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## Homogenization of Forest Plant Communities and Weakening of Species-Environment Relationships via Agricultural Land Use

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# Homogenization of forest plant communities and weakening of species–environment relationships via agricultural land use

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## Summary

**1** Disturbance may cause community composition across sites to become more or less homogenous, depending on the importance of different processes involved in community assembly. In north-eastern North America and Europe local (alpha) diversity of forest plants is lower in forests growing on former agricultural fields (recent forests) than in older (ancient) forests, but little is known about the influence of land-use history on the degree of compositional differentiation among sites (beta diversity).

**2** Here we analyse data from 1446 sites in ancient and recent forests across 11 different landscapes in north-eastern North America and Europe to demonstrate decreases in beta diversity and in the strength of species–environment relationships in recent vs. ancient forests.

**3** The magnitude of environmental variability among sites did not differ between the two forest types. This suggests the difference in beta diversity between ancient and recent forests was not due to different degrees of environmental heterogeneity, but rather to dispersal filters that constrain the pool of species initially colonizing recent forests.

**4** The observed effects of community homogenization and weakened relationships between species distributions and environmental gradients appear to persist for decades or longer. The legacy of human land-use history in spatial patterns of biodiversity may endure, both within individual sites and across sites, for decades if not centuries.

*Key-words:* ancient forest, beta diversity, biotic homogenization, biodiversity, community assembly, forest plants, land-use history, meta-analysis, recent forest, species–environment relationships

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## Introduction

The number of species in an individual habitat patch (alpha diversity) typically represents only a small fraction of the regional species pool (MacArthur 1972). Thus, variation in community composition among habitat patches (beta diversity) is an important component of regional biodiversity (gamma diversity). Studies of spatial variation in community composition have provided key insights into how factors, such as environmental variables, disturbance history and dispersal, influence local biodiversity (Whittaker 1975; Kadmon & Pulliam 1993; McCune & Grace 2002; Cottenie 2005). With data spanning multiple time periods or multiple habitat patches with different histories, one can also test for effects of disturbance or other environmental change on the spatial homogenization or differentiation of communities (e.g. Christensen & Peet 1984; Lepš & Rejmánek 1991) – an issue currently of great interest in ecology and conservation (McKinney & Lockwood 1999; Olden *et al.* 2004). Although the term ‘biotic homogenization’ is most often associated with decreases in beta diversity due to the spread of exotic species, decreases in beta diversity can also result from other causes (Olden & Rooney 2006), such as human land use.

Over the past several centuries, clearance of forests for agriculture and recovery of forests on abandoned fields have transformed biodiversity patterns across much of Europe and north-eastern North America (Whitney 1994; Kirby & Watkins 1998). These regions share a similar climate and dominant natural vegetation (temperate deciduous forest), as well as many genera of plants (e.g. Grubb & Marks 1989). Spatially explicit records of these historical disturbances provide unique opportunities to unravel the fundamental processes involved in community assembly. Ecological studies in many different parts of Europe and north-eastern North America have benefited from exceptionally detailed records of forest history, in some cases dating back > 400 years (Peterken & Game 1984). These records permit the classification of present-day forest patches into those that are known to have grown on former agricultural fields (recent forests) and those that have been continuously forested as far back as the historical record goes (ancient forests; Rackham 2003). Many studies have focused on the understorey plant communities of ancient and recent forests (reviewed in Flinn & Vellend 2005). One generality to emerge from this work is that species richness within forest stands (alpha diversity) remains lower in recent than ancient forests, even when recent forests are decades or centuries old. However, it is not yet clear how land use affects beta diversity, the compositional variability among stands of each forest type.

Agricultural land use, and disturbance in general, could homogenize forest plant communities in several different ways, which correspond to different hypotheses about mechanisms of community assembly (Christensen & Peet 1984; Lepš & Rejmánek 1991). First, if the forests initially cleared for agriculture occur in a narrower

range of environments than remnant forests, environmental control of community composition would lead to lower beta diversity in recent than ancient forests. Second, to the extent that communities on a range of soil types are converted into similar agricultural fields (Foster *et al.* 1998), land use may reduce landscape-scale variation in soil properties, also leading to lower beta diversity in recent forests. Although land-use decisions clearly depend on environmental conditions (e.g. Flinn *et al.* 2005), and agriculture can make lasting changes in forest soils (e.g. Flinn & Marks 2007), it is unknown whether environmental variability among forest patches differs systematically between ancient and recent forests. In this paper we test for differences in environmental variability between ancient and recent forests, regardless of their origin, to assess the potential for such differences to create a disparity in beta diversity between ancient and recent forests.

