

METAPOPULATION DYNAMICS IN CHANGING LANDSCAPES: A NEW SPATIALLY REALISTIC MODEL FOR FOREST PLANTS

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Abstract. In fragmented landscapes, habitat patches are often destroyed and created through time, though most metapopulation models treat patch networks as static. Here we present a generally applicable, modified version of Hanski's Incidence Function Model (IFM) that incorporates landscape dynamics (i.e., habitat patch turnover), and we parameterize the model with data on patch occupancy patterns for forest plants in central Lincolnshire, UK. The modified IFM provided a better, or equally good, fit to species' patch occupancy patterns than logistic regression. Estimated colonization and extinction rates, and the results of logistic regression analyses, varied significantly among species with different life history traits. For example, species with low seed production and predominantly short-distance seed dispersal showed lower rates of colonization and extinction and were more likely to show effects of patch age and connectivity on patch-level presence than species with the opposite set of traits. Model simulations demonstrate a profound negative influence of habitat turnover rate on metapopulation dynamics and persistence, particularly for slow-colonizing species. The incorporation of temporal habitat dynamics into the metapopulation paradigm will permit its application to organisms in a much wider range of real landscapes.

Key words: dynamic landscapes; forest plants; Incidence Function Model; life history traits; metapopulation dynamics and persistence.

INTRODUCTION

The metapopulation concept provides the dominant theoretical paradigm for understanding species dynamics in highly fragmented landscapes (Hanski 1999). Levins' (1969) classic model of colonization and extinction in an infinite number of equally connected habitat patches has since been elaborated on to include spatially explicit colonization (e.g., Durrett and Levin 1994, Bascompte and Solé 1996), variation among patches in area and isolation (e.g., Hanski 1994), rescue from extinction via continued immigration (e.g., Brown and Kodric-Brown 1977), and within-patch population dynamics. However, all of the above-described models take no account of destruction and creation of habitat patches (i.e., landscape dynamics), processes known to characterize many human-dominated landscapes. Incorporating landscape dynamics into the metapopulation paradigm has become an important goal for metapopulation research, in addition to being of potentially great importance for conservation efforts in many parts of the world. Some recent models have revealed important potential effects of landscape dynamics on

metapopulation persistence (e.g., Keymer et al. 2000, Amarasekare and Possingham 2001, Johst et al. 2002, Ellner and Fussmann 2003, Hastings 2003), though parameterization of these models presents a significant challenge. The "spatially realistic" Incidence Function Model (IFM, Hanski 1994) represented a major advance in connecting metapopulation models with data, in that its parameters can be estimated with patch occupancy data of the type often collected by empirical ecologists, but the IFM has yet to be modified to incorporate landscape dynamics.

In this study, we introduce a generally applicable modified version of the IFM that accounts for landscape dynamics and fit it to Peterken and Game's (1984) data on patterns of forest plant patch occupancy in central Lincolnshire (UK), where the history of forest fragmentation and dynamics is well documented (Peterken 1976, Peterken and Game 1984). Insight into metapopulation structure can be gained using the purely statistical approach of relating patch area, isolation, age, and habitat suitability to patch occupancy in a logistic regression framework (e.g., Dupré and Ehrlén 2002, Jacquemyn et al. 2003). Indeed, if independent estimates of the parameters linking patch connectivity to the spatial location of patches are available, fitting the IFM without patch age is done using logistic regression (Hanski 1999:234). However, if one wants to estimate all of the parameters of the IFM using patch

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occupancy data, and if patch age (i.e., habitat turnover) is incorporated (see *Methods*), this is not feasible because it would require the connectivity term to be split into separate terms for each of the potential source patches (in our case >300 patches). Here we first use standard multiple logistic regression to identify significant predictors of patch occupancy for each species, and then estimate parameters of the IFM modified to include patch age. Fitting the IFM yields biologically meaningful parameters that can be used to project metapopulation dynamics under a range of scenarios; here we are particularly interested in the effects of habitat turnover rate on metapopulation persistence. We use the logistic regression results to check for consistency of the two approaches.

The Lincolnshire data set (155 species and 326 patches) holds great potential for studying the effects of patch turnover rate on metapopulation dynamics for a number of reasons: (1) forest cover generally has been constant at ~5% for at least 1000 years; (2) continuous forest destruction, as well as forest reclamation and reforestation have taken place (Peterken 1976), and consequently, present-day forests have variable and known ages; (3) it has been shown that the presence of many forest plants in central Lincolnshire (Peterken and Game 1984) and elsewhere is related to forest age (for a review see Verheyen et al. [2003b]). Both observational (e.g., Matlack 1994, Bossuyt et al. 1999, Verheyen et al. 2003a) and experimental (e.g., Ehrlén and Eriksson 2000, Verheyen and Hermy 2004) research has demonstrated that the limited colonizing capacity of many forest species in Europe is caused mainly by dispersal limitation and not by covariation between habitat suitability and forest age. Hence, we can safely assume that colonization and extinction probabilities do not change with patch age, and that the overall spatiotemporal patch configuration has been more or less stable over time, satisfying the assumption of the IFM that patch-specific colonization and extinction rates are approximately constant.

Furthermore, due to the large number of species for which distribution data were available, we were able to explore the role of species' life history traits in determining rates of colonization and extinction. Theoretical models predict that metapopulation persistence in dynamic landscapes is strongly affected by species' life history traits (e.g., Keymer et al. 2000, Johst et al. 2002), while empirical studies have found relationships between species' traits and frequencies of occurrence in forest patches of different age (e.g., Dupré and Ehrlén 2002, Jacquemyn et al. 2003, Verheyen et al. 2003b). However, it remains unclear if metapopulation dynamics vary systematically among species with different ecological traits.

