

REPORTS

Ecology, 84(5), 2003, pp. 1158–1164
© 2003 by the Ecological Society of America

HABITAT LOSS INHIBITS RECOVERY OF PLANT DIVERSITY AS FORESTS REGROW

MARK VELLEND¹

Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853 USA

Abstract. Agricultural expansion has resulted in loss of natural habitats worldwide, threatening remnant populations and communities. However, during the past several centuries in much of Europe and eastern North America, extensive forest clearance (usually resulting in <20% forest cover) has been followed by widespread expansion of forest onto abandoned agricultural land. Since ancient forests (those remaining at the peak of forest loss) provide seed sources for recolonization of recent (post-agricultural) forests, the extent of forest loss should influence the rate of population recovery in recent forest. Data compiled from the literature for 10 regions of Europe and North America indicate that the proportion of ancient forest in a landscape can account for >65% of the variation in species diversity of “ancient forest herbs” in recent forests relative to ancient forests. This result suggests that ancient-forest loss has had a strong influence on the recovery of herbaceous plant diversity in post-agricultural forests. In addition, a simple mainland–island metapopulation model suggests that with increasing severity of habitat loss the return time to equilibrium patch occupancy in recent forests is greatly extended, perhaps for centuries after forest clearance has ceased and restoration begun.

Key words: *ancient forest; forest herbs; habitat fragmentation; habitat loss; land-use history; primary forest; recent forest; restoration; secondary forest.*

INTRODUCTION

Despite the global abundance of restored land and its potential importance in biodiversity conservation (Dobson et al. 1997), theoretical and empirical research on habitat loss and fragmentation has focused almost entirely on species dynamics in remnant habitat patches (Hanski 1999, Haila 2002). If remnant habitat patches provide the source of colonists for restored patches, it follows that the extent of habitat loss prior to abandonment should influence reestablishment of populations and communities via the reduction of potential sources of colonists. This suggests a potentially important link between two major themes in ecology and conservation biology: habitat loss and habitat restoration.

While the effect of spatial isolation on the rate of migration into local habitat patches is widely recognized (Hanski 1999), to my knowledge there has been no work directly connecting the extent of habitat loss to the rate and extent of population and community recovery in restored habitats at the landscape scale. Some recent simulation models (Tilman et al. 1997, Huxel and Hastings 1999) have shown that with lo-

calized dispersal the recovery of populations in restored habitat patches may lag behind restoration of the habitat itself, though these models do not address variation in the extent of habitat loss among landscapes. In this paper, I use both empirical and theoretical approaches to assess the influence of the extent and timing of forest clearance and subsequent regrowth on the recovery of plant diversity in post-agricultural forests of Europe and eastern North America.

In much of temperate Europe and eastern North America the history of forest cover has been broadly similar over the past several centuries. Agricultural land use reduced the amount of forest cover to some minimum amount (usually <20%), after which farm abandonment allowed forests to regrow in some parts of the landscape (Whitney 1994, Peterken 1996). Forest patches in such landscapes can be classified as either *ancient*—i.e., remnant patches that have been continuously forested since the time of the earliest land use maps, or *recent*—i.e., restored patches on land known to have been in agricultural use at some time since the oldest land-use maps (Rackham 1980). In Europe, “ancient” forests may include both primary forests (i.e., never cleared for agriculture) as well as post-agricultural forests whose origin predates the earliest available maps. In North America, this definition generally includes only primary forests.

Manuscript received 9 July 2002; revised 15 November 2002; accepted 3 December 2002. Corresponding Editor: E. Menges.

¹ E-mail: mv59@cornell.edu

A number of studies on plant colonization in recent forests have paid particular attention to forest herbs and the relative roles of environmental vs. dispersal limitation. Forest herbs typically have highly localized seed dispersal (usually by ants or gravity), prolonged prereproductive life stages, and no persistent seed bank (Bierzuchudek 1982), and are thus expected to be particularly sensitive to landscape history. Environmental conditions may vary between ancient and recent forests (e.g., Petersen 1994), but both observational (e.g., Peterken and Game 1984, Matlack 1994) and experimental (Singleton 1998, Verheyen 2002) studies indicate that dispersal limitation is the dominant force regulating the recovery of forest-herb diversity in recent forests, suggesting that the extent of forest clearance and regrowth should greatly influence the process of population and community recovery.