The process of dispersal may also suppress beta diversity as recent forests regrow. Population-, community- and landscape-level patterns demonstrate that dispersal limitation strongly influences the species composition of recent forests (Verheyen *et al.* 2003; Flinn & Vellend 2005), with strong dispersers (e.g. via animals or wind) over-represented relative to weak dispersers (e.g. via ants or gravity; e.g. Matlack 1994; Verheyen *et al.* 2006). If this dispersal filter is sufficiently influential, recent forests should have lower beta diversity because the same suite of good dispersers would occur across most recent stands, irrespective of local environmental conditions. Because dispersal appears to play a dominant role in forest recolonization, we hypothesize that agricultural land use reduces beta diversity in recent forests by imposing dispersal filters that weaken environmental control on species composition.

This hypothesis makes two specific predictions: (i) variability in species composition among patches (beta diversity) should be greater in ancient than recent forests (Vellend 2004); and (ii) species–environment relationships should be stronger in ancient than recent forests (Harrelson & Matlack 2006). Thus, we expect reduced beta diversity in recent forests even if variability in environmental conditions among patches does not differ significantly between the two forest types. To determine whether past land use caused biotic homogenization, and to evaluate the relative roles of environmental vs. dispersal filters in the assembly of post-agricultural communities, we test these predictions by comparing indices of beta diversity and environmental predictors of plant community composition in ancient and recent forests from 11 different landscapes in north-eastern North America and Europe.

## Methods

### DATA SETS

The authors of this paper contributed 11 data sets on forest plant distributions in ancient and recent forests

**Table 1** Summary of the data sets used in this study

| Location                     | Sampling unit*        | Earliest historical information‡ | Ancient sample size | Recent sample size | References  |
|------------------------------|-----------------------|----------------------------------|---------------------|--------------------|---|
| 1. Central Flanders, Belgium | Stand                 | 1775                             | 12                  | 31                 | Honnay <i>et al.</i> (1999)                             |
| 2. Vlaams-Brabant, Belgium   | Stand                 | 1775                             | 35                  | 204                | Jacquemyn <i>et al.</i> (2001)                          |
| 3. Himmerland, Denmark       | Plot (25 × 25 m)      | 1780                             | 38                  | 10                 | Graae (2000)  |
| 4. North-west Germany        | Stand†                | 1765                             | 29                  | 40                 | Kolb & Diekmann (2004)                                  |
| 5. Prignitz, Germany         | Stand†                | 1767                             | 94                  | 140                | Wulf (2003)   |
| 6. Torup-Skabersjö, Sweden   | Stand                 | 1800                             | 114                 | 155                | Brunet (2004);<br>J. Brunet (unpublished)               |
| 7. Lincolnshire, UK          | Stand                 | 1600                             | 72                  | 254                | Peterken & Game (1984)                                  |
| 8. Franklin County, MA, USA  | Plot (10 × 10 m)      | 1830                             | 18                  | 43                 | Bellemare <i>et al.</i> (2002)                          |
| 9. Petersham, MA, USA        | Plot (20 × 20 m)      | 1830                             | 31                  | 43                 | Gerhardt & Foster (2002)                                |
| 10. Tompkins County, NY, USA | Plot (60 × 1.5 × 2 m) | 1900                             | 28                  | 28                 | Flinn & Marks (2007);<br>Singleton <i>et al.</i> (2001) |
| 11. Tompkins County, NY, USA | Stand                 | 1900                             | 17                  | 10                 | Vellend (2004)  |

\*Stands are discrete patches of forest of variable size; plots are equal-area portions of a forest in which data were collected.

†Only the deciduous portion of each stand was sampled.

‡Forests that established after this date are considered recent; otherwise forests are ancient.

that met the following criteria: (i) the study covered a landscape scale, which we defined as a total study area of > 1000 ha; (ii) each surveyed patch or plot could be classified as ancient or recent forest (for some data sets this meant setting a cut-off for the proportion of the patch that was ancient before considering it an ancient forest); and (iii) the survey included at least 10 patches or plots in both ancient and recent forests. The basic data contributed from each study was a table with the presence or absence of each plant species in each forest patch or plot. When relative abundance data were available, these were converted to presence–absence data to standardize across studies. Detailed information on each data set can be found in the papers cited in Table 1 and in Appendix S1 in Supplementary Material. Only three data sets included information on variation in the ages of recent forests (Appendix S1), so the only temporal information used was the ancient–recent distinction. The date of the earliest historical information in each landscape (Table 1) indicates the maximum age of recent forests.

