Recovery of forest plant communities in post-agricultural landscapes

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As landscapes throughout Europe and eastern North America recover from past agricultural use, forests continue to reflect their agricultural history. For centuries after agriculture has ceased, plant communities on abandoned agricultural lands remain impoverished in herbaceous species characteristic of uncleared forests. To facilitate the recovery of biological diversity in these forests, and to anticipate the effects of future land-use decisions, we need to understand the process of recolonization. The unique interactions between forest herbs and agricultural history also allow us to explore some universal questions in ecology, such as how dispersal and environment limit species distributions.

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The profound impacts of human land use on biological diversity via habitat loss and fragmentation cause intense concern among ecologists and conservationists. Despite the abundance and importance of restored habitats, however, much less attention has focused on how communities respond as landscapes recover from human disturbance. Understanding the long-term consequences of past land-use decisions is critical, not only to inform resource managers about existing communities, but also to predict the effects of future disturbance and environmental change.

Today, many landscapes worldwide continue to bear the imprint of historical land-use patterns. Across much of Europe and eastern North America, for example, phases of forest clearance for agriculture were followed by agricultural abandonment and forest regrowth (Figure 1). In some regions, forests that developed on former agricultural lands represent as much as 80% of current forest cover (Foster 1992; Grashof-Bokdam and Geertsema 1998). These habitats often differ in vegetation and soils from forests that were never cleared for agriculture, even 2000 years after reforestation (Dupouey *et al.* 2002). Such observations lead ecologists to ask whether post-agricultural forests will ever resemble their pre-disturbance condition. If so, how long will it take? Or, has human land use created novel communities that will persist unless active restoration intervenes?

In a nutshell:

- A legacy of past agriculture influences forest plants across much of Europe and eastern North America
- Understory communities in forests that grew on old fields show reduced species richness and altered composition compared to forests that were never cleared
- Many species' distributions appear limited by their ability to disperse to new sites
- Post-agricultural habitats may enhance or depress plant performance
- Forest herb recolonization may take centuries, or require active restoration

At the same time, these patterns raise basic ecological questions about controls on species distribution and abundance. Landscapes with a history of agriculture provide an ideal opportunity to assess the influence of past disturbance versus environmental conditions on current vegetation. In fact, it has become increasingly clear that many modern patterns and processes cannot be explained without taking into account the pervasive and persistent legacies of historical land use. Following the classic work of Rackham (1980) and Peterken (1981) in Britain, ecologists have shown a growing interest in investigating how past land use shapes current communities. While interactions between agricultural history and present-day forest communities have been examined across the neotropics and elsewhere, the past several decades have seen a spate of particularly active research (approximately 100 papers in the past 20 years) focusing on herbaceous understory plants in north-temperate deciduous forests. Here we highlight the key insights that have emerged from this work and discuss new directions.

■ Reconstructing history

All studies of the implications of past land use rely on accurate reconstructions of history. Historical land-use maps and aerial photographs provide the most useful information for documenting forest-cover changes over time (Figure 2). These sources can distinguish remnants of ancient forest from recent, restored forests on former agricultural lands (Panel 1) and establish the

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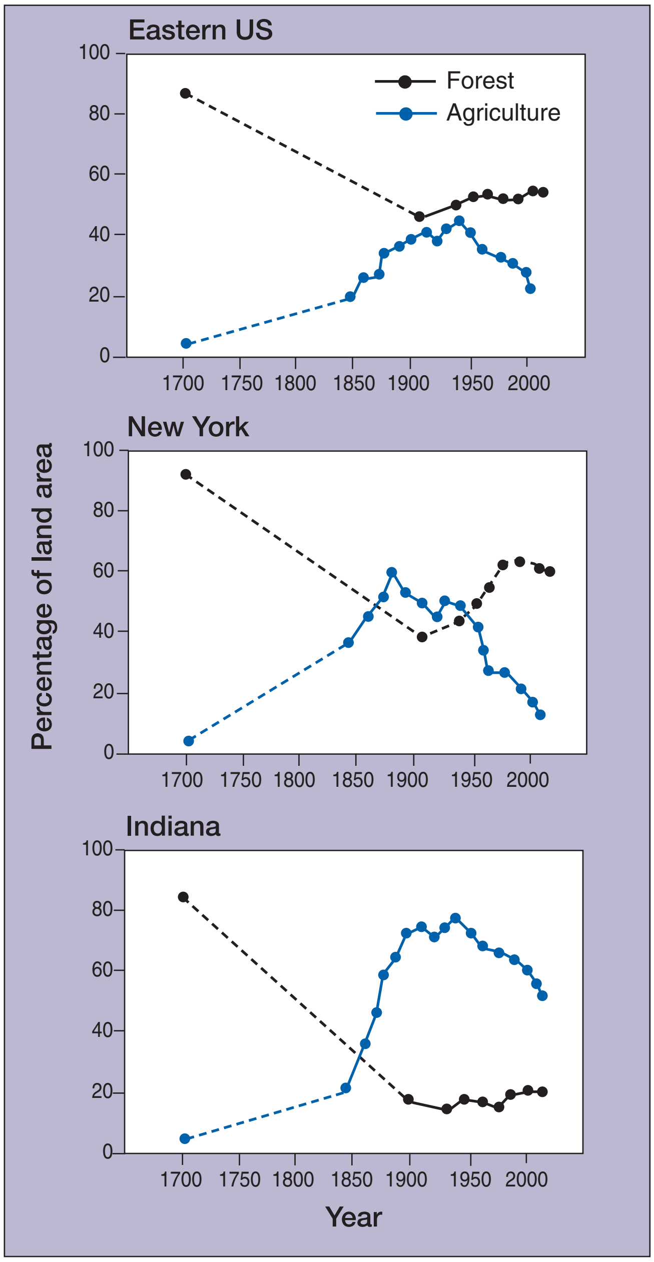