METHODS

Study area and data collection

The study area covered 930 km² in central Lincolnshire (UK) of which only 4950 ha, or 5.3% of the



PLATE 1. *Anemone nemorosa*, a typical slow colonizing forest species. Photo credit: Dries Adriaens.

total land surface, was forested in 1980. Lincolnshire's forests were already highly fragmented during the Roman era, and by AD 1086 (the Domesday Book) forests covered only 4% of the land (Peterken 1976, Rackham 2003). Since then, historical records indicate that overall forest cover has remained within a very narrow range (~4–8%), indicating approximately equal rates of forest creation and destruction. According to Peterken (1976), average forest creation and destruction rates during the past two centuries were respectively 7.8 ha/yr and 10.0 ha/yr (i.e., a yearly turnover of ~0.2%). Creation and destruction of forests results entirely from individual land use decisions, either to convert agricultural fields to forests, or vice versa; forest plant species are highly unlikely to persist through a period of agriculture. In 1980, 326 forest patches were present. Five percent of these originated after 1946, 8% between 1887 and 1946, 31% between 1820 and 1887, and 34% between 1600 and 1820 (dates based on regional forest maps). The remaining patches (22%) were considered "ancient forests," originating before 1600. Between 1972 and 1981, a comprehensive presence-absence list of vascular plant species was compiled for all 326 patches. Only those species typical of forests were recorded (see Plate 1). Trees and shrubs

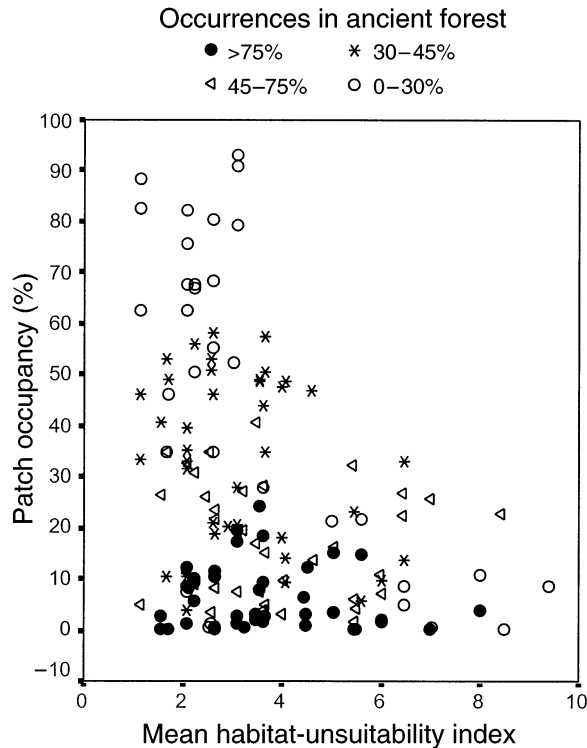


FIG. 1. Relationship between patch occupancy and the mean habitat-unsuitability index for all 155 species (Spearman rank correlation coefficient = -0.317 , $P < 0.001$). The different symbols indicate the percentage of species occurrences that are situated in ancient forest.

were omitted from the analyses because their occurrence in woods may have been deliberately altered by planting and felling. A total of 155 species was recorded, but for statistical reasons only the 63 species with a frequency between 20% and 80% were used for further analyses (see also Fig. 1). We refer readers to Peterken (1976) and Peterken and Game (1984) for more detailed descriptions of the study area and the data collection methods.

Logistic regression analyses

For each species, presence or absence across the 326 patches was first modeled using multiple logistic regression with four explanatory variables: patch area, connectivity, patch age, and a habitat-unsuitability measure described below. It was assumed that any reforestation occurred midway between the dates of two maps (see the previous section). Hence, patch ages in 1980 were 17, 64, 127, and 270 years. The age of the ancient forests was arbitrarily set at 450 years. Patch connectivity was calculated using the following equation (see Moilanen and Nieminen 2002):

$$\text{CON}_i = \sum_{j \neq i}^N \exp(-\alpha d_{ij}) A_j \text{OCC}_j$$

where d_{ij} is the center-to-center distance from patch j

to patch i , A_j is the patch area in square meters, OCC_j is the patch occupancy (0 or 1) of patch j , and N is the total number of patches. The parameter α scales the effect of distance to dispersal and was fixed at 0.002 m^{-1} for all species. This value was similar to the values used by Bastin and Thomas (1999) and Johansson and Ehrlén (2003), studying plants and lichens, respectively. Since no environmental characteristics of the patches had been measured, we relied on Ellenberg's indicator values to assess the suitability of the patches for all 63 species. Based on field observations and, to a lesser extent, on laboratory tests, Ellenberg et al. (1992) assigned scores to Central European plants along an arbitrary nine-point scale, according to their requirements for various ecological factors. Low values of nitrogen, acidity, and humidity scores indicate preferences for nitrogen-poor, acid, and dry conditions, respectively. In this study, we used Ellenberg indicator values revised for the UK (Hill et al. 1999) to calculate a habitat-unsuitability index (h_{ki}) for each species k in every patch i as follows:

$$h_{ki} = |N_k - \text{MIV}_N N_{i(j \neq k)}| + |R_k - \text{MIV}_R R_{i(j \neq k)}| + |F_k - \text{MIV}_F F_{i(j \neq k)}|$$

N_k , R_k , and F_k are the indicator values for soil nitrogen, acidity, and humidity, respectively, for the focal species k ; $\text{MIV}_N N_{i(j \neq k)}$, $\text{MIV}_R R_{i(j \neq k)}$, and $\text{MIV}_F F_{i(j \neq k)}$ are the means of the indicator values of all species j (not including k) present in patch i . High h_{ki} values indicate that the soil preferences of the other species in patch i are different than those of the focal species k , and thus that the environmental conditions in the patch are unlikely to be suitable for the focal species. We acknowledge that Ellenberg values are relatively coarse indicators of site conditions. However, the validity of the index is illustrated in the relationship between mean h_{ki} for each species across all sites against the species' patch occupancy (Fig. 1). As expected (cf. Bastin and Thomas 1999), habitat specialists with limited availability of suitable habitat have low patch occupancy, while habitat generalists can have both high and low occupancies depending on their colonization capacity.

Area and connectivity were \log_{10} -transformed before use in the multiple logistic regression models. A backward variable selection approach was applied and variable removal was based on the probability of the likelihood-ratio statistic, calculated with conditional parameter estimates. The probability for removal was set at 0.001, since the multiple replications of similar tests for each species increase the probability that some significance values would be obtained by chance alone (cf. Cabin and Mitchell 2000). However, at an α -level of 0.001 in analyses for 63 species with four explanatory variables, we would expect less than one relationship to be significant by chance alone.

