, the ability of the Lincolnshire models to predict patch occupancy in Vlaams-Brabant was worse for slow than for fast species. Thus, more than a century after forest fragmentation reached its current level an extinction debt persists for species with low rates of population turnover.

Key words: Europe; extinction debt; forest plants; habitat fragmentation; land use history; metapopulation; relaxation; transient dynamics.

INTRODUCTION

When habitats are fragmented, species are expected to go extinct from small isolated habitat patches, but this process of ''relaxation'' (Diamond 1972) takes time. Until relaxation is complete, such habitat patches are said to have an ''extinction debt'' (Tilman et al. 1994), in that some species are destined to go locally extinct even in the absence of further perturbations. Identifying extinction debts in nature is critically important for assessing the degree to which biological surveys at one point in time provide accurate estimates of the capacity for landscapes to maintain biodiversity, and also for addressing the fundamental question of just how long it takes for populations and communities to come into equilibrium with a given landscape structure following disturbance.

Testing for the presence of an extinction debt requires either long-term data on species losses following habitat fragmentation (e.g., Brooks et al. 1999), or data from multiple similar landscapes with varying histories

of fragmentation (e.g., Berglund and Jonsson 2005). The relative paucity of such data has resulted in few empirical demonstrations of extinction debts. Most studies to date have tested for deviations from statistical predictions of species richness (e.g., based on species-area curves) assuming the extinction debt was already paid off (e.g., Diamond 1972, Cowlishaw 1999, Berglund and Jonsson 2005). These analyses have revealed some clear examples of extinction debt, but focusing on species richness may mask important differences among species in their likelihood of showing an extinction debt. For example, species with relatively high rates of stochastic population extinction and colonization are expected to ''pay off'' their extinction debt quite rapidly compared to species with much lower rates of stochastic extinction (Ovaskainen and Hanski 2002, Vellend 2004*a*). Here we analyze two unusually detailed data sets on plant distributions from different regions of Europe with contrasting histories of land use to test for an extinction debt in relation to species-specific extinction and colonization rates.

Temperate deciduous forests are highly fragmented across all of Europe, but there are important regional variations in the history of land use and forest cover

(Kirby and Watkins 1998). In Lincolnshire, United Kingdom, the first of our two landscapes, forest cover has been relatively stable over the last 1000 years, varying between ~5% and 8% cover (Fig. 1; Peterken 1976, Peterken and Game 1984, Verheyen et al. 2004). In contrast, forest cover in Vlaams-Brabant, Belgium decreased drastically from ~25% in 1775 to <10% a century later, with a further slight decrease to ~6.5% in the present day landscape (Fig. 1; Jacquemyn et al. 2001). Even during periods of relative stability in forest cover, both landscapes have experienced low rates of forest destruction and creation, generally <1% per year. These two regions share a very similar present-day pattern of forest cover and a large number of forest plant species, and their contrasting histories lead to a clear prediction based on extinction debt theory: species' patch occupancy rates should be higher in Vlaams-Brabant than predicted by models parameterized with Lincolnshire data. However, given that the major decrease in forest cover in Vlaams-Brabant occurred more than a century ago, we might expect to find evidence of an extinction debt only for relatively ''slow'' species, if at all.

Our analyses also addressed the closely related issue of how well models parameterized with data in one landscape can predict species' distributions in a second landscape. This question is central to applied branches of ecology (Scott et al. 2002), and is typically addressed by splitting a single data set into a training data set and a test data set (Fielding 2002), rather than using two truly independent data sets. Though we have a specific prediction based on one specific *difference* in land-use history, the two landscapes are otherwise very similar, and have been so for more than a century (Fig. 1). Thus, if species respond to landscape structure in similar ways in different regions, we may expect models parameterized in Lincolnshire to do a reasonable job of predicting distribution patterns in Vlaams-Brabant. Thus, in addition to testing for evidence of an extinction debt, we also assessed the cross-landscape predictive power of these models both quantitatively and qualitatively. That is, even if predicted and observed levels of patch occupancy are quite different, it may still be the case that models capture *relative* variation in occupancy rates among patches with different characteristics, and that variation among species in the patch characteristics they respond to may be correlated across landscapes.