Here I use data compiled from the literature for 10 regions of Europe and eastern North America to test for effects of three landscape variables—proportion ancient forest, proportion recent forest, and time since agricultural abandonment—on the relative diversity of forest herbs in recent vs. ancient forests. Encouraged by the statistical results, I then develop a simple metapopulation model to ask what time course is likely for the recovery of “slow” vs. “rapid” colonizers as habitat is regenerated.

METHODS

Data compilation and analysis

I searched the literature for studies on plant diversity in ancient and recent forests that included: (1) sufficient information to calculate estimates of the proportions of the landscape in ancient (P_A) and recent (P_R) forest; and (2) a table including the frequencies of forest herbs ($n \geq 8$ species) in ancient and recent stands. Ten studies that met these criteria were found (see Appendix A), all of which also included some information about the maximum possible age of recent stands (A_R). Rarely was more specific information provided about stand ages or the spatial arrangement of forest patches, so I focus here on the effects of habitat loss, and not habitat fragmentation per se (sensu Fahrig 1997). I present here an outline of how data were compiled and analyzed, with additional details provided in Appendix B.

In most studies, estimates of the proportions of ancient and recent forest were provided directly (Tack and Hermy 1998, Smith et al. 1993, Wulf 1997, Gerhardt 1998, Graae 2000, Bellemare et al. 2002). Otherwise, forest proportions were estimated by digitizing and analyzing maps in ArcView GIS 3.2 (ESRI, Redlands, California, USA), or by extracting stand areas from species-area graphs in cases where all stands in a given study area were included (see Appendix B).

Studies varied in the extent to which surveys were restricted to “forest” species, or to all plant species regardless of habitat affinity. To objectively delineate

a standardized species pool that was comparable across regions, I included only species whose frequency was greater in ancient than recent stands in a given landscape—“ancient forest herbs.”

In all but one study (Grashof-Bokdam and Geertsema 1998) the raw frequencies of species in ancient and recent stands were provided. For ancient forest herbs, the mean number of species per ancient patch (S_A), and the mean number of species per recent patch (S_R) were calculated by summing all presences of all species in the appropriate stand type, and dividing by the number of stands of that type. As a measure of relative species diversity in recent forests that is comparable among landscapes, I calculated S_R/S_A . Grashof-Bokdam and Geertsema (1998) reported the frequency of each species as a proportion of those sites considered “suitable” for that species. In this case, I estimated S_R and S_A as: (mean proportion of *suitable* stands occupied by a given species) \times (total number of species)/(average number of suitable stands for a given species).

A potentially confounding factor in comparing among studies is the relative areas of ancient vs. recent patches. In three cases (Gerhardt 1998, Singleton et al. 2001, Bellemare et al. 2002) vegetation data were based on equal-area plots, so area was not a factor. In all other studies, species lists were made for whole patches. In Petersen (1994), area was not a significant predictor of species richness (therefore not a confounding factor). In three of the remaining six studies (Peterken and Game 1984, Dzwonko and Loster 1988, 1989, Graae 2000), sufficient information was provided to allow a correction to be made for the difference in area between ancient and recent stands (see Appendix B). To ensure that area differences did not confound the results, data were analyzed in three ways: (1) using the raw uncorrected values of S_R/S_A ; (2) using the three area-corrected values of S_R/S_A in place of their corresponding raw values; (3) using only the seven studies for which either area was not a factor, or a correction for area was possible.

Stepwise linear regression was performed to assess the effects of proportion ancient forest (P_A), proportion recent forest (P_R) and maximum age of recent stands (A_R) on relative species diversity in recent forests (S_R/S_A). Log transformations were applied to P_A and P_R to linearize relationships with S_R/S_A . All possible interaction terms were included as candidate variables in the stepwise procedure, with a cutoff of $P = 0.15$ used for entry or exit from the models (Procedure REG, SAS Version 7.00 [SAS Institute 1998]).