For comparison with the logistic regression and IFM results, we collected data on focal plant species for

TABLE 1. Results of logistic regression analyses predicting presence/absence of area, connectivity, and age effects (see Appendix A) based on species' traits.

Traits	Missing values (%)	Age		Connectivity		Area	
		β †	Sign.	β †	Sign.	β †	Sign.
Regenerative phase							
Seed mass‡	9.8	0.453	*	NE	NS	NE	NS
Seed shape§	6.6	NE	NS	NE	NS	NE	NS
Seed production per plant	50.8	-1.005	**	-0.651	*	NE	NS
Dispersal type	4.9		(*)		*		NS
Wind		-1.299		-2.342		NE	
Vertebrate		-1.435		-0.775		NE	
Ants/ballistic/none							
Seed bank	13.1		*		NS		NS
Transient		1.599		NE		NE	
Short-term persistent		0.251		NE		NE	
Long-term persistent							
Germination requirements¶	9.8	NE	NS	2.521	**	NE	NS
Age of first reproduction#	45.9	0.684	*	NE	NS	NE	NS
Established phase							
Growth form	0		NS		(*)		(*)
Ferns		NE		0.606		0.767	
Graminoids		NE		1.833		-0.693	
Herbs		NE		-6.593		-1.386	
Shrubs							
Life history	1.6		**		NS		*
Annual		-8.327		NE		7.926	
Biennial		10.078		NE		-8.479	
Monocarpic perennial		-8.327		NE		0.417	
Polycarpic perennial							
Lateral spread††	3.3	NE	NS	NE	NS	NE	NS
Maximum height‡‡	6.6	NE	NS	-0.426	(*)	NE	NS
Flowering phenology	9.8		**		*		NS
Spring flowering		2.639		9.069		NE	
Midsummer flowering		0.965		7.699		NE	
Spring-mid summer flowering		-0.305		8.286		NE	
Midsummer-fall flowering							
Leaf phenology	6.6		**		NS		NS
Seasonal aestival		1.214		NE		NE	
Seasonal hibernal		2.773		NE		NE	
Seasonal vernal		10.282		NE		NE	
Always evergreen		0.288		NE		NE	
Partially evergreen							

Notes: Refer to Hodgson et al. (1995) and Verheyen et al. (2003a, b) for more details. "Missing values (%)" refers to the percentage of species for which data on the corresponding trait (e.g., dispersal type) were not available. One statistical test was conducted for each species' trait (listed as the major heading). NE = no effect.

* Significance (Sign.) is indicated as: (*), $0.05 < P \leq 0.1$; * $0.01 < P \leq 0.05$; ** $0.001 < P \leq 0.01$; NS, not significant.

† β value derived from logistic regression.

‡ Eight classes of seed mass: (0) too small to be measured; (1) <0.20 mg; (2) 0.21–0.50 mg; (3) 0.51–1.00 mg; (4) 1.01–2.00 mg; (5) 2.01–10.00 mg; (6) 10.01–100 mg; (7) 100.01–1000 mg.

§ Three classes: (1) length/width ratio <1.5; (2) ratio 1.5–2.5; (3) ratio > 2.5.

|| Five classes: (1) <25; (2) 26–100; (3) 101–1000; (4) 1001–10 000; (5) >10 000.

¶ Three types ranked according to increasing specificity: (1) immediate; (2) dry, chilling, scarification, light; (3) orchid (difficult, warm + chill, chill + warm + chill, chill + wash).

Five classes: (1) 0.25–1 yr; (2) 1–2 yr; (3) 2–3 yr; (4) 3–6 yr; (5) 6–15 yr.

†† Five classes: (1) therophytes; (2) perennials with compact unbranched rhizomes or forming small tussocks; (3) perennials with rhizomatous systems or tussocks attaining 100–250 mm; (4) perennials attaining a diameter of 251–1000 mm; (5) perennials attaining a diameter of >1000 mm.

‡‡ Five classes: (1) <0.1 m; (2) 0.11–0.29 m; (3) 0.30–0.59 m; (4) 0.60–0.99 m; (5) 1.0–3.0 m.

seven regenerative and six vegetative traits (Table 1) using data compilations that can be found in Hodgson et al. (1995) and Verheyen et al. (2003b). Next, trait values were used to predict the presence/absence of significant age, connectivity, or area effects using logistic regressions. Nominal traits were categorized into

x design variables to perform these analyses, with $x =$ number of classes $- 1$ (Hosmer and Lemeshow 1989).

The modified Incidence Function Model (IFM)

According to the IFM, if a given habitat patch i is not occupied ($OCC_i = 0$), it has a constant probability

of being colonized per unit time, C_i ; if it is occupied ($OCC_i = 1$), the patch has a constant probability of going extinct, E_i . The model is thus a Markov chain with two states, and it leads to the following stationary probability (which is called the “incidence”) that the patch is occupied (Hanski 1994):

$$J_i = \frac{C_i}{C_i + E_i}.$$

Calculation of the incidence in this way assumes that the structure of the landscape is static, i.e., there is no habitat destruction or creation. In a dynamic landscape, by definition, a patch is unoccupied at the time it is created ($OCC_i = 0$ at age = 0). To incorporate landscape dynamics into the IFM, we used equations from Feller (1967:432) for the same Markov chain described above to solve for the conditional probability that a patch is occupied at an arbitrary age (i.e., time since creation):

$$J_i(\text{age}) = \frac{C_i - C_i(1 - C_i - E_i)^{\text{age}}}{C_i + E_i}.$$

Without “age” in the model, solving for C_i and E_i can be difficult because very different rates of turnover can sometimes lead to similar patterns of patch occupancy (Hanski 1994). Including “age” in the model not only extends the IFM to dynamic landscapes, but should also improve our ability to estimate parameters because patterns of occupancy in patches of different age should depend strongly on colonization rate.