METHODS

Detailed accounts of the two data sets used here are provided in Peterken and Game (1984) for Lincolnshire, and by Jacquemyn et al. (2001) for Vlaams-Brabant. Briefly, for a 930-km^2 portion of central Lincolnshire, United Kingdom, Peterken and Game (1984) recorded the presence or absence of all woodland vascular plants in 326 patches of forest, which represented all but a very few of the smallest patches in this land-
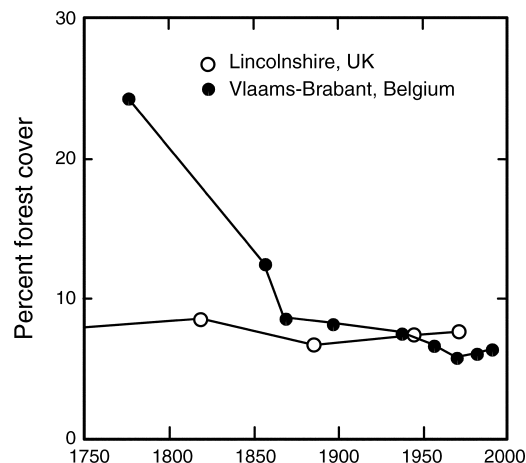

FIG. 1. Changes in percent forest cover in Lincolnshire, United Kingdom, and Vlaams-Brabant, Belgium, since 1750. Forest cover data for Lincolnshire (Peterken 1976) represent a subset of the landscape for which we report analyses here (Peterken and Game 1984). This subset of Lincolnshire probably has slightly higher forest cover than the broader region. In the broader Lincolnshire landscape, 5.6% of the land was forested as of 1980 (Peterken and Game 1984), very close to the percent cover of forest in Vlaams-Brabant as of 1991 (6.5%; Jacquemyn et al. 2001).

scape. For each forest patch, we know its area, its spatial coordinates, and an estimate of its age as the time since the forest established on abandoned agricultural land. Ages were based on historical records and maps, and range from 17 to 450 years; patches assigned to the 450-year-old age class have persisted as forest since at least 1600. Our analyses here focused only on those 36 species present in 20–80% of patches in Lincolnshire (for statistical reasons) and also present in at least some patches in Vlaams-Brabant (for direct cross-landscape comparisons). Further details on the two landscapes are presented in Appendix A.

For these 36 species (and 27 others), we recently reported an analysis using a modified version of Hanski's (1994) incidence function model (IFM) to estimate average species-specific colonization and extinction rates across patches in Lincolnshire (Verheyen et al. 2004). These colonization and extinction rates were tightly correlated across species ($r = 0.75$), so a principal components analysis was used to derive a single variable describing where species fall along the continuum between slow metapopulation dynamics (low colonization and extinction rates) to fast metapopulation dynamics (high colonization and extinction rates). This axis, in turn, was strongly related to species' seed production per plant (Spearman $r = 0.72$, $P < 0.001$), age at first reproduction ($r = {}^-0.41$, $P < 0.02$), and dispersal mode (Verheyen et al. 2004), indicating that it represents a meaningful descriptor of proneness to local extinction and colonization capacity. We refer to this axis as the ''colonization-extinction rate axis,'' and use it to test predictions concerning extinction debts.

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Species with low and high values of this axis are referred to as ''slow'' and ''fast,'' respectively (see also Franco and Silvertown 1996).

The data collected by Jacquemyn et al. (2001) in Vlaams-Brabant was essentially identical to that in Lincolnshire, with species lists recorded for 239 forest patches in a 42-km^2 area. Patch ages ranged from 11 to 250 years, based on historical maps dating back to 1775. Of the 36 above-mentioned species, 21 occurred in 20–80% of the patches in Vlaams-Brabant.

For each of the 36 above-mentioned species, we conducted a multiple logistic regression analysis predicting patch occupancy in Lincolnshire with four independent variables: log-transformed patch area, patch age, a log-transformed index of connectivity, and an index of habitat unsuitability. All of these models were highly statistically significant ($P < 0.001$). We used the species-specific connectivity and habitat unsuitability indices reported in Verheyen et al. (2004). Connectivity is a weighted sum based on the distance of a focal patch to all other occupied patches, and habitat unsuitability is the absolute difference between a given species' Ellenberg indicator value and the mean value for all other species present in the patch, summed across indicator values for soil humidity, acidity, and nitrogen (see Appendix A for details). The resulting parameter estimates in the logistic regression models based on Lincolnshire data were then used to predict the probability of each patch in Vlaams-Brabant being occupied by each species; for these analyses we used the same four independent variables calculated in exactly the same way. In addition, we conducted separate logistic regression analyses based only on Vlaams-Brabant data for the 21 out of 36 species that were present in 20–80% of the patches in Vlaams-Brabant. All of these models were also statistically significant ($P < 0.01$).

