



Promoting the Science of Ecology

---

Historical Landscape Connectivity Affects Present Plant Species Diversity

Author(s): Regina Lindborg and Ove Eriksson

Source: *Ecology*, Vol. 85, No. 7 (Jul., 2004), pp. 1840-1845

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/3450357>

Accessed: 14/11/2010 12:22

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=esa>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).



*Ecological Society of America* is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

## HISTORICAL LANDSCAPE CONNECTIVITY AFFECTS PRESENT PLANT SPECIES DIVERSITY

REGINA LINDBORG<sup>1</sup> AND OVE ERIKSSON

*Department of Botany, Stockholm University, SE-106 91 Stockholm, Sweden*

**Abstract.** Transformation of landscapes is considered to be one of the main drivers behind species loss, regionally and globally. Theory and empirical studies suggest that landscape structure influences species diversity in many habitats. These effects may be manifested at different spatial scales depending on species response to landscape heterogeneity. A similar, but often neglected, scaling issue concerns the temporal scale of species response to landscape change. In this study, we found time lags of 50–100 years in the response of plant species diversity to changing configuration of habitats in the landscape. When analyzing remnants of traditionally managed seminatural grasslands in Sweden, we found that species diversity was not related to present-day connectivity of the investigated sites, irrespective of spatial scale (3.1–12.5 km<sup>2</sup>). However, when using maps depicting landscapes 50 and 100 years ago, respectively, strong positive effects of habitat connectivity appeared, at increasing spatial scale for the older landscapes. Thus, analyses of how species diversity relates to present-day landscapes may be misleading, and future species loss may be expected even if the present landscape is maintained.

**Key words:** *biodiversity; land-use change; land-use history; seminatural grasslands; spatial and temporal scales.*

### INTRODUCTION

Despite a general consensus that ongoing landscape transformation is a major threat to species diversity we are still far from knowing the mechanisms behind species decline and loss (e.g., Harrison and Bruna 1999), and their consequences for ecosystems (e.g., Loreau et al. 2001). So far, much of the research on landscapes and biodiversity has focused on effects of spatial landscape structure on single species and species richness, and has resulted in a growing literature on landscape ecology and conservation (e.g., Hansson 1992, Turner et al. 2001, Bierregaard et al. 2002). A number of important drivers behind species loss have been identified, such as habitat deterioration, reduction of habitat area, increasing isolation of remaining habitats, and increasing susceptibility of fragmented habitats to invasions (Fischer and Stöcklin 1997, Hanski 1999, Harrison 1999, Bruun 2000, Eriksson and Ehrlén 2001, Loreau et al. 2001, Bierregaard et al. 2002). Species may respond to such changes instantaneously, but there may also be a time lag in the response. One form of delayed response causes an extinction debt (Tilman et al. 1994), implying that the conditions for species persistence are no longer met, although the species are still present. This may cause extinctions in the future, but changing conditions may also give threatened species a chance to recover. Thus, a critical issue for conservation biology is not only to assess the effect of spatial structure on biodiversity, but also to include a temporal scale of

the biodiversity response to ongoing landscape transformation (Eriksson and Ehrlén 2001, Hanski and Ovaskainen 2002, Foster 2002).

Studies of historical land-use effects on present-day vegetation have mostly focused on a local scale, i.e., related aspects of species diversity to site-specific management history (e.g., Koerner et al. 1997, Eriksson 1998, Austrheim et al. 1999, Honnay et al. 1999, Bellemare et al. 2002, Cousins and Eriksson 2002, Dupouey et al. 2002). A general conclusion is that such site-specific historical effects are common, and that they may reflect land use as far back as several millennia (Eriksson 1998, Dupouey et al. 2002). However, we are not aware of any study that relates present-day diversity to historical landscape structures, extending beyond the spatial scale of the specific sites under study. The main reason why we should expect that historical landscape structure (i.e., surrounding a target site) should influence species diversity is that site connectivity influences colonization and extinction rates at the site. A highly connected site is expected to be comparatively species rich, because colonization is promoted, and possibly also because the rescue effect (Brown and Kodric-Brown 1977) reduces extinction rates. If landscape structure is altered, but local populations at the site are maintained, either as remnant populations (Eriksson 1996) or as stable albeit isolated populations, sites with high historical connectivity will maintain a high diversity in comparison of sites with lower historical connectivity. This will cause a time-lag in the response of local species richness to landscape changes even if these changes do not directly influence the conditions at the site where the species occur.

