PARALLEL EFFECTS OF LAND-USE HISTORY ON SPECIES DIVERSITY AND GENETIC DIVERSITY OF FOREST HERBS

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Abstract. The two most fundamental levels of biodiversity, species diversity and genetic diversity, are seldom studied simultaneously despite a strikingly similar set of processes that underlie patterns at the two levels. Agricultural land use drastically reduces populations of forest herbs in the north-temperate zone, so that bottlenecks or founder events in forests on abandoned agricultural land (i.e., secondary forests) may have a long-term impact on both species diversity and genetic diversity. Using forest-herb community surveys and molecular-genetic analysis of populations of *Trillium grandiflorum*, a representative species of forest herb, I investigated the influence of land-use history, landscape context, and environmental conditions on diversity and divergence at the population and community levels. Secondary forests (70–100 years old) had reduced diversity of both genes and species relative to primary forests (i.e., stands never cleared for agriculture). The community in secondary forests had an overrepresentation of the most common species in the landscape, though divergence in species' relative abundances within stands suggested an influence of community drift via local bottlenecks. Secondary-forest populations of *T. grandiflorum* were more genetically divergent than those in primary forests, again indicating drift in small populations. Land-use history and the size of populations and communities drove correlations between species diversity and genetic diversity (and community divergence × genetic divergence), though the strength of correlations was relatively weak. These results extend the generality of positive species–genetic diversity correlations previously observed for islands, and they demonstrate a long-term legacy of land-use history at multiple levels of biodiversity.

Key words: biodiversity; forest herbs; genetic diversity; land-use history; species diversity; Tompkins County, New York (USA); forest stands; Trillium grandiflorum.

INTRODUCTION

The second tenet of Antonovics' (1976:238, 2003) ecological geneticist's creed states that ''the forces maintaining species diversity and genetic diversity are similar.'' This idea has been echoed by a number of authors (e.g., Huston 1994, Hairston et al. 1996, Amarasekare 2000, Bell 2001), and is illustrated by considering the principal forces that influence diversity. Community drift consists of random changes in community composition (Hubbell 2001), much as genetic drift consists of random changes in genetic composition; both are an inevitable consequence of finite community or population size. Migration results in the movement of both alleles and species among localities. Selection favors some individuals over others, and these individuals may represent different genotypes of the same species, or different species; for example, if environmental heterogeneity favors different species or genotypes in different places, both species diversity and genetic diversity can be maintained. The influence of these processes on diversity is often manifested as correlations between diversity and attributes of sampling localities, such as area, isolation, environmental conditions, or history (Huston 1994, Frankham et al. 2002). To the degree that these processes influence the two levels of diversity in parallel, we can predict a positive correlation between species diversity and genetic diversity across patches of habitat in a landscape (Antonovics 1976, 1992, Vellend 2003*b*). The relationship between species diversity and genetic diversity has received little attention, despite having been identified as a crucial issue at the interface of ecology and genetics (Antonovics 1976, 1992, 2003); understanding this relationship may contribute to unification of biodiversity research at the levels of genes and species.

Despite the strikingly similar set of forces that may influence species and genetic diversity in parallel, the two are rarely studied simultaneously in the same system. A recent literature compilation of ecological and genetic data from islands demonstrated a general, positive correlation between species diversity in a particular taxonomic group (e.g., birds or plants) and genetic diversity within one species of the same group across islands in an archipelago (Vellend 2003*b*). The magnitude of correlation was highly variable, though never significantly negative, and the influence of island area on both levels of diversity was the principal driver of strong correlations. These results hinted at a potentially

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general pattern in nature, but raised a number of questions (see Vellend 2003*b*), two of which are addressed in the present paper. First, does the species–genetic diversity correlation extend from oceanic islands to "habitat islands" in human-dominated landscapes? Application of theories devised for oceanic islands to habitat islands has been controversial (Haila 2002). Second, can variables other than habitat area drive positive species–genetic diversity correlations? Here I address the effects of land-use history, environment, and landscape structure on species diversity and genetic diversity of herbaceous forest understory plants (forest herbs) in forest fragments of central New York State, USA.

Human land use has had a dramatic impact on the northeastern United States and adjacent Canada over the past several centuries. Landscapes have been transformed first by a massive reduction of forest cover via clearing for agriculture, then by widespread expansion of forest onto abandoned agricultural land (Whitney 1994). Many landscapes in Europe share a similar, though generally more complicated, history of forest clearance and post-agricultural recovery (Kirby and Watkins 1998). Thus, investigating how land-use history interacts with environmental conditions and landscape structure to influence populations and communities is critical to understanding how plant biodiversity is distributed across a large proportion of north-temperate landscapes. Forest herbs represent the majority of plant species diversity in temperate deciduous forests (Whigham 2004), and due to their generally poor colonization ability, forest herbs may be particularly sensitive to land-use history (Honnay et al. 2002, Vellend 2003*a*, 2004, Verheyen et al. 2003).

In several landscapes of northeastern North America, land-use history since European settlement has been reconstructed (Smith et al. 1993, Matlack 1994, Foster et al. 1998, Bellemare et al. 2002), permitting forest stands to be classified as either "primary"—never cleared for agriculture—or "secondary"—growing on abandoned agricultural land (Rackham 1980). Most primary forests have been selectively logged or grazed, but never converted into agricultural fields. Secondary forests include former plowed fields, where forest herbs should have been locally extirpated, and former unplowed pastures, where local forest-herb persistence would have been possible; in either case, a drastic reduction in forest-herb abundance and diversity is expected prior to abandonment and forest recovery (Flinn and Marks 2004). A general pattern has emerged from several studies showing that forest-herb species diversity is reduced in secondary vs. primary forests (e.g., Whitney and Foster 1988, Matlack 1994, Singleton et al. 2001, Bellemare et al. 2002, Flinn and Marks 2004). This pattern can be explained by a combination of environmental limitation and dispersal limitation to colonization, although the bulk of evidence points to dispersal as the dominant limitation. Only one study has

addressed the influence of land-use history on genetic diversity in forest herbs; in a landscape in Belgium, expected heterozygosity (H_e) for AFLP (amplified fragment-length polymorphism) markers was slightly lower in young populations of *Primula elatior* than in older populations, though the difference was not statistically significant (Jacquemyn et al. 2004). The degree to which species diversity and genetic diversity vary in parallel between primary and secondary forests remains unclear.