For all data sets, we analysed only ‘forest plant species’, defined as species that occur primarily in forest (as opposed to open habitats such as grasslands or open fields), but not including trees as these are often directly manipulated by humans. Some data sets originally included only forest plants, whereas others needed to be reduced. Rather than attempt to develop a single list of species that fit this criterion across all regions, we chose to recognize the fact that species may behave differently in different regions (e.g. Hermy *et al.* 1999), so the authors of each study (i.e. local experts) applied this definition independently to their own data set.

Ten of the data sets included at least some environmental variables. In some cases these included a comprehensive suite of measurements characterizing the soil, topography and light environments, while in other

cases ‘environmental’ data included only the assignment of a particular soil type to each site based on regional maps. We recognize that the available environmental data may not represent the most important variables to which the plants respond in all cases. However, these data sets do provide a means to compare the *relative* degree of environmental variability and strength of species–environment relationships in ancient and recent forests. We selected or generated  $\leq 3$  environmental variables from each data set. This was to reduce imbalance across studies in the number of environmental variables, and also because the number of environmental variables approached the number of sites in some data sets. When  $\leq 3$  variables were available, all were used. When > 3 variables were available, we reduced these to three using one of two approaches. When data reduction (via principal components analysis, PCA) had already been conducted as part of earlier studies (sometimes on subsets of the data, such as soil variables separately from topography variables), or when a relatively small set of variables was available to begin with, we selected three variables (which may be PCA axes) previously identified as particularly important in determining vegetation composition. With large suites of raw variables we extracted the first three axes from a PCA of the environmental data. Details on environmental data are provided in Appendix S1.

#### ANALYSIS OF BETA DIVERSITY

Our first question was: does the magnitude of beta diversity differ between ancient and recent forests? For presence–absence data, a large number of coefficients can be calculated to characterize the degree of (dis)similarity between a given pair of sites (Legendre & Legendre 1998; Vellend 2001), but all of the simple, commonly used indices are sensitive to the number of species in

each of the two sites (Koleff *et al.* 2003). For example, Jaccard's similarity index ( $J$ ) is calculated as the ratio of the number of species shared by two sites to the total number of species across the two sites (Legendre & Legendre 1998); a pair of sites with 2 and 10 species, respectively, can share at most 2 species, and must have a minimum combined total of 10, so the theoretical maximum value of  $J$  for these two sites is 0.2. Two sites with 10 species each may have a  $J$ -value anywhere between zero and one. As a result, species-poor sites will appear more differentiated from other sites even if the few species present are random draws from the regional pool. Many studies already show that recent forests have lower species richness (i.e. alpha diversity) of forest plants than ancient forests (reviewed in Flinn & Vellend 2005), and we would like to measure beta diversity independently.

To solve this problem, we used the probabilistic measure of Raup & Crick (1979), which gives the probability that two sites share fewer species than expected under a null model, thus allowing for the observed difference in species richness between the two sites (Vellend 2004). In the null model, the probability of selecting a species from the 'regional' pool is proportional to the number of sites in the data set where the species was present. For sites  $x$  and  $y$  with  $i$  and  $j$  species, respectively, first we calculate the number of species the two sites actually share in common. We then take 1000 draws of  $i$  and  $j$  species from the regional pool, each time counting the number of species the two null communities share in common. The Raup and Crick measure of beta diversity ( $\beta_{RC,x,y}$ ) is calculated as the proportion of pairs of null communities that share the same number or more species in common than sites  $x$  and  $y$ . For a given site, the mean of the pairwise values against all others is that site's degree of community differentiation, or beta diversity (for site  $x$ ,  $\beta_{RC,x}$ ).

In comparing two types of sites (here, ancient and recent forests), we discovered a potential source of bias where there are far more sites of one type than the other. If the two site types differ somewhat in vegetation composition, then sites of the type with higher sample size will potentially have lower mean  $\beta_{RC}$  values for two artifactual reasons. First, the species composition of the site type with higher sample size will largely determine the regional pool, making sites of that type appear more similar to the regional pool. Second, more of the pairwise comparisons made in calculating mean  $\beta_{RC}$  for a given site will be with sites of the type with higher sample size, again causing lower values of  $\beta_{RC}$  for that site type. To remove these two sources of bias, we calculated each species' representation in the regional pool based on the mean of its frequency in ancient forests and in recent forests (rather than its overall frequency), and we calculated mean  $\beta_{RC}$  for a given site as the mean of two means, one against all ancient sites and the other against all recent sites.