Manuscript received 20 February 2004; accepted 3 March 2004. Corresponding Editor: T. J. Stohlgren.

<sup>1</sup> E-mail: regina.lindborg@botan.su.se

In this study, we used species-rich remnants of Swedish seminatural grasslands to address questions of how historical landscape structure surrounding target sites affects local plant species diversity. We analyzed plant species diversity at 30 grassland sites, and by using present-day and historical maps we examined how species diversity depends on surrounding landscape structure over time. We specifically addressed two questions. First, what are the relationships between species diversity at target sites, and present and historical landscape structure? And second, if effects of landscape structure occur, are such effects scale invariant or are they detectable only at certain spatial scales?

## METHODS

### *History of seminatural grasslands*

Historically, seminatural grasslands covered large areas of Scandinavia, due to the need for grazing grounds and for production of winter fodder for livestock (Ekstam and Forshed 2000, Eriksson et al. 2002). Seminatural grasslands were created by agricultural management, mowing or grazing, but have not been fertilized or subjected to plowing. The most intensively used grasslands were either open or semi-open, with scattered trees, but vast areas of forest were also subjected to extensive grazing (Ekstam and Forshed 2000, Eriksson et al. 2002). Seminatural grasslands may contain a remarkable density of flowering plant species: 40–60 species/m<sup>2</sup> (Kull and Zobel 1991, Eriksson and Eriksson 1997). During the last century, land use practices concerning seminatural grasslands have changed drastically (Ekstam and Forshed 2000). In the late 19th century, seminatural grasslands declined rapidly and were replaced by production of ley (cultivated fodder) on arable fields. A large decline of grazed seminatural grasslands commenced some decades later. In the 1940s, a second phase of modernization of agriculture was initiated, leading to the abandonment of a large number of small farms, and as a result, a decline in grazed seminatural grasslands, and especially livestock grazing in forests. Due to new legislation, forests were from now on completely used for commercial production of timber. During the last 80 years, the total area of seminatural grasslands in Sweden has declined by over 90% (Bernes 1994).

### *Field study*

Data on plant species diversity were gathered from 30 target sites, all seminatural grassland, located in three provinces in Sweden: Östergötland, Södermanland, and Uppland (57°50' N to 60°28' N; 15°10' E to 18°25' E). All sites are remnants of traditional land use, with a similar history of hay making or grazing, and were recently subjected to restoration in order to maintain traditional management. Today they are located in landscapes dominated by arable fields and managed forests, habitats that are generally inhospitable to many of the plant species in the seminatural grasslands (Cousins and Eriksson 2001).

Plant species diversity at each site was assessed during the summer 2001 by inventories of 10 randomly placed plots sized 1 m<sup>2</sup>. Two estimates of species diversity were derived for each target site: total species richness (the total number of species recorded in the 10 plots) and species density (average number of species per square meter). Dry-mesic seminatural grasslands in the study areas are very homogeneous and have a high diversity at a small scale, with a high alpha diversity and relatively low beta and total diversity at similar grasslands (Eriksson and Eriksson 1997, Cousins and Eriksson 2002). This holds also for the sites used in this study (Lindborg and Eriksson 2004). Hence, even such a small-scale sampling as ten 1 m<sup>2</sup> picks up a large fraction of the plant species occurring in seminatural grasslands, which may therefore be representative for total species richness at a site. The size of the sites ranged between 3 and 25 ha. Variation in species diversity among the sites was not related to present management or restoration (Lindborg and Eriksson 2004).