Metapopulation model

To explore the degree to which the time course of population recovery in individual species might be retarded by habitat loss, I modeled the proportion of recent forest patches occupied (P_{RO} ; “patch occupancy”) using a mainland–island version of Levins’ (1969) metapopulation model modified to include two types

of suitable habitat. Patch occupancy in remnant habitats (in this case ancient forests) has already been studied with a wide range of models (Hanski 1999). Here the focus is on restored habitats (i.e., recent forests), so for the sake of simplicity I assumed that ancient forest patches comprise a constant proportion of the landscape (P_A), with a constant proportion (P_{AO}) of these patches occupied (i.e., there is no extinction of ancient populations). Occupied ancient patches act as a mainland, providing a source of colonists for recent patches, described by the colonization parameter C_A . Recent forest patches also comprise a constant proportion of the landscape (P_R), and all start out as empty but suitable. Once colonized, populations in recent patches each have a constant probability e of going extinct per year, and may act as sources of colonists for empty patches, described by the colonization parameter C_R .

$$\frac{dP_{RO}}{dt} = (C_A P_A P_{AO} + C_R P_R P_{RO})(1 - P_{RO}) - e P_{RO}. \quad (1)$$

It is recognized that in real landscapes the assumptions of this model are, strictly speaking, all violated to varying degrees. However, despite the simplicity of the Levins model, Ovaskainen and Hanski (2002) have shown that it captures quite accurately the dynamics of much more complex, spatially realistic models. I make simplifying assumptions here with the aim of understanding, in general terms, the expected influence of proportions of ancient and recent forest in the landscape on patch occupancy and time to equilibrium for forest herbs with different colonization abilities. Model output was generated for many parameter combinations, but I focus here on a relatively narrow range of situations most relevant to the empirical data.

Colonization parameters were estimated for two different forest-herb species using data from central New York (USA); one species was a slow colonizer (*Aster divaricatus* L.), the other a relatively rapid colonizer (*Maianthemum canadense* Desf.). Other relatively slow colonizers in this region include *Trillium grandiflorum* (Michx.) Salisb. and *Prenanthes* spp. L.; other rapid colonizers include *Smilacina racemosa* (L.) Desf. and *Circaea* spp. L. (Singleton et al. 2001). For Tompkins County, New York, Smith et al. (1993) provide estimates of P_A and P_R , and Singleton et al. (2001) provide estimates of P_{AO} and P_{RO} for all forest herbs in 25 recent forests that had been abandoned from agriculture for ~80 years, and in 25 ancient forests. The data in Singleton et al. (2001) are especially useful in that all recent forests were approximately the same age. I chose *A. divaricatus* and *M. canadense* because both species had relatively high values of P_{AO} (0.92 and 0.76, respectively), with one species showing relatively low P_{RO}/P_{AO} , and the other species relatively high P_{RO}/P_{AO} (0.43 and 0.89, respectively), indicating differences in colonization ability. High values of P_{AO} were desired

to best approximate the assumption of no extinction in ancient-forest populations. I also assumed that the relative importance as seed sources of ancient stands vs. recent stands that are occupied (i.e., the magnitude of C_A vs. C_R) was a function of their abundances in the two stand types. As such, $C_R/C_A = 0.4$ for *A. divaricatus* and $C_R/C_A = 1$ for *M. canadense* based on data in Singleton et al. (2001). Thus, only one colonization parameter needs to be estimated for each species.

The extinction rate was assumed to be the same for both species, and I used values for e based on literature reports. Repeated vegetation surveys (of all vascular plants) on islands or patches of forest in Europe have resulted in estimates of e ranging from 0.002 to 0.008 (Gibson 1986, Jerling 1998, Roden 1998). Nilsson and Nilsson (1985) estimated that "at most" 0.01 of plant species go locally extinct per year on Swedish islands of similar size and age to the forest patches in studies reviewed here, but given that forest herbs tend to have very low adult mortality rates (Franco and Silvertown 1996), e is unlikely to be as high as 0.01. Separate modeling analyses were conducted with $e = 0.002$, $e = 0.005$, and $e = 0.008$.

Using the above-described parameterizations, the model was solved for values of C_A that could explain the observed P_{RO} for each species 80 years after agricultural abandonment; a different value of C_A was calculated using each of the three values of e . Each value of C_A was then used with its corresponding value of e to explore the influence of variation in P_A and P_R (ranging from 0.01 to 0.5) on patch occupancy in recent forest (P_{RO}) at different times since agricultural abandonment, and on the time to 0.95 of equilibrium patch occupancy.