The analyses of beta diversity presented here are clearly dependent on our definition of the regional spe-

cies pool. The regional pool from which local species composition is derived is impossible to define precisely given that colonization of both ancient and recent forests has occurred over time periods of at least several decades (often much longer), combined with the fact that landscape-scale patterns of forest cover and age distributions have changed considerably over time (Flinn & Vellend 2005). Present-day frequencies of species across forest patches provide what we consider to be the best way to approximate each species contribution to the regional pool that can be applied in an equivalent way across landscapes. We also consider this a major improvement over the implicit assumption when using pairwise values of Jaccard's or related indices that the 'regional' species pool is defined separately for each pair of sites as the list of species currently present only in those two sites.

For each data set, we tested for significant differences in  $\beta_{RC}$  between ancient and recent forests using general linear models in SAS (SAS Institute, Cary, North Carolina, USA). For most data sets,  $\beta_{RC}$  values were square-root or log-transformed to meet assumptions of normality.

#### VEGETATION AND ENVIRONMENT

We used environmental data from 10 of the data sets to address several questions. First, to ask whether any difference between ancient and recent forests in  $\beta_{RC}$  may be due to differences in environmental conditions, we conducted general linear models as described above but with environmental variables included as additional predictors of  $\beta_{RC}$ . Comparing least-squares means for ancient and recent forests from these models provides a measure of how the two forest types differ independent of environmental characteristics.

Next, we asked whether the variability of environmental conditions differed between ancient and recent forests. This analysis was identical to the analysis of  $\beta_{RC}$  except that we used Gower's dissimilarity coefficient (Legendre & Legendre 1998) to characterize the difference in the environmental variables between each pair of sites. Gower's coefficient (denoted here as  $G_{ENV}$ ) was chosen because it can incorporate and combine data in a comparable way for categorical, ordinal and continuous variables (Legendre & Legendre 1998), all of which were represented across the different data sets (see Appendix S1). To calculate  $G_{ENV}$ , first the absolute difference between a pair of sites for each ordinal or continuous variable is divided by the maximum such difference to give a relative difference between 0 and 1 (Legendre & Legendre 1998). For categorical variables, the difference is scored as 1 if the two sites are in different categories (e.g. on different soil types) or 0 if the two sites are in the same category.  $G_{ENV}$  was then calculated as the average of these normalized differences across the different variables in a given data set. Each site was characterized by its mean  $G_{ENV}$  with all other sites (corrected for different sample sizes of ancient and recent forests as for  $\beta_{RC}$ ), and the mean in ancient vs. recent forests was compared as for

**Table 2** Mean beta diversity ( $\beta_{RC}$ ), environmental variability ( $G_{ENV}$ ) and proportion of community composition explained by environment ( $CCA_{ENV}$ ) in ancient and recent forests in 11 data sets. Italics indicate  $P < 0.05$ . Data set numbers correspond to those in Table 1

| Data set   | $\beta_{RC}$ |        |       |               | Gower's dissimilarity, $G_{ENV}$ |        |               |              | $CCA_{ENV}$ |        |
|------------|--------------|--------|-------|---------------|----------------------------------|--------|---------------|--------------|-------------|--------|
|            | Ancient      | Recent | $F$   | $P$           | Ancient                          | Recent | $F$ (or $U$ ) | $P$          | Ancient     | Recent |
| 1. Belg.-1 | 0.245        | 0.145  | 5.53  | <i>0.0236</i> | 0.333                            | 0.289  | 2.06          | 0.1592       | 0.349       | 0.281  |
| 2. Belg.-2 | 0.257        | 0.270  | 0.11  | 0.7378        | 0.262                            | 0.307  | 2474*         | <i>0.007</i> | 0.114       | 0.118  |
| 3. Denmark | 0.316        | 0.348  | 1.1   | 0.2998        | 0.267                            | 0.239  | 0.75          | 0.3908       | 0.263       | 0.250  |
| 4. Germ.-1 | 0.225        | 0.132  | 4.2   | $\leq 0.0001$ | 0.264                            | 0.265  | 0.01          | 0.9132       | 0.219       | 0.164  |
| 5. Germ.-2 | 0.257        | 0.231  | 4.19  | <i>0.0418</i> | 0.241                            | 0.229  | 8023*         | <i>0.004</i> | 0.051       | 0.056  |
| 6. Sweden  | 0.196        | 0.158  | 8.26  | <i>0.0044</i> | –                                | –      | –             | –            | –           | –      |
| 7. UK      | 0.281        | 0.194  | 36.85 | $\leq 0.0001$ | 0.808                            | 0.844  | 7357*         | 0.272        | 0.171       | 0.161  |
| 8. Mass.-1 | 0.313        | 0.320  | 0.05  | 0.8307        | 0.298                            | 0.259  | 1.02          | 0.3165       | 0.215       | 0.175  |
| 9. Mass.-2 | 0.191        | 0.232  | 0.41  | 0.5222        | 0.325                            | 0.317  | 0.35          | 0.5562       | 0.153       | 0.154  |
| 10. NY-1   | 0.363        | 0.347  | 0.27  | 0.6073        | 0.289                            | 0.255  | 3.06          | 0.0882       | 0.198       | 0.181  |
| 11. NY-2   | 0.295        | 0.129  | 16.48 | <i>0.0004</i> | 0.249                            | 0.248  | $< 0.01$      | 0.9506       | 0.401       | 0.369  |