### *Analysis*

The landscape surrounding each target site was analyzed in a Geographical Information System (ArcView GIS 3.2; ESRI, Redlands, California, USA). For each site three maps representing different time layers were analyzed. Cadastral maps were used to analyze the present-day landscape and the landscape around 50 years before present. These maps are based on aerial photographs. For the oldest landscape, 100 years ago, we used land cover maps from around 1900 (*härads-skarta* in Swedish). To make comparisons over time, data on land cover distribution from the oldest map was digitized and rectified using ArcView. A digital method (Cousins 2001) was used to render the land cover maps geometrically accurate and thematically comparable to the cadastral maps. The maps from around 1900 are known to be accurate and carefully constructed. In the 100 years ago land cover map, a major part of the area surrounding the target sites was classified as scattered forests subjected to extensive grazing by livestock. Thus, forests close to farms at that time were potential grazing areas and analyzed as suitable for inhabiting species favored by grazing. Fig. 1 presents an example of grassland distribution for the three time layers for one of the sites.

The landscape was analyzed with regard to target site connectivity at two different spatial scales, defined by circles with radii of 1 and 2 km, respectively, from the center of each target site. These two spatial scales were chosen to include the range from an area that surrounds the target site but still includes other potential sites for grassland species (1-km scale: 3.1 km<sup>2</sup>), to an area that includes the farm with the target site, and other farms in the surroundings (2-km scale: 12.5

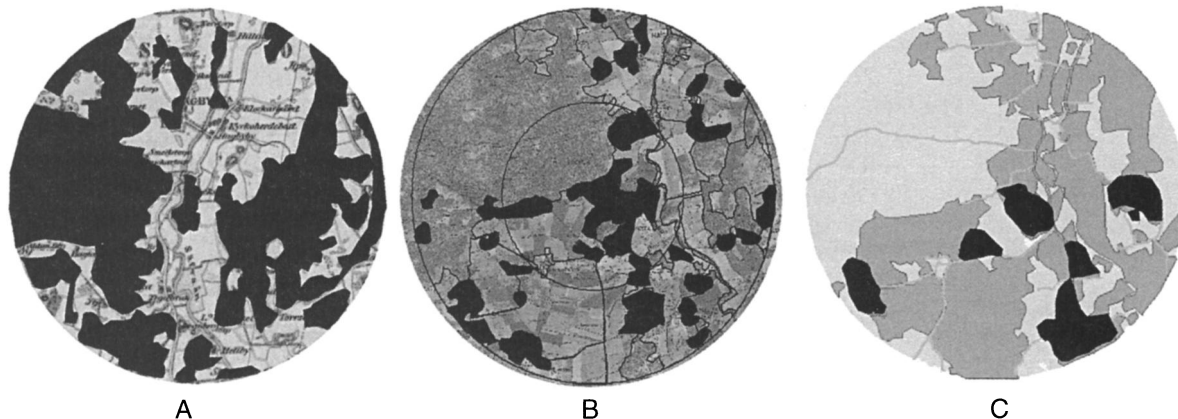


FIG. 1. Distribution of seminatural grasslands (marked in black) in one of the study sites in Sweden representing tree time layers: (A) 1900, (B) 1950, and (C) the present. Each circle has a radius of 2 km.