Another aspect of biodiversity is the divergence among local populations and communities. I define the divergence of a given population or community as the average difference or dissimilarity in composition (species or genetic) from all other sampling localities (see also Petit et al. 2003). If populations in secondary forests derive from relatively few individuals of local origin, bottlenecks or founder effects should reduce within-population diversity and increase among-population genetic divergence for neutral genes in secondary vs. primary populations (Wade and McCauley 1988). To the extent that neutral theory provides an adequate description of community-level patterns (Hubbell 2001), community drift in secondary forests (where the initial number of individuals is small) should also reduce within-stand diversity and cause species composition to diverge at random. In contrast, differences among species in their ability to persist in, or to colonize, secondary forests would cause species composition in secondary forests to converge, rather than diverge.

In this study, I measured the composition and diversity of forest-herb communities, genetic variation in *Trillium grandiflorum* (Michx.) Salisb. (a representative species of forest herb), and several environmental and landscape variables in primary and secondary forests of central New York to address the following questions:

1) Are species diversity and genetic diversity reduced in secondary forests relative to primary forests?

2) Are community divergence and genetic divergence increased (or decreased) in secondary forests relative to primary forests?

3) Do similar sets of environmental and landscape variables predict diversity and divergence at the levels of species and genes?

4) Are species diversity and divergence correlated with genetic diversity and divergence across the landscape?

Study System and Selection of Study Sites

Tompkins County covers ~1300 km² in the Finger Lakes region of central New York State (USA); the history of forest cover has been reconstructed for this county (Smith et al. 1993). Prior to European settlement, which began in the 1790s, the landscape was covered almost completely with temperate mixed deciduous forest, dominated by sugar maple (*Acer saccharum*) and beech (*Fagus grandifolia*) (Marks and

Gardescu 1992); these species remain common in primary forests today. Agricultural land use following European settlement reduced forest cover to <20% by ca. 1900 (the peak of agricultural activity), and forest cover has since risen to >50%, following the abandonment of agricultural land (Smith et al. 1993).

The species pool of forest herbs in Tompkins County was taken from Corbit (1995), with additions made in consultation with P. L. Marks and S. Gardescu (Department of Ecology and Evolutionary Biology, Cornell University). Forest herbs are defined as native herbaceous vascular plant species that occur almost exclusively in forests. This excludes species typical of open habitats (e.g., old-fields) that may also occur occasionally in forests. I chose *Trillium grandiflorum* for genetic analysis because it was common enough in Tompkins County to ensure an adequate sample size of stands, it is representative of many forest herbs in that it is a long-lived perennial with primarily ant-dispersed seeds (though some seeds are dispersed by deer; Vellend et al. 2003), and its lack of clonal growth made identification of genetic individuals unambiguous (see Appendix A for details on *T. grandiflorum* biology).

Twenty-seven forest stands in Tompkins County were used in this study: 17 primary and 10 secondary; all secondary stands were 70–100 years old. The land-use history (i.e., primary vs. secondary) of stands was determined using the maps of Smith et al. (1993), and verified based on field observations in consultation with P. L. Marks. My choice of study sites was based primarily on three criteria. First, *Trillium grandiflorum* had to be present. Second, I selected only stands that were "isolated," in that they were surrounded on all sides by either fields or younger secondary forests. This was done in order to allow unambiguous and non-arbitrary definitions of "community" and "population" as all individuals belonging to the species pool, or to *T. grandiflorum*, respectively, within the stand. Third, after secondary stands were selected, I chose primary stands to cover the same range of soil associations as the secondary stands (based on maps from Neeley [1965], and Tompkins County Planning Department [2000]). In addition, an analysis of soil nutrient data from these 27 stands revealed no significant differences between primary and secondary forests (see Appendix A for additional details on stand selection and characteristics).

METHODS

Forest-herb community surveys

Each of the 27 stands was surveyed for the presence of all forest herbs once in spring (18 April–21 May) and once in summer (4 June–17 July) during 2000–2003. These surveys were conducted by searching for forest herbs along parallel lines, 20 m apart, throughout the entirety of each stand, and along the entire perimeter. To estimate the relative frequencies of species in each stand, I recorded the presence of each species (during summer only, and therefore excluding spring ephemerals) in a stratified random sample of 30 circular plots, each 25 m². These plots were located at random positions along evenly spaced transects traversing each stand (see Appendix A). These data were taken in all but two stands (one secondary and one primary), so N = 25 forest stands (rather than 27) for all analyses of species' relative frequencies within stands.

Trillium *population surveys and genetic analysis*

Population size of *Trillium grandiflorum* was estimated by counting individuals in a sample of plots from each stand, with the number and arrangement of plots tailored to the spatial distribution and density of individuals, and extrapolating to the stand scale (see Appendix A). I analyzed genetic variation in *T. grandiflorum* populations using three classes of molecular markers: allozymes, chloroplast DNA restriction fragment length polymorphisms (cpDNA-RFLP), and microsatellites. Previous studies have employed allozymes (e.g., Broyles et al. 1997, Griffin and Barrett 2004) and cpDNA-RFLPs (Griffin and Barrett 2004) in *T. grandiflorum*. Following initial studies using these markers, I developed microsatellites (highly variable markers) to improve the power of tests concerning genetic diversity and divergence.