\*Mann–Whitney  $U$  statistic with associated  $P$ -value in column to right.

$\beta_{RC}$ . For three data sets the distributions of  $G_{ENV}$  values were multimodal (because of the categorical environmental data); in these cases we used non-parametric Mann–Whitney  $U$ -tests to compare ancient and recent forests.

Finally, we asked whether variation in species composition is more or less predictable based on environmental variables in ancient forests than recent forests. To test this prediction, we conducted canonical correspondence analyses (CCA) on species composition in ancient and recent forests separately in each data set. In CCA,  $n_E$  environmental variables are used to ‘constrain’ the first  $n_E$  axes extracted from the ordination such that the variance on these axes explained by the environmental variables is maximized (McCune & Grace 2002). The sum of the eigenvalues for the constrained axes divided by the sum of all eigenvalues provides a measure of the proportion of variation in community composition accounted for by the environmental variables (denoted here as  $CCA_{ENV}$ ). The denominator of this proportion increases with the number of sites in the analysis (e.g. Cottenie 2005), so for each data set we first conducted a CCA for the forest type with the smaller sample size,  $N_{min}$ . For the forest type with larger sample size we took 50 independent random draws of  $N_{min}$  sites from the data set, and conducted a separate CCA each time. The mean  $CCA_{ENV}$  across simulations was then used to compare with the  $CCA_{ENV}$  value for the forest type with the smaller sample size. These analyses were conducted using Jari Oksanen’s ‘vegan’ package (v. 1.7–82, <http://cc.oulu.fi/~jarioksa/softhelp/vegan.html>) implemented in R.

#### META-ANALYSES

To ask whether  $\beta_{RC}$  and  $G_{ENV}$  differ systematically between ancient and recent forests across studies, we conducted paired  $t$ -tests on the mean values in ancient and recent forests, with individual studies weighted by the inverse variance of the difference between means

(the effect size), as recommended for meta-analysis by Gurevitch & Hedges (1999). If  $s_A^2$  and  $s_R^2$  are the variances (of  $\beta_{RC}$  or  $G_{ENV}$ ) in ancient and recent forests for a given study, the variance of the difference between means is  $s_{A-R}^2 = s_A^2/(n_A - 1) + s_R^2/(n_R - 1)$ , where  $n_A$  and  $n_R$  are the sample sizes of ancient and recent forests, respectively (Zar 1984). In addition to using the raw mean  $\beta_{RC}$  values in ancient and recent forests, we also conducted paired  $t$ -tests for the least-squares means in the two forest types after controlling for environmental variables.