Figure 1. *Changes over time in forest cover and agricultural land area in the eastern US (all states east of the Mississippi River) and the states of New York and Indiana. Land cover estimates for 1700 are approximate. From USDA Forest Inventory and Analysis and Agriculture Census data (Smith* et al. *2004).*

age of recent patches (Smith *et al.* 1993). More specific site histories, including whether a parcel of land was plowed or pastured, can be constructed through interviews with landowners and observations of field evidence such as stone walls, treefall pits and mounds, and open-grown trees (Marks and Gardescu 2001). These methods yield detailed, spatially explicit historical reconstructions that typically span 100–400 years and range from individual woodlots to whole counties. They thereby complement historical information from other approaches, such as palynology and dendrochronology, by providing a unique intermediate time scale and a high level of local detail.

■ Focusing on forest herbs

Agriculture alters entire plant communities, including tree and shrub species composition. After abandonment, old fields are initially colonized by herbaceous species that favor open habitats. A dense thicket of shrubs and trees typically develops within 30–40 years, and a closed tree canopy in about 60–80 years. Dominant tree genera in both European and eastern North American temperate deciduous forests include beech (*Fagus*), maple (*Acer*), basswood (*Tilia*), and oak (*Quercus*), as well as a few conifers such as pine (*Pinus*). The identity and relative abundance of canopy species in post-agricultural forests often differ from communities undisturbed by agriculture (Motzkin *et al.* 1996). However, recolonization by forest herbs has been of particular interest as forests regrow, since herbaceous understory species represent the majority of plant diversity in temperate forests (Figure 3) and, unlike many trees and shrubs, forest herb populations are not altered by planting and harvesting. Forest herbs also share life-history traits that may make them more sensitive to habitat loss and fragmentation, such as short-distance seed dispersal mechanisms, short seed dormancy, low seedling recruitment, and long pre-reproductive periods (Whigham 2004). Post-agricultural landscapes thus provide an opportunity to see how species evidently adapted to temporally stable, spatially continuous habitats respond to dynamic and fragmented landscapes.

■ Dispersal versus recruitment limitation

Having distinguished habitats with different histories and identified species of interest, ecologists can ask, how does vegetation vary with land-use history and, more interestingly, why? To what extent are species distributions determined by the availability of suitable habitat, and to what extent are they determined by chance, history, and limited dispersal? These are fundamental questions in ecology, and to address them in this context it is necessary to assess whether land-use history influences environmental conditions in current forests, as well as what roles land-use history and environmental conditions play in determining plant distribution, diversity, and performance (Figure 4). Types of information collected to date include descriptions of forest environments and vegetation, including their relationships with plant life-history traits and landscape attributes; observational studies of plant performance; and experimental introductions.

■ Environmental characterizations

Agriculture potentially affects vegetation both directly, by locally eliminating plants and propagules of forest species, and indirectly, by altering environmental conditions. To fully assess these impacts, it is important to know how ancient and recent forests differ in the environment they provide for understory plants. Soils recovering from agriculture generally have higher pH and nutrient concentrations and lower organic matter content than soils under continuous forest cover (Koerner *et al.* 1997). However, the magnitude and persistence of these differences show tremendous variation among regions. Recent forest soils may continue to reflect their agricultural history over 100 years after reforestation (Koerner *et al.* 1997; Verheyen *et al.* 1999; Dupouey *et al.* 2002). Alternatively, as an equal number of studies have found, they may become broadly similar to ancient forest soils within that time (Kalisz 1986; Compton and Boone 2000; Flinn *et al.* 2005). This regional variation can be difficult to predict because it depends on complex interactions between inherent soil fertility, the nature and duration of agricultural use, and time since abandonment. Thus, environmentally mediated effects of land use on vegetation may be quite important in some landscapes while nonexistent in others.