Leaf samples (~5 cm²) were collected from 40 three-leaved *T. grandiflorum* plants in each stand. Individuals were chosen haphazardly throughout the entire spatial extent of each population. Allozyme variation was assayed at four loci for all 40 individuals, as described in Appendix A. DNA was extracted from 24 randomly chosen individuals from the sample of 40 individuals in each population using the QIAGEN DNeasy plant mini kit (QIAGEN, Valencia, California, USA). To assay haplotype variation in choloroplast DNA (cpDNA), I amplified one region of the *T. grandiflorum* cpDNA genome (~2.4 kbp) using the *trn*H-*trn*K primer pair from Demesure et al. (1995) in all individuals from which DNA was extracted. PCR (polymerase chain reaction) was conducted in a PTC-100 Programmable Thermal Controller (M. J. Research, Waltham, Massachusetts, USA), and methods of cpDNA analysis followed those of Griffin and Barrett (2004), who initially screened for variation in *T. grandiflorum* using 20 primer pairs and 17 restriction enzymes. Three haplotypes were distinguished based on two polymorphisms in the cpDNA region (see Appendix A). Three polymorphic microsatellite loci for *T. grandiflorum* were developed and analyzed as described in Appendix B. The test of Hardy et al. (2003) indicated that microsatellite allele sizes were not important in determining genetic differentiation among populations (details in Appendix B), so microsatellite data were combined with the allozyme and cpDNA data in all subsequent analyses.

TABLE 1.   Measures of genetic diversity, species diversity, genetic divergence, and community divergence used in this study. See *Methods*: *Measures of diversity and divergence* for additional details of calculation.

Measure	Definition
Genetic diversity	
AR, Allelic richness	Number of alleles or haplotypes observed across all molecular markers in a population, corrected for differences in sample size among populations.
H_e, Expected heterozygosity	Mean probability, across markers, that two randomly chosen alleles or haplotypes within a population are different.
Species diversity	
SR, Species richness	Number of species observed in a given forest stand.
E, Evenness	Probability that two randomly chosen occurrences in a given stand are different species. Occurrence is the presence of a species in 1 of 30 25-m^2 circular plots surveyed in each stand.
Genetic divergence	
F_{ST}-G, Genetic divergence	If H_e is calculated using mean allele/haplotype frequencies across a given *pair* of populations, F_{ST}-G is the proportion of that value of H_e attributable to differences in allele/haplotype frequencies *between* populations. A given population is characterized by its mean value in pairwise comparisons with all other populations.
Community divergence	
β_{RC}, Presence–absence-based community divergence	Probability that a pair of stands shares fewer species in common than expected at random. A given stand is characterized by its mean value in pairwise comparisons with all other stands.
F_{ST}-C, Frequency-based community divergence	Exactly equivalent to F_{ST}-G, except calculated using species' relative frequencies rather than allele/genotype frequencies.

Measures of diversity and divergence

Diversity and divergence at the population and community levels were measured in several different ways, each of which is summarized in Table 1. I calculated two measures of within-population genetic diversity. First, allelic richness (AR) was calculated as the sum of all alleles or haplotypes across loci, rarefied (Leberg 2002) to a sample of 20 individuals in each population (20 was the minimum sample size for any given locus

in a given population). Second, mean Hardy-Weinberg expected heterozygosity (H_e) was calculated as the probability that two randomly chosen alleles or haplotypes at a given locus within a population were different; mean H_e was then calculated across loci.

I calculated the coefficient of inbreeding, F_{ST}, averaged across all loci, as a measure of genetic differentiation among all populations, and between each pair of populations, as $F_{ST} = (H_T - H_S)/H_T$, where H_T is
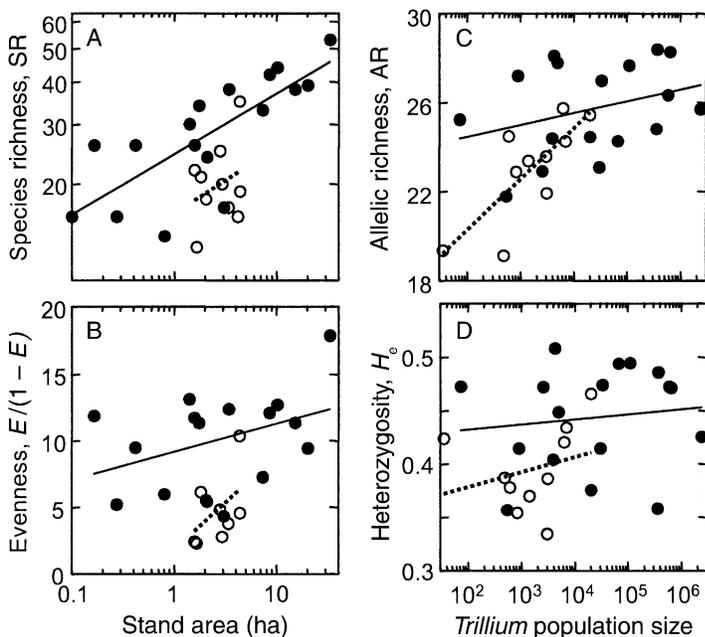

FIG. 1.   Relationships of stand area with (A) species richness and (B) evenness, and of *Trillium grandiflorum* population size with (C) allelic richness and (D) expected heterozygosity. Linear fits to the data are shown for primary forests (closed circles, solid lines) and secondary forests (open circles, dotted lines) separately. Note the $\log_{10}$ scales in the y-axis of (A) and all x-axis scales.

the Hardy-Weinberg expected heterozygosity based on mean allele frequencies across all populations (or the pair of populations), and H_S is the mean of H_e across populations (Nei 1977). As a measure of a given population's genetic divergence from all others, I calculated the mean of the pairwise F_{ST} values for the focal population vs. all others (see also Petit et al. 2003). I denote this measure of population-specific genetic divergence as F_{ST}-G, to distinguish this genetic measure from an equivalent measure of divergence at the community level (see below).

Two measures of species diversity within each stand were calculated. Species richness (SR) was the number of species observed across the full spring and summer surveys in each stand. As a measure of evenness (E) in species abundances, I used the frequency data for summer species to calculate a version of Simpson's (1949) index that is exactly analogous to H_e. Each species relative frequency was first calculated as the proportion of the 30 plots in which it occurred. These frequencies were then normalized to sum to 1, in order to express the proportion of all "occurrences" contributed by each species. If the normalized frequency of species i is f_i ($\Sigma f_i = 1$), E was calculated as $1 - \Sigma f_i^2$, with the f_i^2's summed across species. This represents the probability that two randomly chosen occurrences are of different species. In all analyses, evenness was expressed as an odds ratio, $E/(1 - E)$, to reduce positive skew in the distribution of E (see Rousset [1997] for a similar transformation of F statistics).