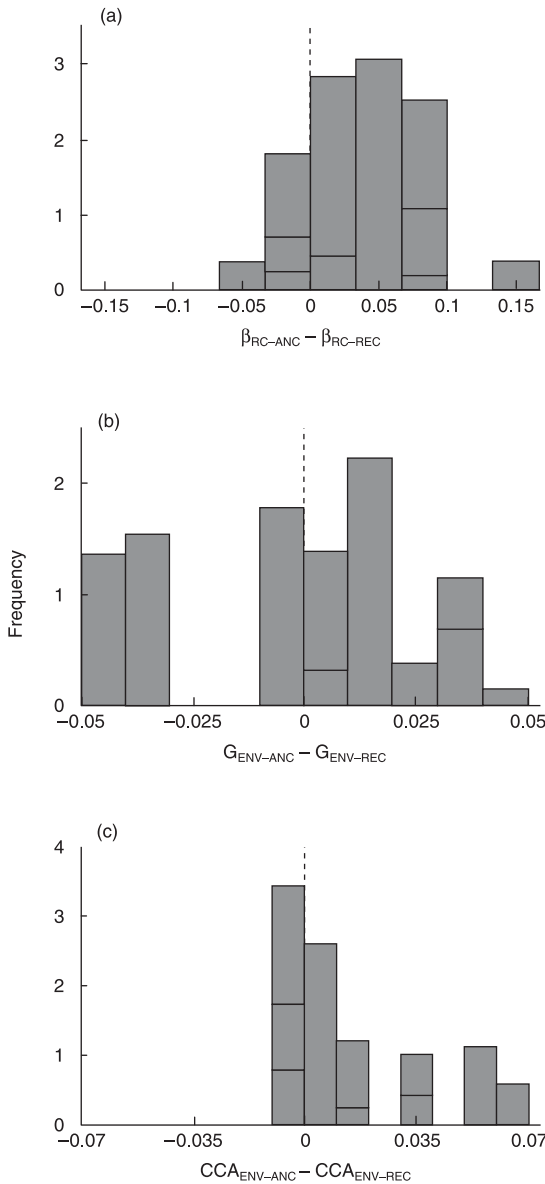
The same approach tested whether  $CCA_{ENV}$  was greater in ancient than recent forests, except that in place of the variances within ancient or recent forests ( $s_A^2$  and  $s_R^2$  above), we used the sum of all eigenvalues from the CCA’s for ancient and recent forests ( $CCA_{TOT-ANC}$  and  $CCA_{TOT-REC}$ ). These quantities are not technically variances, but they do represent the total amount of variation in a species-by-site matrix (McCune & Grace 2002), and thus provide an appropriate method for weighting data sets in a meta-analysis. In this case the inverse ‘variance’ of the mean difference between ancient and recent  $CCA_{ENV}$  was strongly related to sample size in the ordinations ( $r = 0.85$ ), as expected; data sets with larger sample sizes were thus given greater weight in the analysis. Because none of the data sets used here were collected with the purpose of comparing beta diversity between ancient and recent forests (only one data set, Vellend 2004; was previously used in this way), we were not concerned with publication bias in these meta-analyses.

#### Results

In seven of the 11 data sets, mean  $\beta_{RC}$  was greater in ancient than recent forests. The difference in  $\beta_{RC}$  was significant ( $P < 0.05$ ) in six cases (Table 2). Across studies, the weighted mean difference in  $\beta_{RC}$  between ancient and recent forests was significantly greater than zero (mean difference = 0.039,  $P = 0.0177$ ; Table 3, Fig. 1a),

**Table 3** Results of meta-analyses testing for differences between ancient and recent forests. Italics indicate  $P < 0.05$

| Variable     | Analysis                                   | Number of pairwise comparisons | Weighted mean difference (ancient – recent) | SE of weighted mean difference | <i>t</i> | <i>P</i>      |
|--------------|--|--------------------------------|---|--------------------------------|----------|---------------|
| $\beta_{RC}$ | Raw differences                            | 11                             | 0.039                                       | 0.0139                         | 2.83     | <i>0.0177</i> |
|              | Back transformed least-squares differences | 11                             | 0.043                                       | 0.0155                         | 2.76     | <i>0.0220</i> |
| $G_{ENV}$    | Raw differences                            | 10                             | -0.003                                      | 0.009                          | -0.3     | 0.7739        |
| $CCA_{ENV}$  | Raw differences                            | 10                             | 0.017                                       | 0.0076                         | 2.24     | 0.0522        |



**Fig. 1** Weighted histograms of the difference between ancient and recent forests for (a) the Raup-Crick measure of beta diversity for species  $\times$  site data,  $\beta_{RC}$  (b) Gower's dissimilarity coefficient for environmental data,  $G_{ENV}$ , and (c) the proportion of variation in community composition explained by environmental variables in a canonical correspondence analysis,  $CCA_{ENV}$ . In each histogram the summed height of the bars is equal to the number of studies included (11 in a, 10 in b and c), but each study is weighted according to the inverse of the variance of the mean difference between ancient and recent forests (see Methods for details).

and this difference remained significant ( $P = 0.022$ ) after controlling for the influence of environmental variables (Table 3).