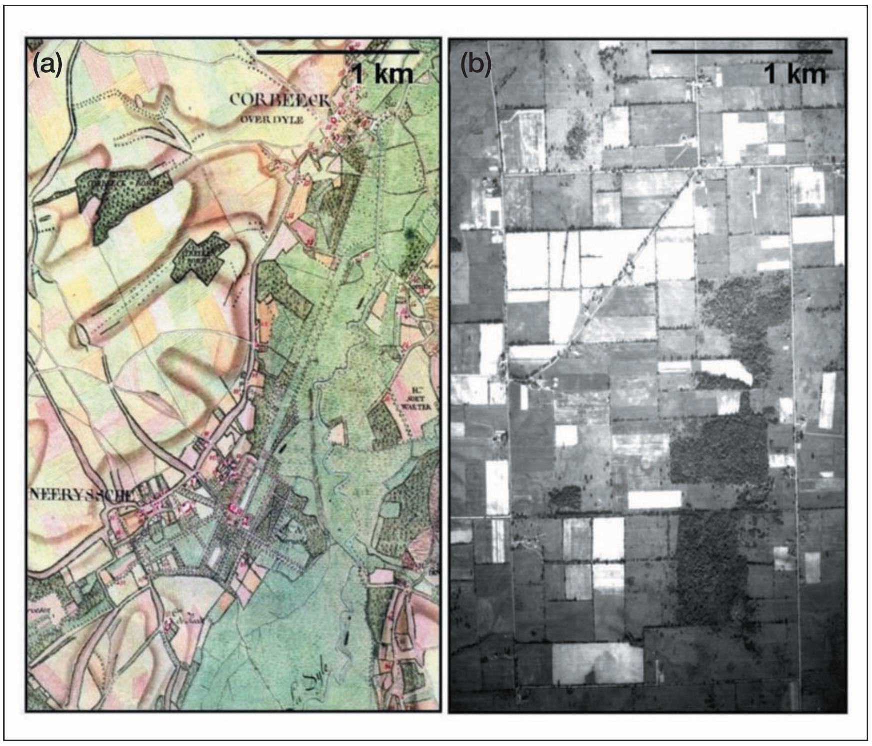


Figure 2. *Sources used to reconstruct past land use include historical maps and aerial photographs. (a) Part of the oldest land-use map covering all of Belgium, made by Count Joseph de Ferraris between 1771 and 1777. This area in the Dijle River valley had forest stands (stippled green), grasslands (light green) and arable fields (yellow). (b) An aerial photograph of central New York taken in 1938, showing patches of ancient forest (dark), abandoned fields with scattered trees, and active agricultural lands (lighter). Hedgerows, often a refuge for forest herbs, are common in both landscapes.*

A major caveat in interpreting environmental differences between ancient and recent forests, as well as the implications for plant communities, is that geographical patterns of land use and environmental variation are often confounded. Steeper slopes, poorer soils, and wetter areas are less likely to be cleared for agriculture and more likely to be abandoned (Foster 1992; Matlack 1997; Flinn *et al.* 2005). Differences in environment and vegetation among current forest types may result from initial conditions rather than agricultural land use itself. Particularly in regions with limited forest cover, investigators must rely on some overlap in environmental conditions between forest types and attempt to isolate the direct effects of land use statistically. One way to control for pre-existing environmental variation is to focus on regions where past land use varies across an area homogenous in topography and soils (Motzkin *et al.* 1996). Within more diverse landscapes, the effects of variation in prior conditions can be eliminated by selecting adjacent pairs of sites that share similar topography and soils, but that differ in history (Kalisz 1986; Singleton *et al.* 2001; Flinn *et al.* 2005).

Panel 1. Defining forest types

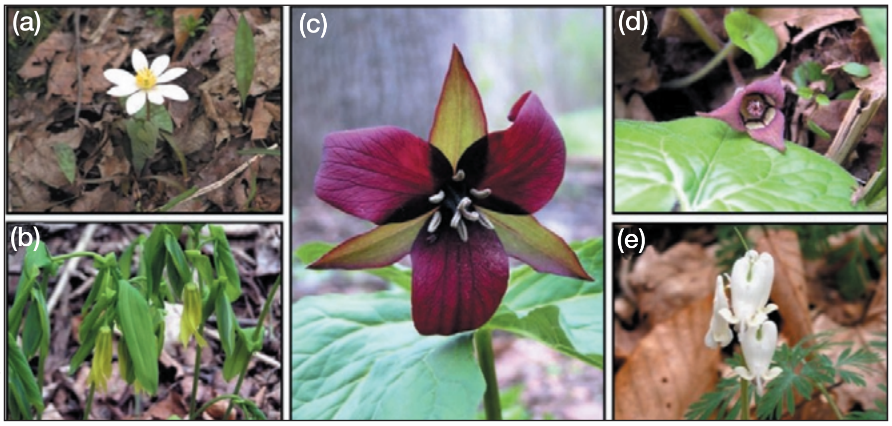
Forest patches in post-agricultural landscapes can be differentiated with two sets of terms (Rackham 1980; Peterken 1981):

Primary forests were never cleared for agriculture, whereas ***secondary*** forests developed on former agricultural land. In most of Europe, where agricultural use and abandonment may predate the oldest land-use maps, identifying primary forests is difficult or impossible. Thus, woodlands are often functionally classified as ***ancient*** – forests that have existed continuously since the time of the earliest land-use maps, or ***recent*** – forests that originated after that time on land known to have been used for agriculture. We use the terms *ancient* and *recent* forest in this paper.

In North America, ancient forests are generally also primary. In Europe, ancient forests may include both primary and ancient secondary forests. Primary forests are not necessarily old-growth forests. In fact, nearly all primary forests have been selectively cut, and many have been grazed by livestock. Clearing and agricultural activities in the surrounding landscape also affect habitats within existing primary forests.

■ Vegetation composition

Differences between the understory communities of ancient and recent forests have been thoroughly documented in regions throughout Europe (Peterken and Game 1984; Dzwonko and Loster 1989; Graae 2000; Wulf 2004) and the northeastern US (Matlack 1994; Motzkin *et al.* 1996; Singleton *et al.* 2001; Bellemare *et al.* 2002). One recent study also compared the vegetation of former coppice woodlands and meadows in Japan (Ito *et al.* 2004). From this body of work, the principal result is abundantly clear: land-use history has a consistently



Courtesy of M Vellend and LM Chan

***Figure 3.** A sample of the forest herb diversity typical of ancient forests in eastern North America: (a) bloodroot (*Sanguinaria canadensis*); (b) bellwort (*Uvularia grandiflora*); (c) purple trillium (*Trillium erectum*); (d) wild ginger (*Asarum canadense*); (e) squirrel corn (*Dicentra canadensis*).*

strong influence on plant diversity and distributions. The impact of past land use on vegetation patterns can equal or even override the effects of topography, soils, subsequent disturbance, and current management (Motzkin *et al.* 1996). In many landscapes, variation in plant community composition largely reflects the former distribution of woodlots and agricultural fields (Glitzenstein *et al.* 1990; Foster 1992; Motzkin *et al.* 1996; Dupouey *et al.* 2002).