I used two methods to quantify the relative divergence in the composition of the forest-herb community in each stand from all other stands: (1) using the presence–absence data of all species (both spring and summer), and (2) using the within-stand frequency data for summer species in 25 of the 27 stands.

To measure pairwise dissimilarity in species composition using presence–absence data, I used the probabilistic measure of Raup and Crick (1979). All simple algebraic indices of pairwise (dis)similarity (e.g., Jaccard's) are biased by differences in the number of species in each site; two sites with very different within-site diversities have a limited number of species they can potentially share, so dissimilarity will tend to be high (Koleff et al. 2003). For my purposes, it was critical to have a measure of compositional dissimilarity that was independent of within-site diversity. Following Raup and Crick (1979), I first calculated the frequency of each species in the "global" pool as the number of stands in which it occurred. These frequencies defined the relative probabilities of choosing each species at random from the pool in a null model analysis. For a given pair of sites, with species richnesses of SR_1 and SR_2, and a_{12} species in common, I then took 1000 random draws of SR_1 and SR_2 species from the global pool, and calculated the number of shared species each time to produce a "null" distribution of a values. The diversity-independent dissimilarity be-

tween the two sites is the proportion of the null distribution greater than a_{12}; this value of "beta diversity" is denoted as "β_{RC};" the mean value of a given site vs. all others is a measure of that site's community divergence.

Using the frequency data, I measured community divergence using a direct analogue of F_{ST}. Treating the entire community as a single "locus," each species was treated like an allele with frequencies that sum to 1 (see description of E above for calculation of normalized species frequencies). Analogues of H_T and H_S at the community level can then be used to calculate the community analogue of F_{ST} between each pair of populations. The mean of the pairwise values for each site vs. all others, F_{ST}-C, provides a measure of community divergence that emphasizes differences in the relative frequencies of species between sites.

Predictor variables for diversity and divergence

The variable of primary interest here is land-use history, treated as a binary variable: primary = 1, secondary = 2. Five additional variables were measured: stand area, isolation, environmental heterogeneity, and two axes of variation in soil characteristics.

Stand area was determined using 1995 aerial photographs in ArcView 8.1.2 (ESRI, Redlands, California, USA). The relative isolation of each stand from potential sources of colonists was estimated by first creating buffers of 100 m, 200 m, 500 m, and 1 km around each stand in ArcView. Within each of four resulting zones (0–100 m, >100–200 m, etc.), the proportion of the landscape in primary forest was estimated. A weighted average of these four proportions was then calculated as a measure of connectivity, with weights determined by the inverse square of the distance from stand edge to the mid-point of each zone (i.e., 50 m, 150 m, etc.). The negative logarithm of these values was used as a measure of isolation (the log transformation reduced considerable skew in the distribution). An index of environmental heterogeneity was calculated as the standard deviation of the slope angle among 10×10 m portions of each stand. Slope angle was estimated in ArcView using a digital elevation model for Tompkins County with a resolution of 10×10 m (USGS 1998).

Standard soil nutrient analyses were conducted on a bulked soil sample from each site (details in Appendix A). Four soil cores (10 cm deep, 3-cm diameter) were collected at random positions along each of five evenly spaced transects traversing each site; the 20 soil cores were thoroughly mixed prior to nutrient analysis. Soils were analyzed by the Cornell Nutrient Analysis Laboratory (Ithaca, New York, USA) for extractable NO_3^-, NH_4^+, P, K, Mg, Ca, Fe, Al, Mn, Zn, and Cu, as well as pH and loss-on-ignition (LOI). Soil drainage was scored on an ordinal scale from 1 to 4 based on a map of soil associations. All soil variables were included in a principal components analysis (PCA). Axis 1 rep-

TABLE 2. Results of stepwise multiple regression analyses predicting species richness (SR), evenness (E), allelic richness (AR), expected heterozygosity (H_e), presence–absence-based community divergence (β_{RC}), frequency-based community divergence (F_{ST}-C), and genetic divergence (F_{ST}-G).

Predictor variable	log(SR) Partial r^2	log(SR) P	$E/(1 − E)$ Partial r^2	$E/(1 − E)$ P	AR Partial r^2	AR P	H_e Partial r^2
Land use	0.24(−)	0.0002	0.40(−)	0.0005	0.09(−)	0.0651	0.22(−)
Log(area)	0.35(+)	<0.0001	0.09(+)	0.065			
Log(pop. size)					0.33(+)	0.0266	
Log(isolation)	0.06(−)	0.0398	†		†		
pH (PCA1)	0.07(−)	0.0108	†		†		
Log(env. het.)‡	†		†		†		
Full model	0.72	<0.0001	0.49	0.0007	0.42	0.0015	0.22

Notes: Land use was included in every model, with a negative effect indicating lower values of the dependent variable in secondary vs. primary forests, and vice versa; additional variables were added if $P < 0.1$. Only significant predictors are shown (soil drainage [PCA2] was not significant in any analyses). The sign (+, −) after the partial r^2 indicates the direction of the effect of the predictor variable. $N = 27$ forest stands for all analyses except for E and F_{ST}-C, for which $N = 25$ stands. Blank cells indicate no data possible, since the independent variable in that row was not used as a potential predictor of the dependent variable in that column.

† The stepwise statistical test did not identify the independent variable in that row as a significant predictor of the dependent variable in that column.

‡ Env. het. = environmental heterogeneity.

resented a soil pH gradient (explaining 49% of the variation in the data), and axis 2 appeared to represent a soil moisture gradient (18% of the variation). These two PCA axes were used to characterize the edaphic environment in all subsequent analysis, and will be referred to as ''soil pH'' and ''drainage,'' respectively.