The relationships of C_i and E_i to patch area (A_i) and connectivity (CON_i) are flexible, and may incorporate information on species-specific habitat suitability (or in this case, habitat unsuitability, h_i). We used the following functional forms:

$$CON_i = \alpha \sum_{j \neq i}^N \exp\left(-\beta d_{ij} - \frac{h_j^2}{\lambda}\right) A_j OCC_j$$

where α , β , and λ are model parameters, d_{ij} is the distance from patch j to patch i , OCC_j is the patch occupancy (0 or 1) of patch j , and N is the total number of patches; and

$$C_i = \frac{CON_i^2}{CON_i^2 + 1} \quad E_i = \min\left\{\frac{\sigma}{\left[A_i \exp\left(-\frac{h_i^2}{\lambda}\right)\right]^\theta}, 1\right\}$$

where σ and θ are two additional model parameters.

We followed Hanski (1994, 1999) for the relationships of A_i and CON_i to E_i and C_i , and incorporated habitat unsuitability, h_i , as a potential reduction in the “effective” area of a habitat patch with respect to extinction probability and the strength of a patch as a potential source of colonists. When λ is large, $\exp(-h_i^2/\lambda) \approx 1$ and habitat unsuitability has little influence on patch occupancy; when λ is small, effective patch area is unaffected in optimal habitat conditions,

but reduced according to a normal distribution with mean zero and variance λ as h_i increases.

We estimated maximum likelihood parameters of the IFM for each species using the *fmincon* function in MATLAB version 6 (The MathWorks Incorporated, Natick, Massachusetts, USA). Starting at 100 random starting points in a broadly defined parameter space, *fmincon* was used to find the parameter combination resulting in the maximum log-likelihood of the model given the observed data. Fifty additional optimizations of the likelihood function were conducted in a more constrained parameter space, with constraints based on the results of the initial 100 optimizations. To compare the fit of the statistical and mechanistic models to the data, Akaike’s Information Criterion (Akaike 1973) was calculated. The sum of AIC across all species indicates which model provides a better fit overall.

For a few species, very different parameter combinations gave similar log-likelihoods, due to parameter trade-offs. However, the mean and median colonization and extinction rates across patches were quite stable for different combinations of high log-likelihood parameters. In addition, median colonization and extinction rates were highly positively correlated across species ($r = 0.75$ for log-transformed median C_i and E_i); this may be because the combination of low colonization and high extinction rates is not viable (the species would be extinct), and high colonization and low extinction would mean that the species is omnipresent, and therefore impossible to analyze in this context. Regardless of its interpretation, this correlation means that the rate of metapopulation dynamics inferred for each species can be characterized by where it falls along the continuum from low to high C_i and E_i . Therefore, we conducted a principal components analysis (PCA) on the median C_i and E_i of each species, and used the value along this axis to characterize the dynamics (i.e., turnover rate) of each species for comparison with plant traits. This PCA axis accounted for 88% of the variance in the two variables; low values represent species with low C_i and E_i , and vice versa. Relationships of this axis with the 13 plant traits were assessed by means of Spearman rank correlation coefficients and the Kruskal-Wallis test for ordinal and nominal traits, respectively (Siegel and Castellan 1988).

To test the sensitivity of the modified IFM to the assumption of constant C_i across time, and to evaluate the parameter estimation procedure, simulation analyses were conducted for two species representing the slow (*Mercurialis perennis*) and fast (*Taraxacum officinale*) ends of the turnover-rate axis. Using our parameter estimates (from real data) for these two species and a habitat destruction/creation rate of 0.002 (see *Methods: Study area and data description*), dynamics were simulated for 500 years in each of 10 replicate simulations. Patch occupancy and age data taken at the end of each simulation (“snapshot” data) were used

to estimate parameters as described above. In these analyses, habitat turnover was incorporated as a constant per-year probability (0.002) of each patch having its occupancy set to zero; in essence, patches that were destroyed were immediately created in the same place in order to maintain constant landscape structure. We used the same patch areas and spatial positions as observed in the empirical data. C_i varied over time according to the changing patterns of occupancy in the landscape.

For *M. perennis* and *T. officinale*, species representing slow and fast colonizers, respectively, we then used the model to assess the influence of habitat turnover rate on patch occupancy and extinction probability at the landscape scale. Both species had similar observed patch occupancy in the real data (0.32 for *M. perennis*; 0.31 for *T. officinale*). For rates of habitat turnover varying from 0 to 0.1, we ran 50 replicate simulations for 500 years each.

RESULTS

For all but two species, reasonable (i.e., Nagelkerke $R^2 > 0.10$) fits to the logistic regression models were obtained (see Appendix A). These two species (*Arrhenatherum elatius* and *Stellaria media*) were omitted from further analysis. Significant effects of the habitat-unsuitability index were obtained for 50 of the remaining 61 species (82%). Significant area, connectivity, and age effects were found for 35 (57%), 17 (28%), and 18 (30%) species, respectively. For all species, the signs of the relationships were either consistently negative (habitat-unsuitability index) or positive (area, connectivity, and age); species were more likely to be present in patches with high suitability (i.e., low unsuitability) and in large, well-connected and/or old patches. The only exception was a negative age effect for *Primula veris*. Species exhibiting a significant age effect were more likely to exhibit a significant connectivity effect ($\chi^2 = 9.73$, $P = 0.002$, $n = 61$), and less likely to exhibit a significant area effect ($\chi^2 = 9.15$, $P = 0.002$, $n = 61$). No association existed between connectivity and area effects ($\chi^2 = 0.02$; $P = 0.887$, $n = 61$).

The procedure for fitting parameters to the IFM was successful. For *Mercurialis perennis* and *Taraxacum officinale*, parameter values estimated using the real data (and used in the simulations) were always within the range of those estimated using the simulated patch occupancy pattern after 500 years (see Appendix B for details). For parameters that varied between species more than twofold (β and σ), there was no overlap in parameters estimates from simulated data. Median E_i estimated from the real data was 0.00067 for *M. perennis*, and did not exceed 0.0027 in the estimates from simulated data; for *T. officinale*, median E_i was estimated at 0.89 using the real data, and was >0.31 in all simulations. A similar pattern was observed for median C_i (Appendix B).