km<sup>2</sup>). Connectivity of each target site, surrounded by  $k$  seminatural grassland sites within the examined circle area, was defined as:  $\sum \exp(-\alpha d_j) A_j$ , where  $A_j$  is the area of the  $j$ th grassland located at a distance  $d_j$  from the target site, for  $j = 1$  to  $k$ . This measure defines connectivity as the sum of areas with suitable habitat within the analyzed circle, weighted by their distance from the target site (Hanski 1999). The value of  $\alpha$ , describing how fast the number of migrants declines with increasing distance, was set to 1 and was not weighted by dispersal ability of the plant species in the community. Different  $\alpha$ -values, ranging from 1 to 5, have been tested earlier in studies at landscape scale (e.g., Bastin and Thomas 1999) on single species or on species groups containing few selected species, and only small differences were detected among  $\alpha$ -values. However, we studied the dispersal range of a whole community and have no basis for distinguishing between different species. The choice of spatial scales and distance decay of dispersal was motivated because a probable major dispersal route for plants in historical landscapes was by transports of animals, tools, and fodder (Poschlod and Bonn 1998). At larger scales, we considered dispersal unlikely except from chance events, which are important but difficult to relate to spatial patterns in landscapes (Cain et al. 2000). Dispersal over long distances cannot be predicted by the use of ordinary dispersal curves (e.g., Cain et al. 1998, 2000, Clark 1998, Bullock et al. 2002), although they might be of importance for migration on a longer time scale. The relationship between the two species richness measures, and connectivity and site area was analyzed for each of the time layers using multiple linear regression.

#### RESULTS

The mean total species richness at the sites were 43.1 (1 SE = 2.5), ranging 19 to 74, and the mean species density at each site was 16.4 (1 SE = 0.9), ranging from 7.3 to 25.5. There were no relationships between any

of the species diversity measures and area of the target sites (Table 1). However, the present-day pattern of species diversity exhibited different relationships to the configuration of the present landscape, the landscape 50 years ago and the landscape 100 years ago (Table 1). Connectivity of the seminatural grasslands in the present-day landscape was not related to total species richness or species density at any of the two spatial scales, 1 km or 2 km. In contrast, total species richness and species density were positively related to the landscape connectivity 50 years ago, but only at the smaller 1-km scale (Table 1). At the oldest time layer, 100 years ago, the landscape structure had an effect on present-day plant species diversity at both the 1-km and the 2-km scale. Connectivity was positively related to both estimates of species diversity, the total species richness and species density (Table 1).

In addition to the finding that effects on plant species diversity of landscape structure only were detected for historical landscapes, the results indicated that the spatial scale of the effects increases as we used older maps, along with an increased connectivity among the investigated sites (Fig. 2). Although, the differences in  $r^2$  between models were small, it is noteworthy that the model with the highest explanatory power was the one for species density, for the 2-km scale, 100 years ago (Table 1).

#### DISCUSSION

From landscape ecological theory (MacArthur and Wilson 1967, Hanski 1999) and previous empirical studies (e.g., Fischer and Stöcklin 1997, Harrison 1999, Bruun 2000), we had a strong expectation that both area and connectivity of the target sites should explain a large portion of the variation in plant species diversity among sites. However, our results indicated that none of these factors, when estimated from the present-day landscape, were related to the two measures of species diversity used, total species richness and species density per square meter. This conclusion held for both of

TABLE 1. Effect of site connectivity and site area on present-day plant species diversity (total species richness and species density) in Swedish seminatural grasslands at two different spatial scales and three different time layers: present, 50 years ago, and 100 years ago.

Time layer and scale	Species diversity measure	Connectivity		Site area		Model $r^2$
		Beta	<i>P</i>	Beta	<i>P</i>	
Present						
1 km	Total species richness	-0.30	0.095	-0.35	0.053	...
	Species density	-0.36	0.053	-0.10	0.566	...
2 km	Total species richness	-0.05	0.793	-0.33	0.108	...
	Species density	-0.19	0.344	-0.03	0.901	...
50 yr BP						
1 km	Total species richness	0.54	<b>0.002</b>	0.11	0.516	0.54
	Species density	0.43	<b>0.020</b>	0.03	0.847	0.43
2 km	Total species richness	-0.03	0.874	0.03	0.884	...
	Species density	-0.14	0.447	-0.04	0.840	...
100 yr BP						
1 km	Total species richness	0.41	<b>0.026</b>	-0.05	0.791	0.41
	Species density	0.49	<b>0.007</b>	-0.13	0.463	0.49
2 km	Total species richness	0.54	<b>0.003</b>	-0.09	0.581	0.53
	Species density	0.57	<b>0.001</b>	-0.15	0.413	0.57