Data analysis

Stepwise multiple regressions were used to determine the significant predictors of species richness (SR), species evenness (E), allelic richness (AR), expected heterozygosity (H_e), presence–absence-based community divergence (β_{RC}), frequency-based community divergence (F_{ST}-C), and genetic divergence (F_{ST}-G). When appropriate, variables were log or square-root transformed to reduce skew. For all analyses $N = 27$ stands, except for those on E and F_{ST}-C, for which $N = 25$ stands. Land use was included in every multiple-regression model, and $P = 0.1$ was used as a cutoff for entry of other variables into the model (SAS, version 8.02: PROC REG [SAS Institute 2001]). For all response variables, soil pH, soil drainage, stand isolation, and environmental heterogeneity were considered as candidate predictors. In addition, *T. grandiflorum* population size was a candidate predictor for genetic measures of diversity and divergence, and stand area was a candidate predictor for community measures. In all regressions, type 3 sums of squares were used to evaluate independent effects of individual variables.

Stepwise multiple regressions were also used to determine significant predictors of pairwise values of the three measures of community and genetic divergence. These analyses were conducted to address the potential importance of geographic separation on genetic and species turnover (sensu Vellend 2001). Pairwise differences in the environmental variables and pairwise

geographic distances were used as potential predictor variables. An additional predictor variable was used to represent land-use history differences between pairs of stands (1 = primary cf. primary; 2 = primary cf. secondary; 3 = secondary cf. secondary). Due to the inflated sample sizes ($N = 351$ pairwise comparisons for β_{RC} and F_{ST}-G; $N = 300$ pairwise comparisons for F_{ST}-C), I used a strict cutoff of $P = 0.001$ for entry into the model. (Even with $P = 0.01$ as a cutoff, variables with partial $r^2 < 0.015$ appear as significant predictors.) For all predictors emerging in the multiple regressions, Mantel tests (Mantel 1967) were conducted as tests of significance; these tests were designed for comparing matrices with far more entries than independent observations (i.e., 27 stands, 351 pairwise comparisons).

To further test for convergence or divergence at the community level, I compared local and global species composition and frequency between primary and secondary stands as follows. First I characterized each species i by its global frequency, g_i (proportion of 27 stands where present) and its mean within-stand relative frequency, RF_i (i.e., mean frequency across stands). For each stand j, I then calculated the average global frequency of the species present ($\Sigma g_i/S_j$, where S_j is the number of species in the subplots of stand j), and the average absolute deviation of each species' local relative frequency from its mean frequency ($\Sigma(|rf_{ij} − RF_i|)/S_j$, where rf_{ij} is the relative frequency of species i in stand j). To test for primary-secondary differences in these two variables, I used a t test and a Kolmogorov-Smirnov test, respectively.

Pearson correlation coefficients were used to test for associations between species diversity and genetic diversity, and between community divergence and genetic divergence. To ask which stand characteristics drive these correlations, partial correlations were also

TABLE 2. Extended.

H_e	β_{RC}		F_{ST}-C		F_{ST}-G	
P	Partial r^2	P	Partial r^2	P	Partial r^2	P
0.0143	0.37(−)	0.0002	0.27(+)	0.005	0.41(+)	0.0058
		†	0.14(−)	0.033		
†					0.07(−)	0.0858
†		†		†		†
†		†		†		†
†	0.11(+)	0.0308		†		†
0.0143	0.48	0.0004	0.41	0.0031	0.48	0.0004

calculated controlling for each of the potential predictor variables. If the raw correlation between two variables is much higher than the partial correlation between the same two variables with a predictor variable held constant, then that predictor variable is likely an important driver of the raw correlation. No corrections were made for multiple statistical tests; inferences were drawn based on the complete set of results.

RESULTS

Seventy-two species of forest herbs were observed across the 27 forest stands. Within-stand richness varied from 13 to 53 species, and evenness varied from 0.70 to 0.95. Apart from *Trillium grandiflorum*, the most frequently observed species across stands were *Erythronium americanum*, *Podophyllum peltatum*, *Smilacina racemosa*, and *Arisaema triphyllum*. The complete community data set is presented in Appendix C.

Across all loci, a total of 40 alleles or haplotypes were found: 11 allozyme alleles, 3 cpDNA haplotypes, and 26 microsatellite alleles (complete data set in Appendix D). Rarefied allelic richness varied among populations from 19.1 to 28.4, and expected heterozygosity varied from 0.33 to 0.51. Summary statistics for all variables (genetic and otherwise) in all stands are presented in Appendix E. Similar results were found for the three classes of molecular markers analyzed separately; here I report only the results for data combined across all markers.

The dominant predictors of species diversity and genetic diversity were land-use history, stand area, and population size. Species richness (SR) was influenced mainly by stand area and land-use history, with minor but significant effects of stand isolation and soil pH (Fig. 1A, Table 2). These four variables explained 72% of the variance in SR, with the highest levels of SR found in large, primary stands with low soil pH and low isolation. The only significant predictors of community evenness (*E*) were land-use history (secondary < primary) and stand area (positive effect), together explaining 49% of the variance in *E* (Fig. 1B, Table 2). *Trillium* population size and land-use history were significant predictors of allelic richness (AR), though the independent effect of land-use history was marginal

(partial $r^2 = 0.09$, $P = 0.065$; total $r^2 = 0.42$, Fig. 1C, Table 2). More alleles were found in large vs. small and primary vs. secondary populations. Expected heterozygosity (H_e) was significantly lower in secondary than primary populations, and no other predictor variables were significant predictors of H_e ($r^2 = 0.22$, Fig. 1D, Table 2).

Presence–absence-based community divergence (β_{RC}) was significantly lower in secondary than primary forests, with a minor though significant effect of environmental heterogeneity, but no effect of area (Fig. 2A, Table 2). However, the positive effect of environmental heterogeneity was due entirely to the one most heterogeneous site having the highest value of β_{RC} (without this site in the analysis, partial $r^2 = 0.008$, $P = 0.59$ for environmental heterogeneity). Interestingly, the opposite trend was observed for frequency-based community divergence (F_{ST}-C), with significantly *higher* F_{ST}-C in secondary than primary forests; stand area was also a significant predictor of F_{ST}-C (Fig. 2B, Table 2). Thus, local abundances appear to have diverged, while species composition has converged, in secondary vs. primary forests, and comparisons of local vs. global species composition and frequency further support this result. Global species' frequencies were greater in secondary than primary stands ($t = 3.69$, $P = 0.001$), indicating a predominance of the most common species in secondary stands. The mean deviation of local vs. mean relative species' frequencies was also greater in secondary than primary stands (Kolmogorov-Smirnov test, $P = 0.004$), indicating local divergence in species' frequencies. Small *Trillium* populations, and those in secondary forest, showed significantly greater genetic divergence (F_{ST}-G) than large, primary populations (Fig. 2C, Table 2). F_{ST}-G (measured among all populations) was higher for chloroplast (cp)DNA (0.46) than for microsatellites (0.13) or allozymes (0.10).