The sum of AIC (Akaike's Information Criterion) across all species was slightly lower for the IFM (19086) than for the logistic regression models (19124), though the two kinds of models provided quite similar results (the two AICs were strongly correlated across species: $r = 0.97$). Furthermore, similar relationships between the plant traits and results of the two kinds of model were found (Tables 1 and 2). Species for which a significant age effect was found in the logistic regressions were characterized by heavy seeds, low seed production, no adaptations for long-distance dispersal, a transient seed bank, and a delayed age of first reproduction (Table 1). These species also tended to flower earlier and were more likely to be evergreen and biennial. Similar, but weaker, relationships were found for connectivity. Although even weaker relationships were found with area effects, their sign was generally opposite to the relationships with age and connectivity effects. From the IFM, the colonization-extinction axis was strongly positively correlated with seed number per plant, and negatively correlated with seed mass, age of first reproduction, and strictness of germination requirements (Table 2, Fig. 2). The colonization-extinction variable was greatest for species with wind-dispersed seeds, intermediate for species with vertebrate-dispersed seeds, and lowest for species with seeds dispersed by ants, by gravity, or ballistic projection (Table 2, Fig. 2). Finally, it appeared that mean scores on the first PCA axis were significantly lower for the species exhibiting a significant age and connectivity effect ($F_{1,59} = 41.08$, $P < 0.001$ and $F_{1,59} = 17.41$, $P < 0.001$) and higher for the species with a significant area effect ($F_{1,59} = 3.51$, $P = 0.066$).

Model simulations indicate that habitat destruction has a much greater effect on a poor colonizer, *M. perennis*, than on a good colonizer, *T. officinale*. The observed patch occupancy for both species (~ 0.3) corresponded quite closely to the estimated rate of habitat turnover in Lincolnshire of 0.002 (i.e., 0.2%; Fig. 3A). However, with no habitat turnover, *M. perennis* should benefit greatly, with patch occupancy almost double that observed in Lincolnshire (Fig. 3A). In contrast, reducing habitat destruction to zero has no effect on patch occupancy of *T. officinale* (Fig. 3B). With increasing habitat destruction, *M. perennis* patch occupancy declines dramatically, and extinction probability rises from zero to almost one across a narrow range of habitat destruction rates (0.01–0.015; Fig. 3). *T. officinale* can persist in the landscape at much higher rates of habitat destruction, though extinction probability exceeds 0.5 when habitat destruction rate > 0.03 (Fig. 3B).

DISCUSSION

In this paper, we presented a modified Incidence Function Model (IFM) incorporating habitat patch turnover, a fundamental feature of many human-dominated landscapes. The model was parameterized using patch

TABLE 2. Relationships between trait values and the colonization–extinction PCA-axis derived from the Incidence Function Model, modified for dynamic landscapes (see legend of Table 1 for explanation of the traits).

Traits	Missing values (%)	Colonization–extinction PCA axis	
		Statistic	Sign.
Regenerative phase			
Seed mass†\$	9.8	−0.29	*
Seed shape†	6.6	NE	NS
Seed production per plant†	50.8	0.72	***
Dispersal type‡	4.9		(*)
Wind		0.47	
Vertebrate		0.03	
Ants/ballistic/none		−0.41	
Seed bank‡	13.1		*
Transient		−0.58	
Short-term persistent		0.19	
Long-term persistent		0.39	
Germination requirements†	9.8	−0.29	*
Age first reproduction†	45.9	−0.41	*
Established phase			
Growth form‡	0		NS
Ferns		NE	
Graminoids		NE	
Herbs		NE	
Shrubs		NE	
Life history‡	1.6		(*)
Annual		0.84	
Biennial		−0.77	
Monocarpic perennial		0.67	
Polycarpic perennial		−0.06	
Lateral spread†	3.3	NE	NS
Max height†	6.6	NE	NS
Flowering phenology‡	9.8		*
Spring flowering		−0.70	
Midsummer flowering		0.07	
Spring-midsummer flowering		0.06	
Midsummer–fall flowering		0.84	
Leaf phenology‡	6.6		**
Seasonal aestival		0.12	
Seasonal hibernal		0.13	
Seasonal vernal		0.20	
Always evergreen		−0.05	
Partially evergreen		−1.84	

Note: NE = no effect.

* Significance (Sign.) is indicated as: (*), $0.05 < P \leq 0.1$; * $0.01 < P \leq 0.05$; ** $0.001 < P \leq 0.01$; *** $P < 0.001$; NS, not significant.

† Nonparametric Spearman rank correlation coefficients.

‡ Nonparametric Kruskal-Wallis tests: mean values on the first PCA axis are given. Low values indicate low colonization and extinction rates, and high values indicate high colonization and extinction rates.

occupancy data from >60 forest plant species in central Lincolnshire, UK, revealing an explicit link between species' life history traits and their rate of population dynamics at the landscape scale. Peterken and Game (1984) originally framed their study in the context of the dynamic theory of island biogeography (MacArthur and Wilson 1967) and demonstrated significant effects of area, age, and connectivity on species richness. Here we demonstrate that the former observations are in fact the sum of individual species responses to landscape structure (cf. Hanski and Ovaskainen 2003). In the following sections we will respectively comment on the model, the results of the case study in central Lincoln-

shire, and on the consequences for conservation and management.