Note: Significant relationships are marked in bold ( $n = 30$ ) and  $r^2$  is shown for models with significant relationships.

the spatial scales used in the analyses, circles with 1 or 2 km radius from the center of the target site. In contrast, connectivity of the target sites 50 years ago was significantly related to both diversity measures, but the effects were only detected for the smallest spatial scale, circles with 1 km radius around the target

sites. Analyzing the maps depicting the landscape 100 years ago, connectivity again revealed an effect on variation in present-day plant species diversity, but the effect was significant also for the larger spatial scale, circles with 2 km radius around the target site. Although effects of site history on local species richness

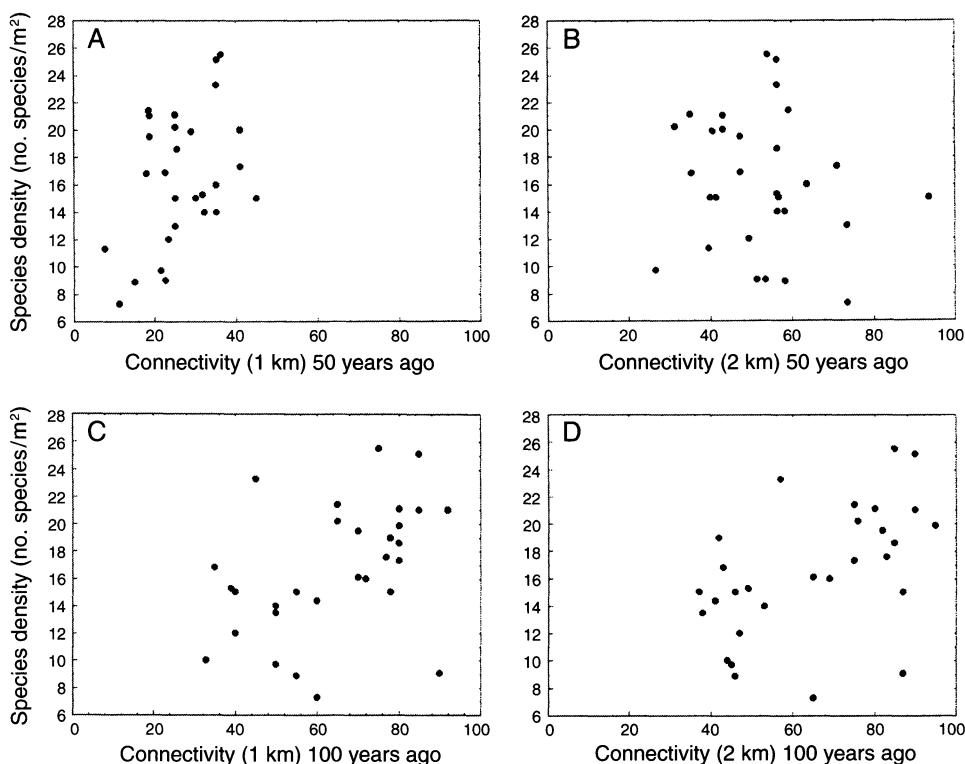


FIG. 2. The relationships between species density (species/m<sup>2</sup>) in Swedish seminatural grasslands and site connectivity 50 and 100 years ago, at two different spatial scales.

are well known (e.g., Peterken and Game 1984, Cousins and Eriksson 2002, Foster 2002), historical effects of landscape structure have, to our knowledge, not been documented previously.