In fact, modern vegetation can be specifically associated with particular types of former agricultural use, such as croplands, pastures, or hay meadows, and species may respond quite differently to different forms of agriculture (Koerner *et al.* 1997; Grashof-Bokdam and Geertsema 1998; Stover and Marks 1998; Wulf 2004). Former pastures tend to be most similar to ancient forests in species richness and composition, in part because the lack of plowing allowed relict populations of forest plants to persist (Glitzenstein *et al.* 1990; Koerner *et al.* 1997; Wulf 2004). Specific agricultural practices have unique effects, and finer categories may be necessary to discern them (cf Verheyen *et al.* 1999).

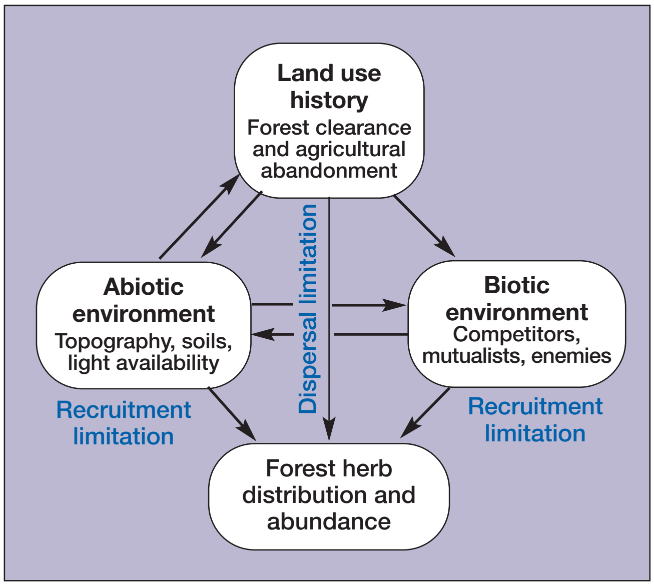


***Figure 4.** Conceptual diagram showing both direct and indirect effects of land-use history on forest herb distribution and abundance. Forest clearance destroys and fragments forest herb communities, and agricultural abandonment creates new, unoccupied habitats, leading to dispersal limitation. Agriculture may also impose recruitment limitation on forest herb populations by altering biotic and abiotic environments.*

Comparing species richness

One way to compare the effects of land-use history across different regions is to examine the species richness of recent forests relative to ancient forests. Comparisons of species richness depend, in part, on how species pools are defined, and these definitions have not been consistent across studies. Some restrict surveys to species that grow exclusively in forests, while others include all species growing in forests, regardless of their habitat affinity. Old-field species that persist as forests develop may contribute to higher total diversity in recent forests. On a Massachusetts sand plain, for example, lands taken out of cultivation 30–50 years before had the highest species richness of any community type, due to a high frequency of weedy and early successional species (Motzkin *et al.* 1996). However, most studies focusing on "native woodland species" or "ancient forest species" have found reduced species richness in understory communities of recent forests as compared to ancient forests (Peterken and Game 1984; Dzwonko and Loster 1989; Matlack 1994; Bossuyt *et al.* 1999; Singleton *et al.* 2001; Vellend 2004; Figure 5).

This result is not universal; some recent forests are apparently old enough to have gained species numbers comparable to those found in ancient forests. In several studies, older recent forests (>70 years old) had similar forest herb species richness to ancient forests, and only younger recent forests had less richness (Bellemare *et al.* 2002). Another case where recent forests may show greater species richness than ancient forests is in regions with acidic, nutrient-poor soils and naturally species-poor communities. Here, disturbance and nutrient enrichment from cultivation may facilitate colonization by a wider range of species (Koerner *et al.* 1997). In this respect, Graae (2000) provides an interesting contrast between two regions of Denmark, Hornsherred and Himmerland. Hornsherred has more nutrient-rich soils and more species-rich communities, and in this region ancient forests had greater species richness than recent forests. In Himmerland, with more sandy, acidic soils and generally lower species richness, ancient and recent forests had similar numbers of species. Nonetheless, the general reduction in diversity in recent versus ancient forests demonstrates that some forest herb distributions must be limited either by their ability to disperse to new habitats, their ability to establish and persist there, or both. Some species that are relatively common in ancient forests may remain almost entirely absent from recent forests, and the metapopulation persistence of these species may be threatened.

Relationships with life-history traits

Knowing which life-history traits characterize species that successfully occupy recent forests may suggest what processes control colonization of post-agricultural landscapes by forest herbs. Of these traits, dispersal mechanisms have received by far the most attention. If dispersal ability primarily limits species distributions, then better dispersers should be more abundant than other species in recent forests. A number of studies have found evidence to support this prediction. Species with adaptations for dispersal by vertebrates and wind tend to have considerably higher migration rates than species dispersed by ants and those that lack morphological adaptations for dispersal (Dzwonko and Loster 1992; Matlack 1994; Grashof-Bokdam and Geertsema 1998; Brunet and von Oheimb 1998; Figure 6). Nevertheless, many studies have failed to find associations between dispersal mode and colonization ability (Mabry *et al.* 2000; Singleton *et al.* 2001; Ito *et al.* 2004; Wulf 2004). Although an intuitively attractive approach, attempts to relate dispersal mode to colonization ability have not always been successful, in part because dispersal classes based on seed morphology may poorly represent realized dispersal distances (Vellend *et al.* 2003).