Our modified version of the IFM successfully recovered parameters in simulated data, and provided a slightly superior fit to the data than logistic regression. However, the logistic regression results were quite comparable to the IFM results, as indicated by similar sets of correlations with species' traits and a very strong correlation across species of the AIC values for the two models. The data set used in this study included all 326 forest patches in Lincolnshire, where it is reasonable to assume approximately constant rates of patch-specific colonization and extinction rates over

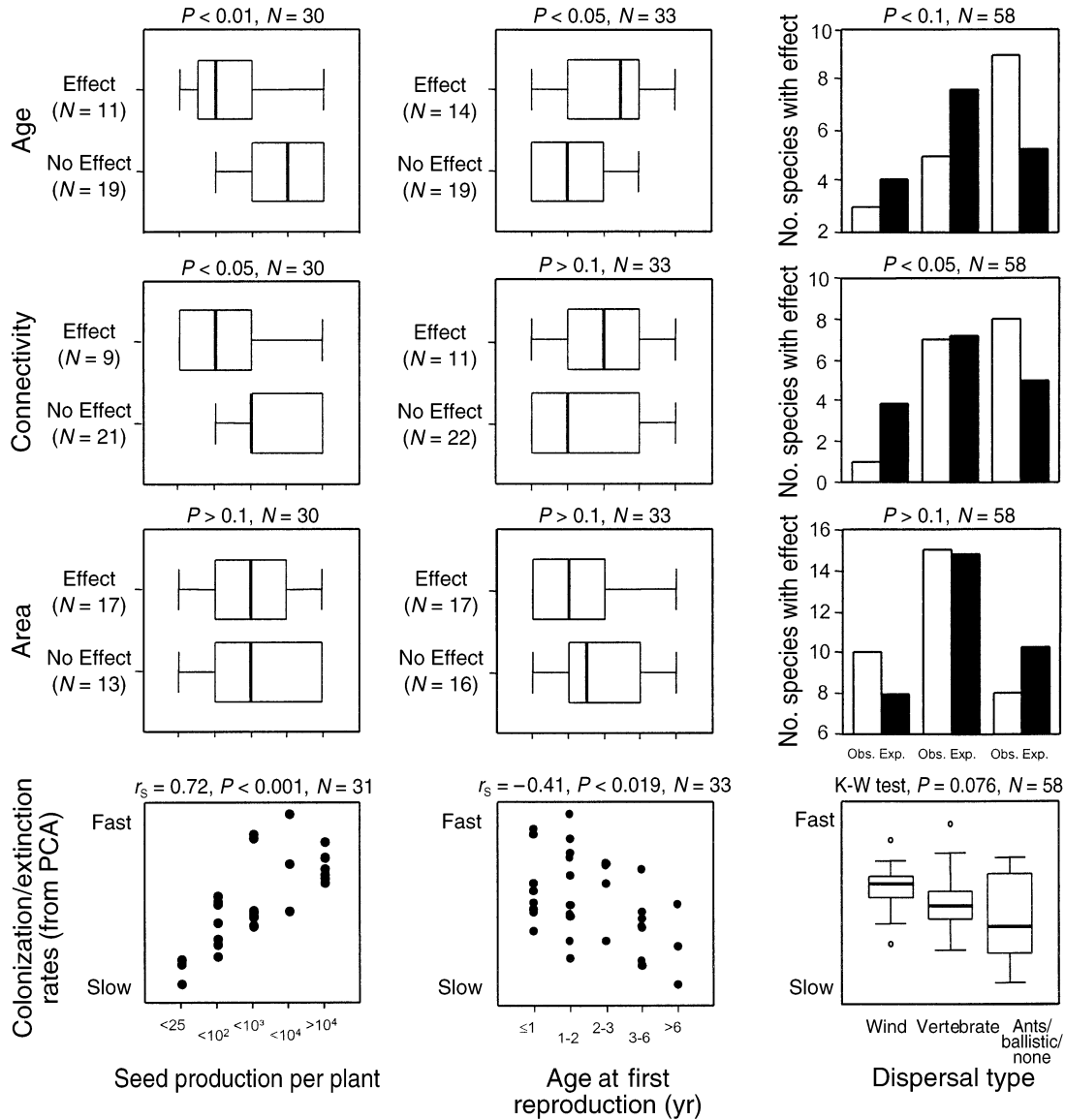


FIG. 2. Relationships between three selected life history traits (diaspore production, age of first reproduction, and dispersal mode) and the presence/absence of age, connectivity, and area effects in the logistic regressions, and the colonization–extinction PCA axis derived from the modified Incidence Function Model. Box plots are used for diaspore production and age of first reproduction, while the observed (open bars) vs. the expected (solid bars) number of cases exhibiting age, area, and connectivity effects are depicted for agency of dispersal. Kruskal-Wallis (K-W) tests, Spearman rank correlations (r_s), and logistic regressions (all others) were used to conduct statistical tests. Small open circles in the bottom right plot are outliers.

time, owing to the constancy in forest cover. Our results suggest that where these requirements are not met (and therefore where the IFM cannot be applied), logistic regression can provide important qualitative insights into the dynamic processes underlying patterns of patch occupancy (cf. Hanski 1999). Where data requirements and model assumptions are met, our modified IFM can be used to quantitatively characterize metapopulation dynamic rates in dynamic landscapes. For species such as forest plants, for which empirical data on coloni-

zation and extinction rates are very hard to obtain due to their slow population turnover rates, this is extremely useful. Difficulty in measuring these rates was one of the reasons that Freckleton and Watkinson (2002) were skeptical about the application of metapopulation theory to describe the regional dynamics of plants. Hence, although time scales of colonization and extinction may be on the order of hundreds of years, both have been observed in European forest fragments (Petterken and Game 1984, Harmer et al. 2001, Jacquemyn

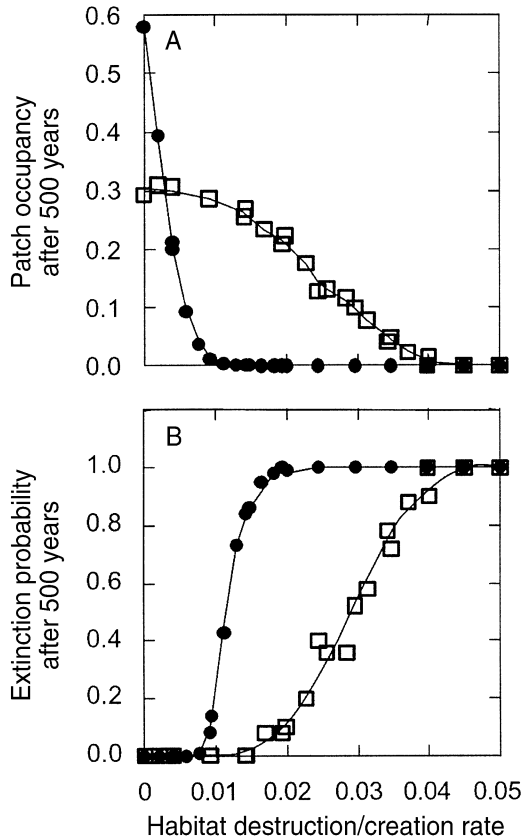


FIG. 3. The effect of habitat destruction rate on (A) patch occupancy and (B) extinction probability after 500 years for *Mercurialis perennis* (solid circles) and *Taraxacum officinale* (open squares). Each data point in panel (A) represents the mean of 50 simulations; in panel (B), the y-axis is the proportion of simulations in which the species went extinct.