The above-described analyses resulted in two sets of predictions for Vlaams-Brabant. First, for 36 species we had predicted probabilities of occupancy for each patch based on the models estimated with the entirely independent Lincolnshire data. The mean of these predicted probabilities across all patches represents the predicted overall patch occupancy for a given species, which we compared with observed patch occupancy across species by simple correlation. We then calculated the difference between observed and predicted patch occupancy for each species, and used linear regression to ask whether this difference varied according to the colonization–extinction rate axis. The prediction is a negative relationship, with slow species showing elevated patch occupancy as a signature of extinction debt.

The second set of predicted probabilities of occupancy in each patch was for 21 species based on the model estimated with the Vlaams-Brabant data themselves. The predictions of this latter model necessarily provide a better fit to the data (e.g., log-likelihood) than the Lincolnshire model because the parameters were
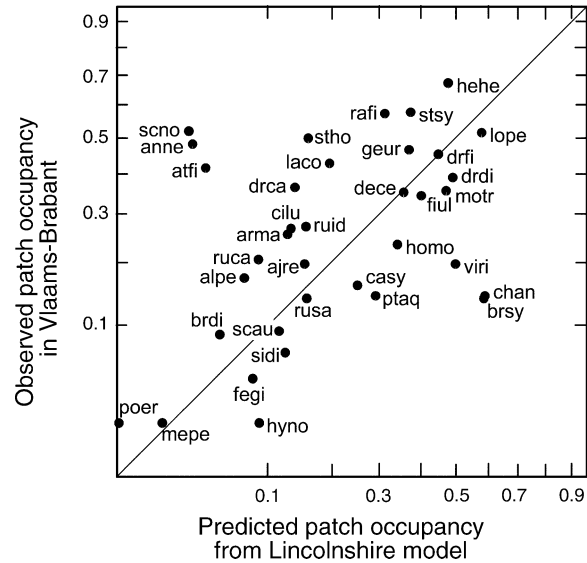

FIG. 2. Observed average patch occupancy for 36 species in Vlaams-Brabant vs. predicted patch occupancy based on logistic regression models parameterized with data from Lincolnshire ($r = 0.43$, $P = 0.009$). The diagonal is the 1:1 line. Species abbreviations are as follows: ajre, *Ajuga reptans*; alpe, *Alliaria petiolata*; anne, *Anemone nemorosa*; arma, *Arum maculatum*; atfi, *Athyrium filix-femina*; brdi, *Bryonia dioica*; brsy, *Brachypodium sylvaticum*; casy, *Carex sylvatica*; chan, *Chamerion angustifolium*; cilu, *Circaea lutetiana*; dece, *Deschampsia cespitosa*; drca, *Dryopteris carthusiana*; drdi, *Dryopteris dilatata*; drfi, *Dryopteris filix-mas*; fegi, *Festuca gigantea*; fiul, *Filipendula ulmaria*; geur, *Geum urbanum*; hehe, *Hedera helix*; homo, *Holcus mollis*; hyno, *Hyacinthoides non-scripta*; laco, *Lapsana communis*; lope, *Lonicera periclymenum*; mepe, *Mercurialis perennis*; motr, *Moehringia trinervia*; poer, *Potentilla erecta*; ptaq, *Pteridium aquilinum*; rafi, *Ranunculus ficaria*; ruca, *Rubus caesius*; ruid, *Rubus idaeus*; rusa, *Rumex sanguineus*; scau, *Scrophularia auriculata*; scno, *Scrophularia nodosa*; sidi, *Silene dioica*; stho, *Stellaria holostea*; stsy, *Stachys sylvatica*; viri, *Viola riviniana*.