Environmental dissimilarity ( $G_{ENV}$ ) differed significantly between ancient and recent forests in only two data sets (in opposite directions, Table 2), and the weighted mean difference in  $G_{ENV}$  between ancient and recent forests was not significantly different from zero (mean difference =  $-0.003$ ,  $P = 0.77$ ; Table 3, Fig. 1b). The weighted mean proportion of variance in vegetation composition explained by the environment ( $CCA_{ENV}$ ) was greater in ancient than recent forests (mean difference =  $0.017$ ,  $P = 0.052$ ; Table 3, Fig. 1c), and raw  $CCA_{ENV}$  values were greater in ancient than recent forests in 7 of the 10 data sets used in these analyses (Table 2).

## Discussion

### ENVIRONMENTAL CONTROL AND DISPERSAL LIMITATION IN ANCIENT AND RECENT FORESTS

Based on the hypothesis that the relative importance of environmental control vs. dispersal limitation is greater in ancient than recent forests, we predicted higher beta diversity and stronger species–environment relationships in ancient forests. The data generally supported these predictions, while we found no evidence for a difference in environmental variability between the forest types. Although some data sets included only limited environmental variables, differences in environmental variability between ancient and recent forests were lacking even in data sets with fairly detailed environmental data (e.g. data sets 4 and 8–11 in Table 2), and differences were in opposite directions for the two individual data sets with significant results (Table 2). Fully evaluating whether agricultural land use alters environmental variability among habitat patches will require more comprehensive environmental data from studies designed to distinguish the environmental causes and effects of disturbance. At present, our results simply provide no evidence that differences in environmental variability between the forest types contribute to the observed differences in beta diversity. Rather, lower beta diversity in recent than ancient forests is most likely to result from ecological filters constraining the pool of species that colonize recent forests.



These ecological filters could operate at any stage of the colonization process. For example, recent forests could show reduced beta diversity if habitat specialists were less successful colonists than generalist species. While further work may reveal multiple types of ecological filters governing recent forest colonization, results to date suggest that dispersal limitation is at least one key component of these filters. Multiple studies in this system have found disproportionate representation of strong dispersers in recent forests (e.g. Matlack 1994; Verheyen *et al.* 2006), strong effects of spatial isolation on species richness (e.g. Jacquemyn *et al.* 2001) and increased recruitment with experimental introductions (e.g. Graae *et al.* 2004; reviewed in Flinn & Vellend 2005). Thus, our results suggest that ecological filters, including dispersal, lead not only to reduced alpha diversity in recent forests, as previously documented quite generally (Flinn & Vellend 2005), but also to homogenized species composition across the landscape. Most of the recent forests in this study were at least several decades old, so human land use appears to make enduring changes in patterns of biodiversity at multiple spatial scales.

Christensen & Peet (1984), drawing on earlier suggestions by Margalef (1963) and others, hypothesized that, as succession proceeds and species ultimately reach most of the sites across the landscape with suitable environmental conditions, beta diversity should increase along with the environmental predictability of species composition. Consistent with our results, Christensen & Peet (1984) found support for this trend in forests ranging from 20 years old to > 80 years old in North Carolina. Furthermore, Harrelson & Matlack (2006) recently found weakened species–environment relationships in recent vs. ancient forests in Ohio. For forests growing on former agricultural fields in northeastern North America and Europe, our study demonstrates a general decoupling of species composition from environmental gradients that may persist for decades or longer, at least in some landscapes.

Although we found significant tendencies for lower beta diversity and weaker species–environment relationships in recent than ancient forests, there was considerable variation among data sets (Fig. 1, Table 2). On one hand, we can interpret the meta-analyses as estimating the true mean difference between ancient and recent forests, with the point estimate from each study representing a random sample from a distribution with this true mean. This is the interpretation we have emphasized thus far. Alternatively, we could posit that at least some of the variability among point estimates has a deterministic explanation. In this case we might focus on the result that 6 of 11 studies showed significantly lower beta diversity in recent than ancient forests, the rest showed no significant difference, and, importantly, none showed the opposite trend. (Note that this issue is not unique to meta-analyses, but applies to any analysis in which we might like to make sense of individual data points). We may conclude

strongly that, in this sample of landscapes, beta diversity is, on average, lower in recent than ancient forests. While we hesitate to read too deeply into the differences among individual data sets, given the difficulty of determining if these differences are ‘real’, here we do offer some speculation on one intriguing result: significant differences were found in 5 out of 7 European landscapes but only 1 out of 4 North American landscapes (Table 2). Three plausible factors could help explain this difference. First, the period of agricultural land use preceding recent forest establishment is typically much shorter in North America than Europe, such that the possibility of persistence of forest plants on site or in adjacent hedgerows is higher (e.g. Bellemare *et al.* 2002). Second, percentage forest cover is typically higher in North American than European landscapes, such that individual forest patches are less isolated from potential seed sources (Vellend 2003). These two differences may decrease the relative importance of dispersal limitation during recent forest colonization. Finally, all four of the studies in which plots rather than whole stands were sampled showed no significant difference in beta diversity between forest types, and three of these four were in North America; this would be important if much of the community differentiation among sites is due to relatively uncommon species that are less likely to be observed in plots. Each of these factors could contribute to the apparent difference between beta diversity patterns in North America and Europe.