The two historical time layers analyzed, around 50 and 100 years ago, cover a period of drastic land use changes in Sweden, and our results suggest that the present-day variation in plant species diversity in seminatural grasslands is largely a legacy of land use still occurring 50–100 years ago. Thus, plant species diversity patterns in the present-day landscape have been formed under landscape conditions no longer existing. The finding that the effect of spatial scale on connectivity decreases over time, from past to present, is likely to reflect that the large areas in the surroundings of the present-day target sites were used for grazing around 1900, and that these areas had been reduced 1950. It is also plausible that land use close to the farms was more intensive and that human-induced dispersal of seeds at the 1-km scale was more effective due to transportation of animals, hay, and tools (Poschod and Bonn 1998). Usage of the grasslands, e.g., livestock grazing and hay-making, also delay succession compared to more extensive grazed areas at the larger 2-km spatial scale, 50 years ago. A general explanation for connectivity effects is that connected habitats increase the effective dispersal of species, creating larger and more persistent regional populations (Hanski 1999). Our results indicate that the source areas for diaspores deposited at what we now define as target areas have declined over the last century.

Population studies of single plant species in the region have suggested that there may be considerable time lags between the onset of habitat change and the final demise of populations (Eriksson and Ehrlén 2001). Such time lags reflect the capacity of local plant populations to persist not only under deteriorating local conditions, but also in isolation. Thus, in addition to the effects of historical source populations, the capacity to develop remnant populations is a prerequisite for the time lag in the response of site specific diversity to landscape changes. Species that are subjected to faster turnover, or are not capable of maintaining populations over extended periods of slow population decline, are not expected to exhibit distributions reflecting historical landscapes. Although this was beyond the scope of our study, we may speculate that diversity of short-lived and mobile organisms such as insects or birds do not reflect landscape history in the same way as long-lived plants.

Our results have several implications for conservation biology. Analyses of spatial biodiversity patterns that fail to find landscape effects today may give a misleading impression that landscape structure surrounding sites identified as valuable for conservation are of no importance for biodiversity. If the buildup of locally high species richness is a legacy of historically higher connectivity, the lack of relationship between

plant species diversity and landscape configuration in the present-day landscape suggests that future loss of species locally may not be compensated for by new colonizations. Development of conservation programs based on spatial analyses of changing landscapes should therefore consider not only effects of area, isolation, corridors and edge effects (Hanski 1999, Bierregaard et al. 2002), but also the history of the investigated landscape, especially if conservation concerns long-lived less mobile organisms.

#### ACKNOWLEDGMENTS

We are grateful to J. Ehrlén, S. A. O. Cousins and two anonymous reviewers for comments on the manuscript, to T. Håkansson and M. Isaeus for GIS-technical support, and to Formas and the Mistra program "Seminatural grasslands—economy and biodiversity" for financial support.

#### LITERATURE CITED

- Austrheim, G. E., G. A. Olsson, and E. Grøntvedt. 1999. Land-use impact on plant communities in semi-natural sub-alpine grasslands of Budalen, central Norway. *Biological Conservation* **87**:369–379.
- 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.
- Bernes, C. 1994. Biological diversity in Sweden [In Swedish: Biologisk Mångfald i Sverige]. Naturvårdsverket Förlag, Solna, Sweden.
- Bierregaard, R. O., T. E. Lovejoy, C. Gascon, and R. Mesquita, editors. 2002. *Lessons from Amazonia: the ecology and conservation of a fragmented forest*. Yale University Press, New Haven, Connecticut, USA.
- Brown, J. H., and A. Kodrick-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**:445–449.
- Bruun, H-H. 2000. Patterns of species richness in dry grassland patches in an agricultural landscape. *Ecography* **23**: 641–650.
- Bullock, J. M., I. M. Moy, R. F. Pywell, S. J. Coulson, A. M. Nolan, and H. Caswell. 2002. Plant dispersal and colonization processes at local and landscape scale. Pages 279–302 in J. M. Bullock, A. Kenward, and R. Hails, editors. *Dispersal ecology*. Blackwell Science, Oxford, UK.
- Cain, M. L., H. Damman, and A. Muir. 1998. Seed dispersal and the Holocene migration of woodland herbs. *Ecological Monographs* **68**:325–348.
- Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany* **87**:1217–1227.
- Clark, J. S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist* **152**:204–224.
- Cousins, S. A. O. 2001. Analysis of land-cover transitions based on 17th and 18th century cadastral maps and aerial photographs. *Landscape Ecology* **16**:41–54.
- Cousins, S. A. O., and O. Eriksson. 2001. Plant species occurrences in a rural hemiboreal landscape: effects of remnant habitats, site history, topography and soil. *Ecography* **24**:461–469.
- Cousins, S. A. O., and O. Eriksson. 2002. The influence of management history and habitat on plant species richness in a rural hemiboreal landscape, Sweden. *Landscape Ecology* **17**:517–529.