estimated specifically to maximize the likelihood of having observed the data given the model. However, this model involved estimating five parameters (including a constant term) from the data, compared to the zero free parameters involved in making predictions using the Lincolnshire model. Thus, we compared predictions based on the two models using the Akaike Information Criterion (AIC, see Burnham and Anderson 2003), which ''penalizes'' models for their number of free parameters. The difference in AIC values for the two models (denoted Δ_i) was used to compare their relative fits to the data (Burnham and Anderson 2003), and we predicted that Δ_i would vary negatively with the colonization–extinction rate axis. That is, data from Lincolnshire should provide a relatively poor basis for predicting patch occupancy of slow species in Vlaams-Brabant because their distributions are less likely to have reached equilibrium with current landscape structure than fast species. This analysis complements the analysis based on simple differences between mean ob-
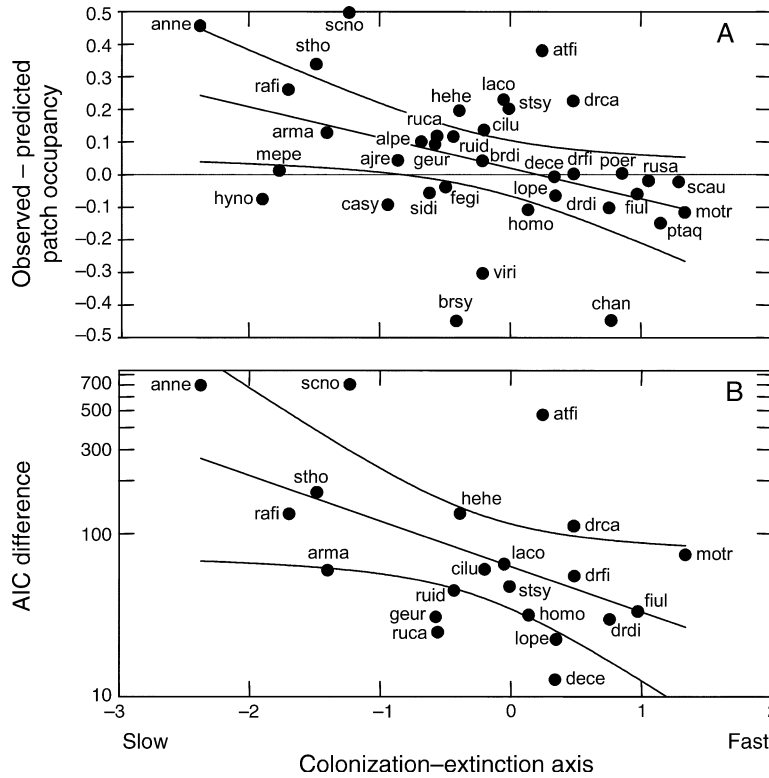
FIG. 3. (A) The difference between observed and predicted patch occupancies (see Fig. 2) vs. species' positions on a colonization–extinction axis for 36 species ($r^2 = 0.18$, $P = 0.009$). Colonization and extinction rates increase from left to right (see *Methods* for details). (B) For 21 species, the difference in the Akaike Information Criterion (AIC) between a model parameterized in Lincolnshire and a model parameterized using Vlaams-Brabant data vs. species' positions on a colonization–extinction axis ($r^2 = 0.28$, $P = 0.013$). The log-likelihood for the predictions of each model (used to calculate AIC) was calculated based on comparisons with observed patch occupancy in Vlaams-Brabant. In both panels, the regression line with 95% confidence intervals is shown. Species abbreviations are as in Fig. 2.

served and predicted patch occupancy by using a more comprehensive measure of model-data fit.

To provide a visual assessment of how predicted patch occupancy from the Lincolnshire models relates to observed patch occupancy in Vlaams-Brabant, for each species we first divided the 239 patches into four quartiles based on the value of predicted patch occupancy from the Lincolnshire model. We then plotted the predicted vs. observed mean patch occupancy within each quartile of data.

RESULTS AND DISCUSSION

Observed patch occupancy per species in Vlaams-Brabant was positively correlated with patch occupancy predicted from the Lincolnshire models, but there was considerable scatter in this relationship (Fig. 2; square-root transformed data, $r = 0.43$, $P = 0.009$). As predicted based on extinction debt theory, the difference between observed and predicted patch occupancy showed a significant negative relationship with the colonization–extinction axis (Fig. 3A, $r^2 = 0.18$, $P = 0.009$). Slow species showed higher levels of patch occupancy than predicted based on the Lincolnshire models, with the 95% confidence intervals not over-

lapping with zero, whereas fast species showed no such difference (Fig. 3A). For the 21 species for which logistic regression analyses were also conducted using the Vlaams-Brabant data, the difference in AIC between the Lincolnshire and Vlaams-Brabant predictions was also significantly negatively related to the colonization extinction axis (Fig. 3B; $r^2 = 0.28$, $P = 0.013$). That is, the ability of the Lincolnshire models to predict patch occupancy in Vlaams-Brabant (relative to models parameterized in Vlaams-Brabant) was worse for slow than fast species, as predicted by extinction debt theory. Details of the logistic regression analyses are presented in Appendix B.