RESULTS

In the empirical data, the proportion of ancient forest in the landscape (P_A) was a significant predictor (with positive coefficients) of relative diversity in recent forests, regardless of whether area corrections were used or not (Fig. 1, Table 1). The logarithm of P_A alone explained 66–76% of the variation in S_R/S_A (the mean number of species per recent patch divided by the mean number of species per ancient patch) ($P < 0.03$), depending on which data set was used. The maximum age of recent stands (A_R) was not a significant predictor of S_R/S_A when the raw data were used, but was at least marginally significant (with positive coefficients) in both analyses that included area corrections ($P < 0.06$; Table 1). However, the partial r^2 for A_R was only 0.16–0.21, compared to 0.66–0.69 for P_A . Though there was a positive correlation between P_A and P_R (the proportion of landscape in recent forest) ($r = 0.7$, $P < 0.03$), it is important to note that the result described above (for P_A as a predictor of S_R/S_A) is not akin to a species–area relationship, because diversity was expressed *within* recent forest patches relative to ancient patches, not across the entire landscape.

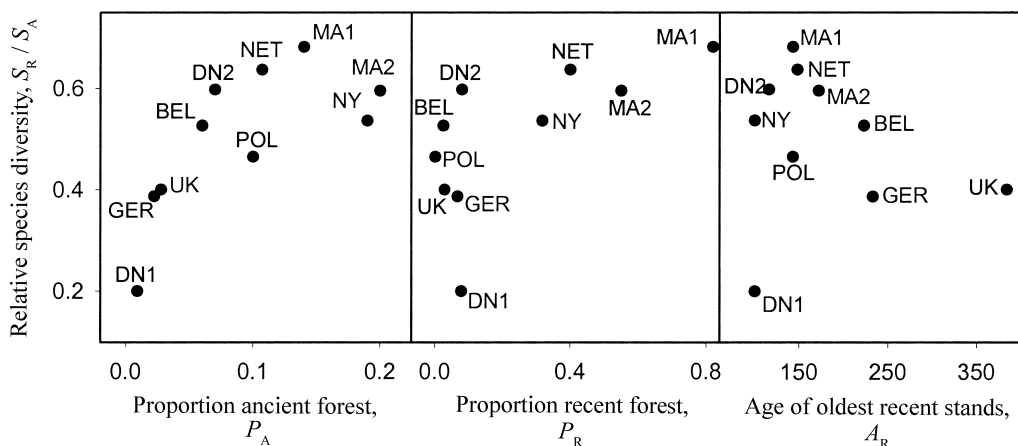


FIG. 1. Relationships among landscape variables. Proportion ancient forest (P_A), proportion recent forest (P_R), and age of oldest recent stands (A_R) are plotted against relative species diversity (S_R/S_A) for 10 landscapes of Europe and eastern North America. Landscape abbreviations are: BEL, Flanders, Belgium (Honnay et al. 1998, Tack and Hermy 1998); DN1, Røsnaes, Denmark (Petersen 1994); DN2, Himmerland, Denmark (Graae 2000); GER, Lower Saxony, Germany (Wulf 1997); MA1, Petersham, Massachusetts, USA (Gerhardt 1998); MA2, towns of Shelburne and Conway, Massachusetts, USA (Bellemare et al. 2002); NET, Twente region, The Netherlands (Grashof-Bokdam and Geertsema 1998); NY, Tompkins County, New York, USA (Smith et al. 1993, Singleton et al. 2001); POL, Western Carpathian foothills, Poland (Dzwonko and Loster 1988, 1989); UK, Lincolnshire, UK (Peterken and Game 1984).

There were some differences in the quantitative details of the model output using different values of e , though the qualitative results were very similar. I present here the graphical output for the case where $e = 0.005$ (C_A [the colonization parameter] = 0.039 for slow colonizer, $C_A = 0.069$ for rapid colonizer), and note the few differences that depend on the value of e between 0.002 and 0.008.

As a greater proportion of ancient forest is left in a landscape following clearance, patch occupancy in recent forest is higher (Fig. 2A and B), and equilibrium is reached more quickly for a slow colonizer (Fig. 2C). At equilibrium there is a steep decline in patch occupancy, and a steep rise in the time it takes to reach equilibrium, as ancient forest decreases below 10–15%, particularly when recent forest is also low (Fig. 2B and C). With <5% ancient forest, it should take ≥ 240 years, and as many as 800 or more years, depending on the proportion of recent forest (Fig. 2C). The maximum time to equilibrium was >1200 years using $e = 0.002$, and >600 years using $e = 0.008$.