Interpretation of multiple-regression results may be influenced by covariance among predictor variables. The only significant relationships between pairs of predictor variables were for *Trillium* population size × land-use history (secondary < primary population size, *t* test, $t = 2.98$, $P = 0.006$), and for stand area ×
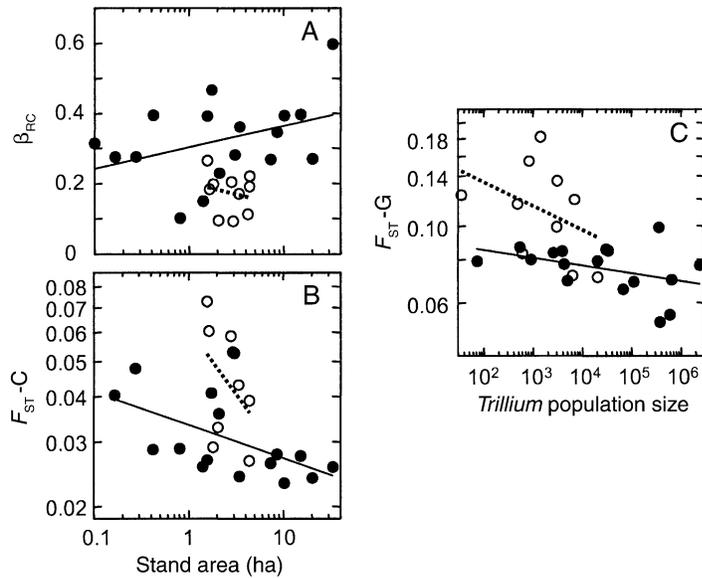
FIG. 2. Relationships of stand area with (A) presence–absence-based community divergence (β_{RC}) and (B) frequency-based community divergence (F_{ST}-C) and (C) relationship of *Trillium grandiflorum* population size with genetic divergence (F_{ST}-G). Linear fits to the data are shown for primary forests (closed circles, solid lines) and secondary forests (open circles, dotted lines) separately. Note $\log_{10}$ scales in *y*-axes of panels (B) and (C) and all *x*-axis scales.

environmental heterogeneity ($r = 0.57$, $P = 0.002$). A multiple regression of population size on all other predictor variables revealed significantly lower population size in secondary than primary forests, independent of differences in other variables ($P = 0.0002$). The only other significant predictor of population size was stand area ($P = 0.0004$). These results indicate that effects of land-use history on genetic diversity and divergence may be mediated by population size; independent effects of land-use history indicate effects disproportionate to differences in population size between primary and secondary stands. Effects of land-use history were not due to confounding environmental differences between primary and secondary stands.

Geographic distance had no influence on pairwise community differentiation, but a strong positive effect on pairwise genetic differentiation (Fig. 3, Table 3). Consistent with the previous results, secondary-secondary pairwise comparisons showed greater F_{ST}-C and F_{ST}-G, but lower β_{RC} than primary-primary comparisons; primary-secondary pairwise comparisons tended to be intermediate (Fig. 3, Table 3). Additional significant predictors of pairwise differentiation were differences in area (for β_{RC} and F_{ST}-C), and pH (for β_{RC}) (Table 3).

Positive correlations were observed in each of the four pairwise comparisons of species diversity and genetic diversity (Fig. 4A–D). All four correlations (SR × AR, SR × H_e, E × AR, E × H_e) were >0.3 ($P <$ 0.15), but the only correlation significant at $P < 0.05$ was between E and H_e ($r = 0.51$, $P = 0.01$). Genetic divergence (F_{ST}-G) was negatively correlated with β_{RC} ($r = -0.45$, $P = 0.02$), and positively correlated with F_{ST}-C ($r = 0.48$, $P = 0.01$) (Fig. 4E, F). In all partial correlation analyses, land-use history and population size caused the greatest reductions in the raw corre-

lations, and none of the partial correlations controlling for these two variables simultaneously was significant ($P > 0.15$; see Appendix F).

DISCUSSION

Diversity and divergence of forest herbs at the levels of genes and species were driven primarily by the size and history of populations and communities (summarized in Fig. 5). Species diversity and genetic diversity were generally reduced in small vs. large populations and communities, and in secondary vs. primary forests. Species diversity was also influenced by stand isolation and soil conditions, although these effects were relatively minor, likely due to the relatively narrow range of variation among stands in these variables. The parallel effects of size and history on the two levels of diversity drove positive correlations between species diversity and genetic diversity across the landscape; however, the magnitude of these correlations was only weak to moderate ($r = 0.31–0.51$). Nonetheless, the species–genetic diversity correlation appears to apply to habitat fragments in a human-dominated landscape, as well as to islands in oceanic archipelagos (Vellend 2003*b*), and the land-use history of forest fragments is a potential cause of the correlation.