Studies of forest plant distributions in relation to land-use history in the north temperate zone have provided a powerful system for addressing the time scale of biotic responses to disturbance (Flinn and Vellend 2005, Honnay et al. 2005). Studies to date have convincingly demonstrated that the process of colonization in post-agricultural forests may continue for several centuries, with 100–200-year-old recent forests still having lower species richness of forest herbs than ancient forests (e.g., Jacquemyn et al. 2001, Vellend 2003, 2004*b*). In the terms of Hanski (2000), it takes a long
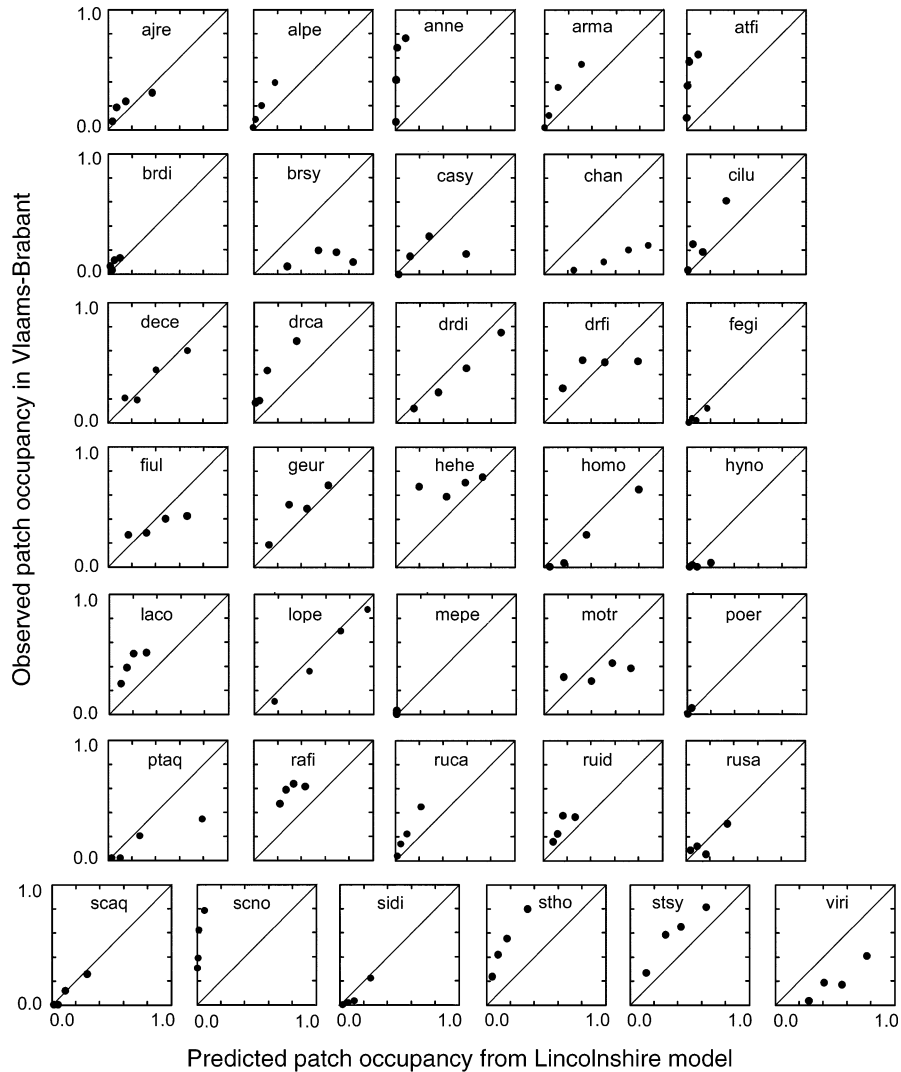
FIG. 4. Predicted vs. observed patch occupancy for 36 species. For these graphs, data for each species were divided into four quartiles based on predicted values (the *x*-axis), and the average predicted and observed patch occupancies in each quartile were plotted against one another. Species abbreviations are as in Fig. 2. Diagonals are 1:1 lines.

time for the ''species credit'' in post-agricultural forests to be accrued. However, although models of plant responses to land-use history have suggested the potential for long delays between fragmentation and paying of the extinction debt (Vellend 2004*a*), this has yet to be demonstrated empirically. Here we have shown that more than a century after the main phase of forest fragmentation was complete in Vlaams-Brabant (Fig. 1), clear evidence of an extinction debt persists (Fig. 3). Detecting this would have been difficult without a priori knowledge of which species were more or less likely to show signs of an extinction debt, suggesting that future studies of extinction debt would benefit from such an approach. As forests are created and destroyed in the north-temperate zone, extended time lags on the order of centuries should be expected both in terms of

species accumulation and species loss in different forest patches.