For a rapid colonizer, proportion of ancient forest also has a strong influence on patch occupancy in recent forest, but as equilibrium is approached this effect can be offset to a large degree by a relatively high proportion of recent forest (Fig. 2D–F). (Only with $e = 0.002$ was there an indication for the slow colonizer that recent forest could compensate somewhat for a low proportion of ancient forest.) For a rapid colonizer there is again a steep decline in equilibrium patch occupancy as both ancient and recent forest fall below $\sim 10\%$ (Fig. 2E), though the steep rise for time to equilibrium occurs only when proportion of recent forest is also relatively

low (Fig. 2F). For all three extinction rates, the maximum time to equilibrium was >450 years.

DISCUSSION

Here I first address the comparability of the empirical data and the model. This is followed by a discussion of the expected and observed influence of P_A , P_R , and A_R (the proportion of the landscape in ancient and recent forest and the maximum age of recent stands, respectively) on patch occupancy and species diversity, and the time course of post-agricultural colonization.

Despite the fact that the empirical data are for whole species assemblages, and the model for individual species, the two can in fact be compared (at least qualitatively) because species diversity is simply the sum of individual species' patch occupancies. However, we cannot use mean values of colonization and extinction parameters across species to model S_R/S_A as if it were an estimate of P_{RO}/P_{AO} (i.e., [the proportion of recent forest patches occupied]/[the proportion of ancient forest patches occupied]) or simply P_{RO} if $P_{AO} = 1$, because in this case the function of the means is not equal to the mean of the functions. Nonetheless, because variation among landscapes in S_R/S_A should be driven largely by the patch occupancy patterns of relatively poor colonizers, we should expect a qualitative agreement between the data and the poor-colonizer model.

In the empirical data there was a strong, positive, and nonlinear effect of proportion of ancient forest (P_A) on relative species diversity in recent forests (Fig. 1). This pattern was mirrored in the model by a positive effect of P_A on patch occupancy in recent forest, both at equilibrium and as equilibrium was approached (Fig.

TABLE 1. Results of stepwise multiple-regression analyses predicting relative species diversity of ancient forest herbs in recent vs. ancient forests (S_R/S_A) with three candidate variables (log proportion ancient forest, $\log P_A$; log proportion recent forest, $\log P_R$; and maximum age of recent forests, A_R).

Analysis†	Individual significant variables			Full model (with intercept)‡					
	Variable	Partial r^2	F	P	Model ss (df)	Error ss (df)	Total ss (df)	F	P
1	$\log P_A$	0.76	25.3	0.001	0.14 (1)	0.045 (8)	0.19 (9)	25.3	0.001
2	$\log P_A$	0.69	18.2	0.003	0.14 (2)	0.024 (7)	0.17 (9)	20.9	0.001
	A_R	0.16	7.9	0.026
3	$\log P_A$	0.66	9.9	0.026	0.12 (2)	0.017 (4)	0.14 (6)	14.3	0.015
	A_R	0.21	7.0	0.057

† Analysis 1 used the raw uncorrected values of S_R/S_A , analysis 2 used the three area-corrected values of S_R/S_A in place of their corresponding raw values, and analysis 3 used only the seven studies for which either area was not a factor, or a correction for area was possible.

‡ ss = sum of squares; df = degrees of freedom, in parentheses.

2). The only theoretical situation in which this was not the case was at equilibrium for a rapid colonizer when a large proportion of the landscape was recent forest (high P_R). In this case, occupied recent stands ultimately become more important than ancient stands as sources of colonists for empty recent patches. For poor colonizers, the effect of P_A on P_{RO} was effectively independent of P_R , and very similar in shape after 100 years as at equilibrium. Therefore, the model predicts a positive relationship between P_A and P_{RO} even among

landscapes differing in the age of recent forests, just as was found in the empirical relationship between P_A and S_R/S_A . Thus, it appears that habitat loss inhibits the recovery of species diversity in recent forests, likely by effectively reducing the colonization rate ($C_A P_A$) of already poor colonizers.