Relationships with time and distance

Predictions that diversity in recent forests should increase with age and decrease with isolation also rest on the hypothesis that dispersal controls species distributions. Many studies have documented increases in understory species richness with recent forest age (Dzwonko and Loster 1992; Brunet and von Oheimb 1998; Grashof-Bokdam and Geertsema 1998; Bossuyt *et al.* 1999; Flinn and Marks 2004; Figure 5). Although recent forests gain measurable numbers of species over timescales of decades, both empirical observations and models indicate that full recovery will take several centuries at least (Vellend 2003).

Declines in diversity with distance from source habitats have been equally well documented. Recent forests adjacent to ancient forests tend to have greater species richness than isolated recent forests (Peterken and Game 1984), and among isolated recent forests, those closer to ancient forests tend to have higher levels of diversity (Dzwonko and Loster 1992; Matlack 1994; Flinn and Marks 2004). Within adjacent stands, species richness often declines with distance from the ancient forest boundary (Matlack 1994; Brunet and von Oheimb 1998; Bossuyt *et al.* 1999; Singleton *et al.* 2001). Several studies have examined patch occupancy patterns of individual species in greater detail. For example, Verheyen *et al.* (2003) created unusually fine-scale species distribution maps to analyze the influences of forest age, distance from species-specific colonization sources, and environmental variables on colonization patterns. They found the joint effects of time and distance were by far the most important factors explaining the distributions of most species. Taken together, the association of colonization success with recent forest age and isolation, and with species' dispersal-related traits, all point to dispersal as a major driver of post-agricultural forest colonization.

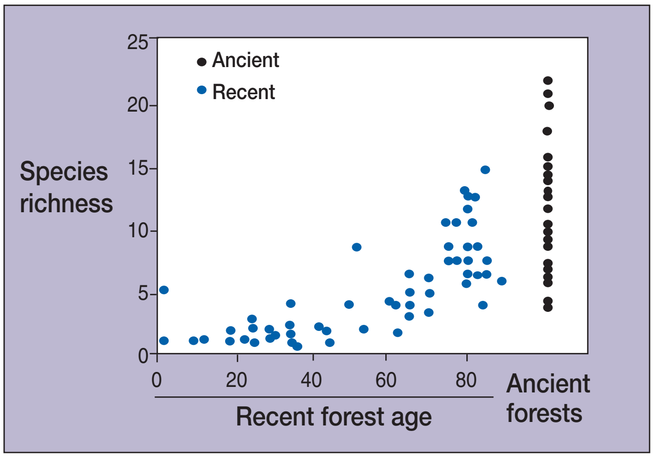


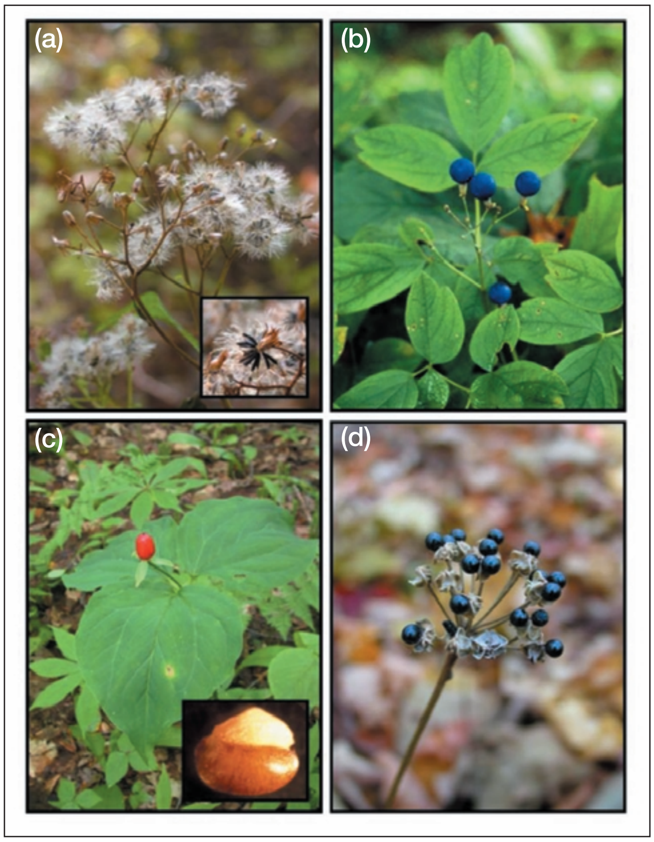
Figure 5. *Species richness of recent forests (number of forest herb species per 180-m^2 area) increases through time (years since abandonment from agriculture), approaching the range spanned by ancient forests. From a synthesis of vegetation surveys in central New York (Flinn and Marks 2004).*

■ Performance observations

To test the hypothesis that depressed demographic performance in recent forests may also limit species distributions, a few studies have compared plant performance between ancient and recent forests. Contrary to predictions, performance in recent forests has often been similar or even enhanced in some species. In wintergreen (*Gaultheria procumbens*), a woody, clonal understory species largely restricted to ancient forests in central Massachusetts, various measures of vegetative and reproductive performance were either similar or higher in recent forests than in ancient forests (Donohue *et al.* 2000). Endels *et al.* (2004) also found generally better performance in recent forests, including higher densities of seedlings and juveniles, for three forest herbs in central Belgium. In contrast, white trillium (*Trillium grandiflorum*) plants of the same age were smaller and less likely to flower in recent forests than in ancient forests in central New York, at sites with high soil pH (Vellend 2005). Clearly, individual species interact differently with the habitats created by past land use, and many of these interactions still need to be investigated.