- 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.
- Ekstam, U., and N. Forsh, editors. 2000. Swedish semi-natural grasslands—history and ecology [In Swedish: Svenska naturbetesmarker—historia och ekologi]. Naturvårdsverket Förlag, Stockholm, Sweden.
- Eriksson, Å. 1998. Regional distribution of *Thymus serpyllum*: management history and dispersal limitation. *Ecography* **21**:35–43.
- Eriksson, Å., and O. Eriksson. 1997. Seedling recruitment in semi-natural pastures: the effects of disturbance, seed size, phenology and seed bank. *Nordic Journal of Botany* **17**:469–482.
- Eriksson, O. 1996. Remnant dynamics of plants: a review of evidence for remnant, source–sink and metapopulations. *Oikos* **77**:248–258.
- Eriksson, O., S. A. O. Cousins, and H.-H. Bruun. 2002. Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. *Journal of Vegetation Science* **13**:743–748.
- Eriksson, O., and J. Ehrlén. 2001. Landscape fragmentation and the viability of plant populations. Pages 157–175 in J. Silvertown and J. Antonovics, editors. Integrating ecology and evolution in a spatial context. Blackwell, Oxford, UK.
- Fischer, M., and J. Stöcklin. 1997. Local extinctions of plants in remnants of extensively used calcareous grasslands 1950–1985. *Conservation Biology* **11**:727–737.
- Foster, D. R. 2002. Thoreaus country: a historical-ecological perspective on conservation in the New England landscape. *Journal of Biogeography* **29**:1537–1555.
- Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, UK.
- Hanski, I., and O. Ovaskainen. 2002. Extinction debt at extinction threshold. *Conservation Biology* **16**:666–673.
- Hansson, L. 1992. Ecological principles of nature conservation. University Press, Cambridge, UK.
- Harrison, S. 1999. Local and regional diversity in a patchy landscape: native, alien and endemic herbs on serpentine. *Ecology* **80**:70–80.
- Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* **22**:225–232.
- Honnay, O., M. Hermy, and P. Coppin. 1999. Effects of area, age and diversity of forest patches in Belgium on plant species richness, and implications for conservation and reforestation. *Biological Conservation* **87**:73–84.
- Koerner, W., J. L. Dupouey, E. Dambrine, and M. Benoit. 1997. Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. *Journal of Ecology* **85**:351–358.
- Kull, K., and M. Zobel. 1991. High species richness in an Estonian wooded meadow. *Journal of Vegetation Science* **2**:711–714.
- Lindborg, R., and O. Eriksson. 2004. Effects of restoration on plant species richness and composition in Scandinavian semi-natural grasslands. *Restoration Ecology*, *in press*.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**:804–808.
- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.
- 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.
- Poschlod, P., and S. Bonn. 1998. Changing dispersal processes in the central European landscape since the last ice age: an explanation for the actual decrease of plant species richness in different habitats? *Acta Botanica Neerlandica* **47**:27–44.
- Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. *Nature* **371**:65–66.
- Turner, M., G. R. H. Gardner, and R. V. O'Neill. 2001. Landscape ecology in theory and practice: pattern and process. Springer-Verlag, New York, New York, USA.