No effect of proportion recent forest (P_R) on relative species diversity in recent forest was found in the empirical data. Again, this pattern was mirrored in the model output, with the effect of P_R on P_{RO} only be-

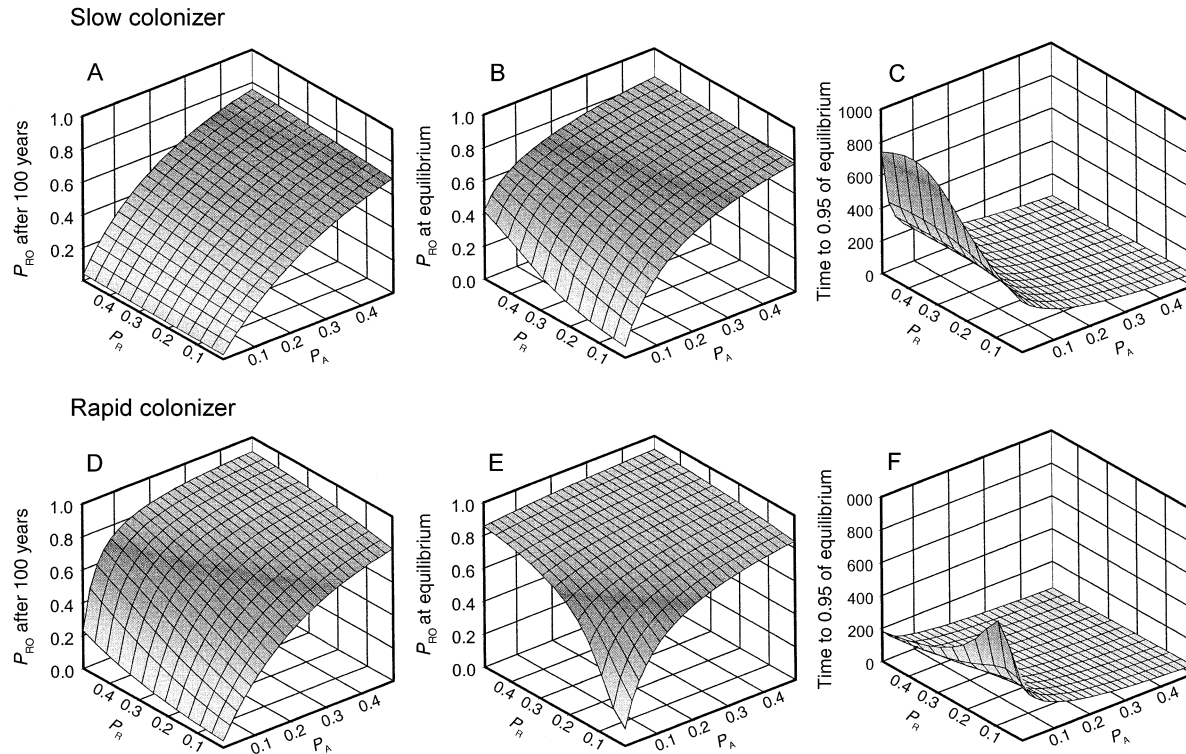


FIG. 2. Patch occupancy in recent forest (P_{RO}) after 100 years and at equilibrium, and time to 0.95 of equilibrium, in relation to proportion of ancient forest (P_A) and proportion of recent forest (P_R) predicted by a mainland-island metapopulation model for a relatively slow colonizer ($C_A = 0.039$, $C_R/C_A = 0.4$, panels A–C) and a relatively rapid colonizer ($C_A = 0.069$, $C_R/C_A = 1$, panels D–F). In both cases, e (probability of going extinct per year) = 0.005.

coming important for rapid colonizers at equilibrium in landscapes with very low P_A . Therefore, if P_R influences P_{RO} in real landscapes, the effects would only become detectable close to equilibrium, and with a sample of landscapes covering a wide range of P_R at low P_A . Appropriate data, and perhaps even appropriate landscapes, are not currently available to test this. The data and model together suggest that the extent of recent forest creation is far less important than ancient forest preservation for the recovery of diversity in recent forests.