■ Experimental introductions

Several recent studies have experimentally introduced forest herb species into restored habitats. Successful seed sow-



Courtesy of J Bellemare and M Vellend

Figure 6. *Dispersal mechanisms of forest herbs. (a) The tiny seeds of white snakeroot (*Eupatorium rugosum*) have bristles (inset) to aid in wind dispersal. (b) Birds and mammals eat the bright fruits of blue cohosh (*Caulophyllum thalictroides*). (c) Painted trillium (*Trillium undulatum*) was traditionally thought to be dispersed by ants, since the fat-rich elaisomes on its seeds attract ants (inset), but deer have been found to eat* Trillium *fruits as well (Vellend* et al. *2003). (d) Wild leek (*Allium tricoccum*) seeds have no special adaptation for dispersal.*

ings and adult transplants in unoccupied recent woods suggest that seed dispersal limits some species distributions (Petersen and Philipp 2001; Heinken 2004), but they are difficult to interpret without comparisons to ancient forests and unsown control plots. Experimental populations in ancient and recent forests often perform equally well. For example, planted seeds and adults of four forest herb species showed no consistent differences between forest types in seed germination, seedling survival, or adult performance (Singleton 1998). Where differences between forest types have arisen, plants in recent forests have sometimes shown better survival and performance. In Verheyen and Hermy's (2004) experiment, two of four planted species had higher seedling survival and adult performance in recent than in ancient forest. Likewise, Graae *et al.* (2004) sowed seeds of eight species in both ancient and recent forests. Seed addition increased establishment of four species, and for three species, seedling establishment increased to a much greater extent in recent than in ancient forest. This result clearly indicates that, at least for these species, seed limitation was stronger in recent forest than in ancient, and conditions for seedling establishment in recent forest were favorable – possibly more favorable than in ancient forest. Nevertheless, these studies have been relatively short term compared to the life spans of these species, and it remains an open question whether their results will hold over longer time scales.

■ New directions

Much progress has been made in elucidating the influence of past land use on present-day patterns of forest herb distribution and diversity. The arrival of seeds in recent forests appears to be a critical step limiting the colonization process, and at least for some species, environmental conditions that inhibit establishment or population growth may also slow colonization. Thus, simple seed introductions may go a long way towards restoring plant communities in recent forests, though overcoming environmental limitations may prove more complex. Results to date also point to some important directions for future research.

Population ecology

Patterns of post-agricultural colonization have been extensively documented, but the population-level processes underlying them remain poorly understood. Perhaps the first priority for future work should be detailed studies of individual species' ecology that can unambiguously identify these processes. In particular, the indirect methods applied so far tend to oversimplify the dichotomy between dispersal and recruitment limitation. The two are not mutually exclusive; in fact, many plant populations may be limited by a combination of seed and microsite availability (Eriksson and Ehrlén 1992). Though several studies have measured seed germination and establishment or adult plant performance, only Donohue *et al.* (2000) estimated demographic rates for different life stages with population models. Such studies are essential for evaluating population viability in forests with different land-use histories, as well as for identifying the demographic transitions most critical to population establishment and growth. Since most forest herbs are long-lived perennials (Whigham 2004), demographic studies of at least 3–4 years are greatly needed.

A few studies have used molecular markers to document the impacts of land-use history on genetic variation (Jacquemyn *et al.* 2004; Vellend 2004). Where bottlenecks have reduced genetic diversity (Vellend 2004), forest herb populations in recent forests can suffer from inbreeding depression, which may further hinder colonization. Finer-scale genetic studies may yield important insights into the demographic history and mating patterns of recent populations.

Community interactions

While some studies have correlated plant performance with abiotic environmental conditions such as soil pH, the biotic environment has received little attention. Plant mutualists and enemies often play an important role in determining patterns of spread (Torchin and Mitchell 2004), but their role in this context is unclear. An exception is the study by Mitchell *et al.* (2002), which showed that a lack of seed-dispersing ants cannot explain limited forest herb colonization of recent forests in the southern Appalachians. In European recent forests, competition with a dense cover of nettle (*Urtica dioica*) may inhibit colonization by forest herbs (Endels *et al.* 2004; De Keersmaeker *et al.* 2004). However, in general we simply do not know how the presence or abundance of pollinators, herbivores, mycorrhizal fungi, pathogens, and other organisms influence forest herb colonization of post-agricultural forests.

The interaction between land-use history and herbivory may prove a particularly fruitful area for future research. Deer populations have grown considerably over the past 100 years in both Europe and eastern North America, in part because old fields and developing forests provide ideal habitat and abundant forage (Côté *et al.* 2004). Herbivory by deer can have severe detrimental effects on the growth and reproduction of forest herbs, reducing the abundance of preferred browse plants such as *Trillium* species (Russell *et al.* 2001). However, deer also disperse the seeds of at least some forest herbs (Vellend *et al.* 2003), so an evaluation of their net effect on plant communities must consider both herbivory and seed dispersal. In the context of forest herb recovery, one key unanswered question is whether deer have differential effects in ancient versus recent forests. If deer prefer post-agricultural habitats, herbivory might slow the recovery of forest herb populations.