Of course the Lincolnshire and Vlaams-Brabant data sets differ in more than just their land-use history. For example, the two data sets were collected ~20 years apart, during which time the impact of nitrogen deposition on vegetation has likely been greater in Vlaams-Brabant than Lincolnshire. Species' behavior may also vary among regions (e.g., Hermy et al. 1999). However, there are no apparent differences between the two landscapes, apart from the difference in land-use history, that can explain the significant tendency in Vlaams-Brabant for patch occupancy to be elevated in slow species but not fast species.

Our ability to quantitatively predict patch occupancy patterns in Vlaams-Brabant based on models parame-

terized in Lincolnshire appears to be limited. For interpreting differences in AIC between competing models (Δ_i), Burnham and Anderson (2003) provide some rules of thumb. For all 21 species, Δ_i was >10 (Fig. 3B), indicating that the level of empirical support for the Lincolnshire model is ''essentially none'' (Burnham and Anderson 2003), despite having no free parameters compared to the five parameters estimated for the Vlaams-Brabant models. Given that Lincolnshire and Vlaams-Brabant are likely as similar as we might reasonably expect landscapes in two regions to be (despite the difference in history), it seems unlikely that predicting patterns of distribution across other pairs of fragmented landscapes would fare much better. Good predictive ability has been demonstrated for models focused on distribution patterns at much coarser scales (e.g., 10×10 km portions of a country), in which cases environmental conditions predicting distributions in one region may be applicable in others (Scott et al. 2002). In fragmented landscapes, patterns of patch occupancy are created, in large part, by the stochastic processes of colonization and extinction (Hanski 1999), such that our predictive ability may be inherently poor relative to broad-scale analyses in which deterministic forces (e.g., environmental tolerance limits) predominate. Our conclusion is that if we are interested in quantitatively predicting patch occupancy in a given fragmented landscape, we need to study that landscape directly. This concords with the conclusion of Hermy et al. (1999) that ancient forest indicator species also vary among different regions of Europe.

If we are interested in qualitative predictions across landscapes the outlook is more positive. First, there is a significant positive correlation between predicted and observed patch occupancy across species (Fig. 2). Second, if we compare parameters of the two independent sets of logistic regression models for 21 species, there are significant positive correlations across species (constant, $r = 0.45$, $P = 0.04$; area, $r = 0.49$, $P = 0.02$; age, $r = 0.61$, $P = 0.003$; habitat unsuitability, $r = 0.49$, $P = 0.02$; connectivity, $r = 0.27$, $P = 0.24$). This means that species that tend to show a strong effect of a particular variable on patch occupancy in one landscape also show a relatively strong effect of that variable in the other. Third, even though the precision of predictions across landscapes was quite low, for most species the Lincolnshire model accurately predicted variation among patches in their probability of occupancy in Vlaams-Brabant (Fig. 4). For many species there was a bias in that average patch occupancy was either higher or lower than predicted, regardless of the predicted values, but patches for which a *relatively* high level of patch occupancy was predicted, this was also observed (Fig. 4). For 17 of the 36 species, the rank order correlation between predicted and observed patch occupancy in the four quartiles of data was one. In sum, these results indicate that in the absence of data from Vlaams-Brabant, the models from Lincolnshire

can provide at least a qualitative guide as to which species might be more or less sensitive to different aspects of landscape structure, which are likely to be relatively common vs. rare, and which patches are more or less likely to contain particular species.

This study has several important practical implications. In Vlaams-Brabant and other landscapes that have experienced a decline in forest cover within the last couple of centuries, such as many parts of North America and the tropics, we can expect that the process of relaxation is still underway. Thus, present-day surveys may provide an overly optimistic assessment of the degree to which local forest patches can support biodiversity. On the other hand, the fact that it takes so long for the extinction debt to be paid off indicates that even a century after forest clearance reached a maximum, there is still an opportunity to prevent further local extinctions by increasing forest cover or the spatial structure of forests. An understanding of local landscape history appears critical for understanding how biodiversity is distributed across the landscape, and how future changes in land use may impact species distributions.

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APPENDIX A

Additional methodological details, including background information of the study sites and explanations of the calculations of patch connectivity and habitat unsuitability (*Ecological Archives* E087-030-A1).

APPENDIX B

A table showing coefficients from logistic regression analysis in Lincolnshire and Vlaams-Brabant. (*Ecological Archives* E087-030-A2).

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