Because agricultural fields generally do not contain ancient forest herbs, species diversity necessarily increases through time in recent forest patches, thus leading to a relationship between diversity and patch age within landscapes (e.g., Grashof-Bokdam and Geertsema 1998). By extension, in landscapes where recent forest patches are relatively old (on average), diversity should be higher than where recent forests are younger. This is a trivial prediction of the model in which patch occupancy in recent forest starts at zero and increases through time. However, this prediction is difficult to test empirically because of tremendous variation in recent patch ages within landscapes. The maximum age of recent patches (A_R) is a very crude indicator of recent forest age at the landscape scale (most studies present insufficient data to improve upon this), but despite this, A_R was a marginally significant predictor of S_R/S_A in two of the three analyses. Concerning the question of habitat loss influencing restoration, the only important conclusion is that the effect of P_A on S_R/S_A was not confounded by the age of recent patches. The weakness of the A_R effect in the empirical analysis may be due to limitations of the data, or to the overwhelming influence of P_A on diversity in recent forests.

The preceding paragraphs show that the data and model present a consistent picture of how landscape proportions of ancient and recent forest influence species diversity in recent forests, thus lending support to the use of the model for exploring how time to equilibrium patch occupancy is influenced by landscape composition. Several authors have suggested that centuries will be required for certain plant species to reestablish populations in recent forests (e.g., Peterken 1996, Bellemare et al. 2002). The model results reported here support this suggestion, and go a step further to suggest that both patch occupancy and the time course for post-agricultural colonization should depend strongly on the initial extent of habitat loss. Where habitat loss is most severe, the expected time to equilibrium is longest. Even in landscapes with a relatively large proportion of ancient forest (~20%), as in many areas of eastern North America (Smith et al. 1993, Bellemare et al. 2002), colonization is expected to be a slow process. Across a range of reasonable extinction rates and corresponding colonization rates estimated from data, the model predicts that the recovery process will take at least several centuries when forest clear-

ance is most severe, even for rapid colonizers. At the very least, it can be concluded that severe habitat loss greatly delays the process of natural restoration.

This paper has provided evidence, both empirical and theoretical, for a strong and enduring influence of habitat loss on the recovery of populations and communities in restored habitat patches. Establishment of forests on former agricultural land is taking place throughout the world (Whitney 1994, Peterken 1996, Dobson et al. 1997), and the recovery of diversity in these forests will likely depend on the extent to which the forest was initially cleared, and to a lesser degree on the extent to which agricultural land is abandoned. If remnant habitats are more favorable for populations than restored habitats, as is generally the case in both temperate and tropical forests (Dobson et al. 1997), the effects of habitat loss and fragmentation will extend beyond the much-studied persistence vs. extinction of whole metapopulations, and will continue long after habitat loss has ceased and restoration begun.

ACKNOWLEDGMENTS

I thank Stephen Ellner, Peter Marks, Monica Geber, Sana Gardescu, Nelson Hairston, Jr., Peter Kareiva, Robert Harris, and Dan Ardia for invaluable discussion and comments throughout this project, and Kris Verheyen, David Foster, and Jesse Bellemare for access to unpublished data. Two anonymous reviewers provided helpful comments on the manuscript. Funding was provided by a training grant in Human Accelerated Environmental Change from the National Science Foundation, and a STAR fellowship from the U.S. Environmental Protection Agency.

LITERATURE CITED

- 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.
- Bierzychudek, P. 1982. Life histories and demography of shade-tolerant temperate forest herbs: a review. *New Phytologist* **90**:757–776.
- Dobson, A. P., A. D. Bradshaw, and A. J. M. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. *Science* **277**:515–522.
- Dzwonko, Z., and S. Loster. 1988. Species richness of small woodlands on the western Carpathian foothills. *Vegetatio* **76**:15–27.
- Dzwonko, Z., and S. Loster. 1989. Distribution of vascular plant species in small woodlands on the Western Carpathian foothills. *Oikos* **56**:77–86.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* **61**:603–610.
- Franco, M., and J. Silvertown. 1996. Life history variation in plants: an exploration of the fast–slow continuum hypothesis. *Philosophical Transactions of the Royal Society of London B* **351**:1341–1348.
- Gerhardt, F. 1998. Physiographic and historical influences on forest composition in central New England, USA. Thesis. Department of Forest Science, Harvard University, Cambridge, Massachusetts, USA.
- Gibson, C. W. D. 1986. Management history in relation to changes in the flora of different habitats on an Oxfordshire estate, England. *Biological Conservation* **38**:217–232.
- Graae, B. J. 2000. The effect of landscape fragmentation and forest continuity on forest floor species in two regions of Denmark. *Journal of Vegetation Science* **11**:881–892.