Landscape-level approaches

The wealth of descriptive data on forest herb distributions has created excellent opportunities to observe vegetation changes directly, rather than infer them from chronosequences. Colonization and extinction, the processes that determine metapopulation dynamics and viability at the landscape scale, are usually difficult to study in long-lived plants. However, since initial surveys of some landscapes were conducted over 25 years ago (Peterken and Game 1984), resurveys could yield direct estimates of colonization and extinction rates. Harmer *et al.* (2001), for example, compared multiple surveys spanning 100 years of forest development on two abandoned arable fields. More systematic efforts across entire networks of sites could produce valuable information on landscape-scale metapopulation dynamics.

In the same way, the accumulation of similar studies from different regions generates great potential for comparison and synthesis across landscapes. Within regions, we may understand what drives variation among forest patches in species diversity and composition, but we know much less about how landscape-level differences in land-use history or environmental conditions may shape vegetation. For example, habitat destruction may cause delayed extinctions of long-lived plants, so that landscapes fragmented relatively recently may show elevated levels of patch occupancy for poor colonizers compared to landscapes fragmented earlier. Comparative and synthetic research across landscapes can begin to address such issues.

Predictive models

Finally, predicting the influence of future land-use decisions on forest herb distributions and diversity will require the development of mathematical models. In fragmented habitats, the metapopulation framework provides a powerful tool for modeling landscape-scale dynamics. However, most metapopulation models treat habitat patch networks as static, whereas the most interesting feature of many landscapes is habitat turnover – the creation and destruction of forests through time. Recent progress has been made in constructing models applicable to dynamic, north-temperate landscapes (Matlack and Monde 2004; Verheyen *et al.* 2004), but parameterization of such models presents considerable challenges. Direct estimates of colonization and extinction rates from resurvey studies could be highly valuable in this regard. As forest clearance and agricultural abandonment continue worldwide, both models and empirical work will provide knowledge essential for understanding current plant communities, guiding conservation efforts, and informing land-use decisions.

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■ References

Bellemare J, Motzkin G, and Foster DR. 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *J Biogeogr* **29**: 1401–20.

Bossuyt B, Hermy M, and Deckers J. 1999. Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. *J Ecol* **87**: 628–38.

Brunet J and von Oheimb G. 1998. Migration of vascular plants to secondary woodlands in southern Sweden. *J Ecol* **86**: 429–38.

Compton JE and Boone RD. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. *Ecology* **81**: 2314–30.

Côté SD, Rooney TP, Tremblay J-P, *et al.* 2004. Ecological impacts of deer overabundance. *Annu Rev Ecol Evol Syst* **35**: 113–47.

De Keersmaeker L, Martens L, Verheyen K, *et al.* 2004. Impact of soil fertility and insolation on diversity of herbaceous woodland species colonizing afforestations in Muizen forest (Belgium). *Forest Ecol Manag* **188**: 291–304.

Donohue K, Foster DR, and Motzkin G. 2000. Effects of the past and the present on species distribution: land-use history and demography of wintergreen. *J Ecol* **88**: 303–16.

Dupouey JL, Dambrine E, Laffite JD, and Moares C. 2002. Irreversible impact of past land use on forest soils and biodiversity. *Ecology* **83**: 2978–84.

Dzwonko Z and Loster S. 1989. Distribution of vascular plant species in small woodlands on the Western Carpathian foothills. *Oikos* **56**: 77–86.

Dzwonko Z and Loster S. 1992. Species richness and seed dispersal to secondary woods in southern Poland. *J Biogeogr* **19**: 195–204.

Endels P, Adriaens D, Verheyen K, and Hermy M. 2004. Population structure and adult plant performance of forest herbs in three contrasting habitats. *Ecography* **27**: 225–41.

Eriksson O and Ehrlén J. 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia* **91**: 360–64.

Flinn KM and Marks PL. 2004. Land-use history and forest herb diversity in Tompkins County, New York, USA. In: Honnay O, Verheyen K, Bossuyt B, and Hermy M (Eds). Forest biodiversity: lessons from history for conservation. Wallingford, UK: CABI.

Flinn KM, Vellend M, and Marks PL. 2005. Environmental causes and consequences of forest clearance and agricultural abandonment in central New York. *J Biogeogr* **32**: 439–52.

Foster DR. 1992. Land-use history (1730-1990) and vegetation dynamics in central New England, USA. *J Ecol* **80**: 753–72.

Glitzenstein JS, Canham CD, McDonnell MJ, and Streng DR. 1990. Effects of environment and land-use history on upland forests of the Cary Arboretum, Hudson Valley, New York. *B Torrey Bot Club* **117**: 106–22.

Graae BJ. 2000. The effect of landscape fragmentation and forest continuity on forest floor species in two regions of Denmark. *J Veg Sci* **11**: 881–92 .

Graae BJ, Hansen T, and Sunde PB. 2004. The importance of recruitment limitation in forest plant species colonization: a seed sowing experiment. *Flora* **199**: 263–70.

Grashof-Bokdam CJ and Geertsema W. 1998. The effect of isolation and history on colonization patterns of plant species in secondary woodland. *J Biogeogr* **25**: 837–46.