Comparing divergence at the population and community levels revealed some discordant patterns. Increased genetic divergence (F_{ST}-G) of secondary populations relative to primary populations is consistent with the effect of genetic drift via population bottlenecks or founder events (Wade and McCauley 1988). The effect of land-use history, therefore, is likely mediated by a reduction in the effective population size of *Trillium grandiflorum*. This is illustrated in Fig. 1C, where the smallest secondary populations show reduced allelic richness compared to primary populations
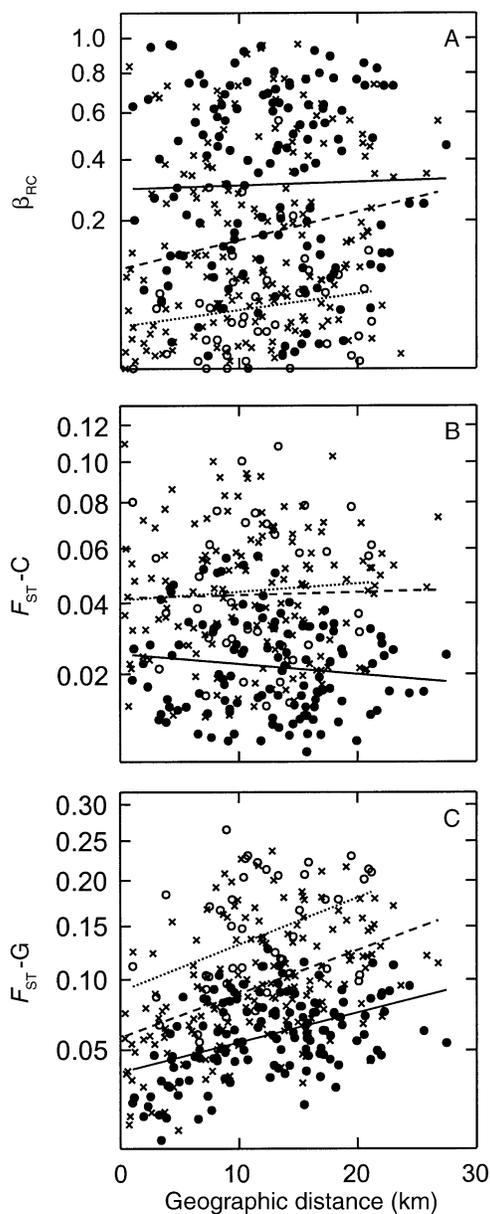
FIG. 3. Relationships of pairwise geographic distance with (A) pairwise presence–absence-based community divergence, (B) frequency-based community divergence, and (C) genetic divergence. Linear fits to the data are shown for primary vs. primary pairwise comparisons (closed circles, solid lines), secondary vs. secondary comparisons (open circles, dotted lines), and primary vs. secondary comparisons ($\times$ symbols, dashed lines). The y-axes in (A)–(C) are all square-root transformations.

of comparable census size, suggesting that the ratio of effective:census population sizes is lower for secondary than primary populations. Likewise, increased community divergence (F_{ST}-C) in secondary forests is consistent with a reduction of effective community size via localized "community bottlenecks." However,

when only the identity of species (not their relative abundances) is taken into account, community divergence (β_{RC}) has, in fact, decreased in secondary relative to primary forests. Therefore, it appears that selective forces determine a set of species most likely to disperse to, persist in, or establish in secondary forests, a result consistent with other analyses of forest-herb species composition in post-agricultural forests (reviewed by Verheyen et al. [2003]). However, the relative abundances of species in secondary vs. primary forests are rarely analyzed, and the results here suggest that they are prone to community drift in depauperate secondary forest communities.

A positive relationship between pairwise genetic divergence and pairwise geographic distance (Fig. 3C) is consistent with neutral genetic variation structured by a balance between local drift and spatially restricted gene flow (Hutchison and Templeton 1999). If the spatial scale of seed and pollen movement in *T. grandiflorum* is representative of forest herbs in general (likely a reasonable assumption—see *Introduction* and Appendix A), then the absence of such a pattern at the community level points to the likely importance of selective forces (i.e., environment) in determining local community composition, notwithstanding some localized drift in species' abundances in secondary stands. This interpretation is supported by the result that the pairwise difference in soil pH was a significant predictor of pairwise presence–absence-based community divergence (β_{RC}; Table 3). Thus, coordinating studies of species diversity and genetic diversity may not only address the issue of whether the two levels of diversity are influenced by parallel processes, but may also lead to novel insights into controls on biodiversity that would not result from analysis of either level alone. Both neutral and non-neutral processes contribute to patterns of diversity and divergence in secondary relative to primary forests.

The influence of agricultural land-use history on the diversity and composition of forest herbs has received considerable attention in eastern North America and Europe (e.g., Peterken and Game 1984, Whitney and Foster 1988, Matlack 1994, Bellemare et al. 2002, Honnay et al. 2002, Vellend 2003*a*, 2004, Verheyen et al. 2003). These studies have revealed reductions of species diversity in post-agricultural forests that may persist for decades or centuries, and compositional differences that often relate to species' life-history traits. Far less is known about how land-use history influences population-genetic variation. Grashof-Bokdam et al. (1998) attempted to determine the source of nine individual *Lonicera periclymenum* plants across three planted woodlots in The Netherlands using RAPD markers, although the analysis was unable to distinguish among many potential parents in older woodlots. Jacquemyn et al. (2004) found slightly lower genetic diversity in *Primula elatior* populations from forests <35 years old ($H_e = 0.28$) than in older forests ($H_e =$

TABLE 3.   Results of stepwise multiple regression analyses predicting pairwise community differentiation (β_{RC}, F_{ST}-C) and genetic differentiation (F_{ST}-G).

Predictor variable	β_{RC}			F_{ST}-C			F_{ST}-G		
	Partial r^2	Mantel r	P	Partial r^2	Mantel r	P	Partial r^2	Mantel r	P
Land use	0.17	−0.24	0.002	0.22	0.49	0.0005	0.28	0.33	0.0004
Geographic distance			†			†	0.13	0.34	0.0012
Area‡	0.08	0.40	0.0001	0.04	−0.34	0.0009			
pH‡	0.09	0.28	0.0008			†			†
Full model	0.35			0.26			0.41		

Notes: Variables entered the model only if $P < 0.001$, and only significant predictors in at least one analysis are shown. Raw differences between each pair of sites were calculated for each variable and then transformed to reduce skew in distributions (therefore, some transformations are different than in the analyses on raw variables). Mantel tests were performed for each variable suggested to be significant in the multiple regression analysis. For β_{RC} and F_{ST}-G there were 351 pairwise comparisons; for F_{ST}-C, 300 pairwise comparisons. Blank cells indicate no data possible, since the independent variable in that row was not used as a potential predictor of the dependent variable in that column.

  † The stepwise statistical test did not identify the independent variable in that row as a significant predictor of the dependent variable in that column.

  ‡ Based on square root of values.