et al. 2003, Verheyen et al. 2003a), and we believe that the application of the metapopulation framework is justified here (cf. Ehrlén and Eriksson 2003). Development and parameterization of spatially realistic metapopulation models for systems where habitat suitability or landscape structure changes dramatically over time remains an important challenge for future research.

The forest history in Lincolnshire is broadly representative of northwestern Europe, and to a lesser extent eastern North America, where human land use has resulted in a patchwork of forests varying in area, isolation, and age (Whitney 1994, Kirby and Watkins 1998). Applied to the Lincolnshire data set, the modified IFM has provided novel insights in the landscape-scale population dynamics of (forest) plants in highly fragmented and dynamic landscapes. A substantial body of research has focused on the colonization of restored recent forests from source populations in remnant ancient forests in Europe (e.g., Grashof-Bokdam 1997, Bossuyt et al. 1999, Verheyen et al. 2003a) and in North America (e.g., Matlack 1994, Bellemare et al. 2002, Flinn and Marks 2004). In a formal metapopu-

lation context, ancient and recent forests have been previously treated as a mainland-island system (Vellend 2003). However, and this is particularly true for the northwestern European landscape, forest destruction (and creation) has been an ongoing process since at least the Roman era (e.g., Dupouey et al. 2002), and consequently, a more realistic framework relaxing the formal distinction between ancient and recent forest was warranted (see also Vellend 2004). Our results indicate that, due to continuous patch turnover, species such as *M. perennis* that are known to be slow colonizers in central Lincolnshire (cf. Peterken and Game 1981) have much lower patch occupancies than those expected if the landscape were static (Figs. 1 and 3). Furthermore, the maximum rate of patch turnover that allows persistence is several times lower for slow-colonizing species than for species known to be rapid colonizers, such as *T. officinale*.

Species' sensitivity to landscape structure and dynamics is expected to depend on their life history traits. Simulations by Johst et al. (2002) predicted that species characterized by small local population growth rates and short-range dispersal were particularly vulnerable in highly dynamic and fragmented landscapes, and that the upper limit of patch turnover rate allowing metapopulation persistence was greater for long-distance dispersers. By analyzing slow-colonizing forest plant species from across Europe and eastern North America, Verheyen et al. (2003b) found that these species were generally characterized by long generation times, and that they produced relatively few, heavy seeds that lacked adaptations for long-distance dispersal and did not form a persistent seed bank. Here we found similar traits to be correlated with colonization and extinction rates (Tables 1 and 2, Fig. 2). The nature of the trait correlations, together with the infrequent co-occurrence of both age and area effects in the logistic regression models (see also Ouborg 1993, Grashof-Bokdam 1997), therefore suggest that life history trade-offs (e.g., many small vs. few large seeds) result in a colonization-extinction trade-off as well. Species that are capable of rapid colonization tend to be extinction prone at the patch scale, and vice versa.

Finally, our findings also have implications for management and conservation. Most conservation efforts have been oriented toward the establishment and protection of ancient forest reserves (Peterken 1996), so that a fraction of the patches become static. Our results emphasize the importance of this strategy, in that some species (e.g., *M. perennis*) are extremely sensitive to habitat turnover, and may benefit greatly from habitat protection. Also, knowing a species' traits is surprisingly informative regarding the rate of metapopulation dynamics (Fig. 2), and since species with slow dynamics are particularly sensitive to landscape change, knowledge of species' traits can also help determine which species to monitor or use as indicators in a conservation context. Considerable at-

tention has been paid to the effect of landscape structure on metapopulation dynamics and persistence (e.g., Bascompte and Solé 1996). Our results provide both theoretical and empirical evidence of an equally important influence of temporal landscape dynamics on the viability of metapopulations. Destroying and creating patches of habitat is profoundly different than leaving habitat patches alone.