Harmer R, Peterken G, Kerr G, and Poulton P. 2001. Vegetation changes during 100 years of development of two secondary woodlands on abandoned arable land. *Biol Conserv* **101**: 291–304.

Heinken T. 2004. Migration of an annual myrmecochore: a four year experiment with *Melampyrum pratense* L. *Plant Ecol* **170**: 55–72.

Ito S, Nakayama R, and Buckley GP. 2004. Effects of previous land-use on plant species diversity in semi-natural and plantation forests in a warm-temperate region in southeastern Kyushu, Japan. *Forest Ecol Manag* **196**: 213–25.

Jacquemyn H, Honnay O, Galbusera P, and Roldán-Ruiz I. 2004. Genetic structure of the forest herb *Primula elatior* in a changing landscape. *Mol Ecol* **13**: 211–19.

Kalisz PJ. 1986. Soil properties of steep Appalachian old fields. *Ecology* **67**: 1011–23.

Koerner W, Dupouey JL, Dambrine E, and Benoît M. 1997. Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. *J Ecol* **85**: 351–58.

Mabry C, Ackerly D, and Gerhardt F. 2000. Landscape and species-level distribution of morphological and life history traits in a temperate woodland flora. *J Veg Sci* **11**: 213–24.

Marks PL and Gardescu S. 2001. Inferring forest stand history from observational field evidence. In: Egan D and Howell EA (Eds). The historical ecology handbook: a restorationist's guide to reference ecosystems. Washington, DC: Island Press.

Matlack GR. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* **75**: 1491–1502.

Matlack GR. 1997. Land use and forest habitat distribution in the hinterland of a large city. *J Biogeogr* **24**: 297–307.

Matlack GR and Monde J. 2004. Consequences of low mobility in spatially and temporally heterogeneous ecosystems. *J Ecol* **92**: 1025–35.

Mitchell CE, Turner MG, and Pearson SM. 2002. Effects of historical land use and forest patch size on myrmecochores and ant communities. *Ecol Appl* **12**: 1364–77.

Motzkin G, Foster D, Allen A, *et al*. 1996. Controlling site to evaluate history: vegetation patterns of a New England sand plain. *Ecol Monogr* **66**: 345–65.

Peterken GF. 1981. Woodland conservation and management. London, UK: Chapman and Hall.

Peterken GF and Game M. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *J Ecol* **72**: 155–82.

Petersen PM and Philipp M. 2001. Implantation of forest plants in a wood on former arable land: a ten year experiment. *Flora* **196**: 286–91.

Rackham O. 1980. Ancient woodland: its history, vegetation and uses in England. London, UK: Edward Arnold.

Russell FL, Zippin DB, and Fowler NL. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *Am Midl Nat* **146**: 1–26.

Singleton R. 1998. Recovery of the forest herb community in post-agricultural forests in central New York: pattern and process (PhD dissertation). Ithaca, NY: Cornell University.

Singleton R, Gardescu S, Marks PL, and Geber MA. 2001. Forest herb colonization of post-agricultural forests in central New York State, USA. *J Ecol* **89**: 325–38.

Smith BE, Marks PL, and Gardescu S. 1993. Two hundred years of forest cover changes in Tompkins County, New York. *B Torrey Bot Club* **120**: 229–47.

Smith WB, Miles PD, Vissage JS, and Pugh SA. 2004. Forest resources of the United States, 2002. General Technical Report NC-241. St. Paul: USDA Forest Service, North Central Forest Experiment Station.

Stover ME and Marks PL. 1998. Successional vegetation on abandoned cultivated and pastured land in Tompkins County, New York. *J Torrey Bot Club* **125**: 150–64.

Torchin ME and Mitchell CE. 2004. Parasites, pathogens, and invasions by plants and animals. *Front Ecol Environ* **2**: 183–90.

Vellend M. 2003. Habitat loss inhibits recovery of plant diversity as forests regrow. *Ecology* **84**: 1158–64.

Vellend M, Myers JA, Gardescu S, and Marks PL. 2003. Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. *Ecology* **84**: 1067–72.

Vellend M. 2004. Parallel effects of land-use history on species diversity and genetic diversity of forest herbs. *Ecology* **85**: 3043–55.

Vellend M. 2005. Land-use history and plant performance in populations of *Trillium grandiflorum*. *Biol Conserv* **124**: 217–24.

Verheyen K, Bossuyt B, Hermy M, and Tack G. 1999. The land use history (1278–1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. *J Biogeogr* **26**: 1115–28.

Verheyen K, Guntenspergen GR, Biesbrouck B, and Hermy M. 2003. An integrated analysis of the effects of past land use on forest herb colonization at the landscape scale. *J Ecol* **91**: 731–42.

Verheyen K and Hermy M. 2004. Recruitment and growth of herb-layer species with different colonizing capacities in ancient and recent forests. *J Veg Sci* **15**: 125–34.

Verheyen K, Vellend M, van Calster H, *et al*. 2004. Metapopulation dynamics in changing landscapes: a new spatially realistic model for forest plants. *Ecology* **85**: 3302–12.

Whigham DF. 2004. Ecology of woodland herbs in temperate deciduous forests. *Ann Rev Ecol Evol Sys* **35**: 583–621.

Wulf M. 2004. Plant species richness of afforestations with different former use and habitat continuity. *Forest Ecol Manag* **195**: 191–204.