- Grashof-Bokdam, C. J., and W. Geertsema. 1998. The effect of isolation and history on colonization patterns of plant species in secondary woodland. *Journal of Biogeography* **25**:837–846.
- Haila, Y. 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecological Applications* **12**:321–344.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford, UK.
- Honnay, O., B. Degroote, and M. Hermy. 1998. Ancient-forest plant species in western Belgium: a species list and possible ecological mechanisms. *Belgian Journal of Botany* **130**:139–154.
- Huxel, G. R., and A. Hastings. 1999. Habitat loss, fragmentation, and restoration. *Restoration Ecology* **7**:309–315.
- Jerling, L. 1998. Linnaeus' Flora Kofsöensis revisited—floristic changes during 260 years in a small island of the lake Mälaren. *Nordic Journal of Botany* **18**:667–675.
- Levins, R. 1969. Some demographic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**:237–240.
- Matlack, G. R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* **75**:1491–1502.
- Nilsson, I. N., and S. G. Nilsson. 1985. Experimental estimates of census efficiency and pseudoturnover on islands: error trend and between observer variation when recording vascular plants. *Journal of Ecology* **73**:65–70.
- Ovaskainen, O., and I. Hanski. 2002. Transient dynamics in metapopulation response to perturbation. *Theoretical Population Biology* **61**:285–295.
- Peterken, G. F. 1996. *Natural woodland: ecology and conservation in northern temperate regions*. Cambridge University Press, Cambridge, UK.
- Peterken, G. F., and M. Game. 1984. Historical factors affecting the number and distribution of vascular plant species in woodlands of central Lincolnshire. *Journal of Ecology* **72**:155–182.
- Petersen, P. M. 1994. Flora, vegetation, and soil in broad-leaved ancient and planted woodland, and scrub on Røsnæs, Denmark. *Nordic Journal of Botany* **14**:693–709.
- Rackham, O. 1980. *Ancient woodland: its history, vegetation and uses in England*. Edward Arnold, London, UK.
- Roden, C. M. 1998. Persistence, extinction and different species pools within the flora of lake islands in western Ireland. *Journal of Biogeography* **25**:301–310.
- SAS Institute. 1998. *SAS version 7.0*. SAS Institute, Cary, North Carolina, USA.
- Singleton, R., S. Gardescu, P. L. Marks, and M. A. Geber. 2001. Forest herb colonization of postagricultural forests in central New York State. *Journal of Ecology* **89**:325–338.
- Singleton, T. A. 1998. *Recovery of the forest herb community in post-agricultural forests in central New York: pattern and process*. Dissertation. Cornell University, Ithaca, New York, USA.
- Smith, B. E., P. L. Marks, and S. Gardescu. 1993. Two hundred years of forest cover changes in Tompkins County, New York. *Bulletin of the Torrey Botanical Club* **120**:223–247.
- Tack, G., and M. Hermy. 1998. Historical ecology of woodlands in Flanders. Pages 283–292 in K. J. Kirby and C. Watkins, editors. *The ecological history of European forests*. CAB International, New York, New York, USA.
- Tilman, D., C. L. Lehman, and P. Kareiva. 1997. Population dynamics in spatial habitats. Pages 3–20 in D. Tilman and P. Kareiva, editors. *Spatial ecology*. Princeton University Press, Princeton, New Jersey, USA.
- Verheyen, K. 2002. *The relative importance of seed and recruitment limitation of vascular plants in secondary forest succession*. Dissertation. University of Leuven, Leuven, Belgium.
- Whitney, G. G. 1994. *From coastal wilderness to fruited plain*. Cambridge University Press, Cambridge, UK.
- Wulf, M. 1997. Plant species as indicators of ancient woodland in northwestern Germany. *Journal of Vegetation Science* **8**:635–642.

APPENDIX A

Data on landscape properties and plant species diversity in ancient and recent forests of Europe and eastern North America are available in ESA's Electronic Data Archive: *Ecological Archives* E084-025-A1.

APPENDIX B

Details on methods of data acquisition and analysis for studies on plant diversity in ancient and recent forests that includes sufficient information to calculate estimates of the proportions of the landscape in ancient (P_A) and recent (P_R) forest are available in ESA's Electronic Data Archive: *Ecological Archives* E084-025-A2.