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LITERATURE CITED

- Akaike, H. 1973. Information theory and the maximum likelihood principle. Pages 267–281 in B. N. Petrov and F. Csàki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.
- Amarasekare, P., and H. Possingham. 2001. Patch dynamics and metapopulation theory: the case of successional species. *Journal of Theoretical Biology* **209**:333–344.
- Bascompte, J., and R. Solé. 1996. Habitat fragmentation and extinction thresholds in explicit models. *Journal of Animal Ecology* **65**:465–473.
- Bastin, L., and C. D. Thomas. 1999. The distribution of plant species in urban vegetation fragments. *Landscape Ecology* **14**:493–507.
- Bellemare, J., G. Motzkin, and D. R. Foster. 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *Journal of Biogeography* **29**:1401–1420.
- Bossuyt, B., M. Hermy, and J. Deckers. 1999. Migration of herbaceous plant species across ancient–recent forest ecotones in central Belgium. *Journal of Ecology* **87**:628–638.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effects of immigration on extinction. *Ecology* **58**:445–449.
- Cabin, R. J., and R. J. Mitchell. 2000. To Bonferroni or not to Bonferroni: when and how are the questions. *Bulletin of the Ecological Society of America* **81**:246–248.
- Dupouey, J. L., E. Dambrine, J. D. Laffite, and C. Moares. 2002. Irreversible impact of past land use on forest soils and biodiversity. *Ecology* **83**:2978–2984.
- Dupré, C., and J. Ehrlén. 2002. Habitat configuration, species traits and plant distributions. *Journal of Ecology* **90**:796–805.
- Durrett, R., and S. A. Levin. 1994. The importance of being discrete (and spatial). *Theoretical Population Biology* **46**:363–394.
- Ehrlén, J., and O. Eriksson. 2000. Dispersal limitation and patch occupancy in forest herbs. *Ecology* **81**:1667–1674.
- Ehrlén, J., and O. Eriksson. 2003. Large-scale spatial dynamics of plants: a response to Freckleton and Watkinson. *Journal of Ecology* **91**:316–320.
- Ellenberg, H., H. E. Weber, R. Düll, V. Wirth, W. Werner, and D. Paulissen. 1992. *Zeigerwerte von Pflanzen in Mitteleuropa*. Verlag Erich Goltze, Göttingen, Germany.
- Ellner, S. P., and G. Fussmann. 2003. Effects of successional dynamics on metapopulation persistence. *Ecology* **84**:882–889.
- Feller, W. 1967. *An introduction to probability theory and its applications*. Wiley, New York, New York, USA.
- Flinn, K. M., and P. L. Marks. 2004. Land-use history and forest herb diversity in Tompkins County, New York, USA. Pages 81–95 in O. Honnay, K. Verheyen, B. Bossuyt, and M. Hermy, editors. *Forest biodiversity: lessons from history for conservation*. CAB International, Wallingford, UK.
- Freckleton, R. P., and A. R. Watkinson. 2002. Large-scale spatial dynamics of plants: metapopulations, regional ensembles and patchy populations. *Journal of Ecology* **90**:419–434.
- Grashof-Bokdam, C. 1997. Forest species in an agricultural landscape in the Netherlands: effects of habitat fragmentation. *Journal of Vegetation Science* **8**:21–28.
- Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* **63**:151–162.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford, UK.
- Hanski, I., and O. Ovaskainen. 2003. Metapopulation theory for fragmented landscapes. *Theoretical Population Biology* **64**:119–127.
- Harmer, R., G. Peterken, G. Kerr, and P. Poulton. 2001. Vegetation changes during 100 years of development of two secondary woodlands on abandoned arable land. *Biological Conservation* **101**:291–304.
- Hastings, A. 2003. Metapopulation persistence with age-dependent disturbance or succession. *Science* **301**:1525–1526.
- Hill, M. O., J. O. Mountford, D. B. Roy, and R. G. H. Bunce. 1999. Ellenberg's indicator values for British plants. Institute for Terrestrial Ecology, Huntingdon, UK.
- Hodgson, J. G., J. P. Grime, R. Hunt, and K. Thompson. 1995. *The electronic comparative plant ecology*. Chapman and Hall, London, UK.
- Hosmer, D. W., and S. Lemeshow. 1989. *Applied logistic regression*. John Wiley and Sons, New York, New York, USA.
- Jacquemyn, H., J. Butaye, and M. Hermy. 2003. Influence of environmental and spatial variables on regional distribution of forest plant species in a fragmented and changing landscape. *Ecography* **27**:768–776.
- Johansson, P., and J. Ehrlén. 2003. Influence of habitat quantity, quality and isolation on the distribution and abundance of two epiphytic lichens. *Journal of Ecology* **91**:213–221.
- Johst, K., R. Brandl, and S. Eber. 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. *Oikos* **98**:263–270.
- Keymer, J. E., P. A. Marquet, J. X. Velasco-Hernández, and S. A. Levin. 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. *American Naturalist* **156**:478–494.
- Kirby, K. J., and C. Watkins. 1998. *The ecological history of European forests*. CAB International, Wallingford, UK.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**:237–240.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Matlack, G. R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* **75**:1491–1502.
- Moilanen, A., and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. *Ecology* **84**:1131–1145.
- Ouborg, N. J. 1993. Isolation, population-size and extinction. The classical metapopulation approaches applied to vascular plants along the Dutch Rhine-system. *Oikos* **66**:298–308.

- Peterken, G. F. 1976. Long-term changes in the woodlands of Rockingham forest and other areas. *Journal of Ecology* **64**:123–146.
- Peterken, G. F. 1996. Natural woodland. Ecology and conservation in northern temperate regions. Cambridge University Press, Cambridge, UK.
- Peterken, G. F., and M. Game. 1981. Historical factors affecting the distribution of *Mercurialis perennis* in central Lincolnshire. *Journal of Ecology* **69**:781–796.
- Peterken, G. F., and M. Game. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *Journal of Ecology* **72**:155–182.
- Rackham, O. 2003. Ancient woodland, its history and uses in England. Castlepoint Press, Colvend, UK.
- Siegel, S., and N. J. Castellan. 1988. Non parametric statistics for the behavioral sciences. McGraw-Hill, New York, New York, USA.
- Vellend, M. 2003. Habitat loss inhibits recovery of plant diversity as forests regrow. *Ecology* **84**:1158–1164.
- Vellend, M. 2004. Metapopulation dynamics following habitat loss and recovery: forest herbs in ancient and recent forests. Pages 163–177 in O. Honnay, K. Verheyen, B. Bossuyt, and M. Hermy, editors. Forest biodiversity: lessons from history for conservation. CAB International, Wallingford, UK.
- Verheyen, K., G. Guntenspergen, B. Biesbrouck, and M. Hermy. 2003a. An integrated analysis of the effects of past land-use on forest plant species colonization at the landscape scale. *Journal of Ecology* **91**:731–742.
- Verheyen, K., and M. Hermy. 2004. Recruitment and growth of herb-layer species with different colonizing capacities in ancient and recent forest. *Journal of Vegetation Science* **15**:125–134.
- Verheyen, K., O. Honnay, G. Motzkin, M. Hermy, and D. Foster. 2003b. Response of forest plant species to land-use change: a life-history based approach. *Journal of Ecology* **91**:563–577.
- Whitney, G. G. 1994. From coastal wilderness to fruited plain. Cambridge University Press, New York, New York, USA.

APPENDIX A

Results of logistic regression analyses and fitting the incidence function model for all species are available in ESA's Electronic Data Archive: *Ecological Archives* E085-115-A1.

APPENDIX B

Simulation results to test the parameter-fitting procedure for the modified incidence function model are available in ESA's Electronic Data Archive: *Ecological Archives* E085-115-A2.