The arguments in the preceding paragraph make it clear that community dynamics in networks of north-temperate forest patches are driven by explicit spatial and temporal processes. However, in the present paper we have only directly addressed the ancient–recent distinction in terms of time, and average differences among sites in terms of space. Data limitations prevent us from more explicit spatial and temporal analyses that can be compared across all of these landscapes, although this limitation has not prevented us from revealing some general patterns. Previous papers on particular landscapes have incorporated spatial and temporal considerations somewhat more explicitly, demonstrating important consequences for community dynamics of both spatial isolation of individual habitat patches (e.g. Jacquemyn *et al.* 2001), and of continuous destruction and creation of forest patches over time (Verheyen *et al.* 2004). In any detailed modelling of these landscapes space and time must be considered together because the spatial context of a given habitat patch can change considerably over time due to changes in forest cover in the surrounding area (Vellend *et al.* 2006). This presents a considerable challenge to constructing realistic spatio-temporal models of community dynamics (Verheyen *et al.* 2004). Particularly promising for future studies is the possibility of directly addressing the issue of temporal change in species composition and diversity by re-surveying forests whose initial surveys were conducted two or more decades ago (e.g. Peterken & Game 1984).

BROADER SIGNIFICANCE: SELECTIVE  
DISPERSAL ASSEMBLY AND BIOTIC  
HOMOGENIZATION

In the parlance of the current debate over niche vs. neutral theory in community ecology, the term 'niche assembly' is typically used to stress the importance of local competitive interactions among ecologically differentiated species in determining local species composition (Chase & Leibold 2003). 'Dispersal assembly' is typically used to describe the neutral standpoint in which species composition is determined at random via dispersal of ecologically equivalent species (Hubbell 2001). However, dispersal itself may have an important non-random component if species differ in dispersal ability. Our results, in combination with previous studies examining dispersal limitation in detail and across data sets (e.g. Verheyen *et al.* 2003), suggest that assembly of forest plant communities in recent forests may be best described as 'selective dispersal assembly'. In this study, if dispersal were predominantly random, and the species composition of recent forests had been determined primarily by which species happened to occur nearby, dispersal limitation may have led to increased differentiation among recent forests. In fact, however, dispersal contributed to homogenized species composition by acting as an ecological filter, variably permeable to different species.

A great deal of attention has recently been paid to the issue of biotic homogenization via the spread of generalist exotic species and the decline of specialist natives (McKinney & Lockwood 1999; Olden *et al.* 2004). However, biotic homogenization may occur via a variety of mechanisms (Olden & Rooney 2006). For example, intense deer herbivory in Wisconsin forests is suspected as the cause of the increased abundance of already common native species and the decline of other, usually rarer, native species (Wiegmann & Waller 2006). Here we have demonstrated an additional mechanism of biotic homogenization – habitat turnover via human land use. The destruction and creation of forests increases the representation of recent stands, thereby homogenizing regional vegetation.

A mixture of forests of different ages characterizes many landscapes throughout the globe, but the history of forest cover and the rate of habitat turnover vary greatly among regions (Whitney 1994; Kirby & Watkins 1998). In north-eastern North America, a period of forest clearance for agriculture, largely in the 19th century, was followed by widespread establishment of forests on abandoned fields (Whitney 1994). Across this region we can thus predict an increase in beta diversity in the future, with a concomitant increase in the strength of species–environment relationships. Ongoing afforestation schemes in Europe (e.g. Madsen 2002) should lead to an initial decrease in beta diversity as average forest age decreases, followed by an increase in beta diversity as these forests mature. To the extent that our results apply elsewhere, we should expect a similar

outcome to the massive afforestation projects in parts of China (Fang *et al.* 2001) and to the widespread reforestation of degraded tropical landscapes (Lamb *et al.* 2005). Human land use continues to change the landscape-scale distribution of forest ages, and we can expect such changes to leave an enduring legacy in spatial patterns of biodiversity.

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## Supplementary material

The following supplementary material is available for this article:

### Appendix S1 Description of data sets

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2007.01233.x>

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