0.29), although the difference was not statistically significant. In contrast to the present study, F_{ST} among populations of *P. elatior* was slightly higher in old (0.035) than young (0.019) forests, although the spatial proximity of young relative to old populations made interpretation of this pattern difficult (Jacquemyn et al. 2004). Here I found significantly lower genetic diversity in *Trillium grandiflorum* populations in secondary forests than in primary forests. For allelic richness, the effect of land-use history was not independent of population size, although it is important to recall that population size itself was significantly lower in secondary than primary stands, independent of stand area. In other words, land-use history likely influences genetic diversity via reduced effective population size. Thus, a legacy of past land-use persists for at least 70–100 years in the contemporary biota of forest fragments at multiple levels of biodiversity. An important question

for future research is whether species diversity and genetic diversity vary in parallel through time in secondary forests, or whether the two levels of diversity recover at significantly different rates. Comparative genetic studies across species in the same landscape that vary in their colonization ability hold great potential for contributing to our understanding of the process of biodiversity recovery in post-agricultural forests.

Agricultural land use decimates populations of forest herbs, potentially to the point of local extirpation. In general, plowing is expected to completely extirpate forest herbs, so that populations on former plowed fields are likely to originate via colonization (Singleton et al. 2001), whereas populations on former unplowed fields (as in the present study) may derive from on-site persistence (Stover and Marks 1998). However, this simple dichotomy is complicated considerably by the presence of hedgerows, which are ubiquitous features
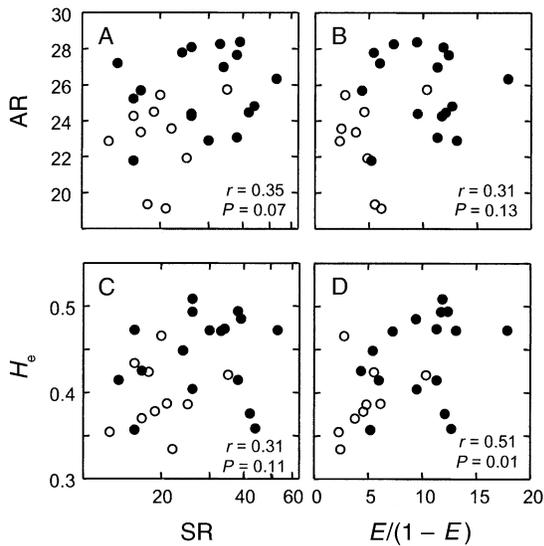

FIG. 4.   (A–D) Relationships between species diversity (species richness, SR; evenness, E) and genetic diversity (allelic richness, AR; expected heterozygosity, H_e). (E–F) Relationships between community divergence (presence–absence based, β_{RC}; frequency-based, F_{ST}-C), and genetic divergence (F_{ST}-G). Note the y-axes $\log_{10}$ scales in panels (E) and (F) and x-axes $\log_{10}$ scales in panels (A), (C), and (F).
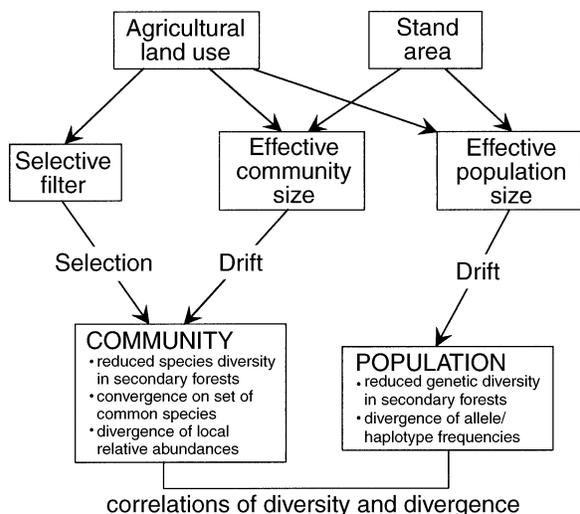
Fig. 5.　Schematic summary of results concerning the influence of land-use history and forest stand area on diversity and divergence at the levels of genes and species.

of northeastern landscapes, and which often harbor populations of forest herbs (Corbit et al. 1999). Even in secondary forests on former plowed fields that are distant from older forests, the source of forest-herb colonists may be quite nearby in adjacent hedgerows. Indeed it is extremely difficult to find a secondary forest in Tompkins County that is not adjacent either to primary forest or to a remnant hedgerow (*personal observation*). Thus, the difference between former plowed and unplowed fields is one of degree and not of kind—population size may be reduced to a very small number, or to zero. The present study has revealed an enduring impact of community and population bottlenecks in secondary forests, though it was not possible to distinguish local persistence from colonization. In theory, genetic data could be used to distinguish these alternatives, though this would require information on local demography, long-distance seed dispersal, and pollen movement that is much more detailed than presently available.

A parallel influence of size (i.e., effective area or population size) on species and genetic diversity was observed in this study, and in a study of diversity patterns on islands (Vellend 2003*b*). These empirical results, and the close theoretical parallel between predictions regarding size in the neutral theories of populations genetics (Kimura 1983) and community ecology (Hubbell 2001), points to a fundamental unity across disciplines concerning the effect of population and community size on diversity. Many studies have also revealed important effects of environmental conditions, habitat isolation, and disturbance regimes on diversity (Huston 1994, Frankham et al. 2002), but it remains unclear to what degree these variables may influence species diversity and genetic diversity in par-

allel. Such patterns seem likely to be influenced by the choice of species pools and genetic traits (e.g., molecular vs. quantitative). Morishima and Oka (1978) found a positive correlation between weed species diversity in rice fields and seed-morphological variation (presumably genetic) in rice plants, suggesting the potential for environmental heterogeneity to drive correlations between the two levels of diversity. Determining the generality and domain of application of the species–genetic diversity correlation will require additional studies on both species diversity and genetic diversity from a range of systems; such studies promise to yield fresh insights into controls on patterns of biodiversity.

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APPENDIX A

Additional details on the study system and methods are available in ESA's Electronic Data Archive: *Ecological Archives* E085-100-A1.

APPENDIX B

Information on isolation and characterization of microsatellite DNA markers in *Trillium grandiflorum* is available in ESA's Electronic Data Archive: *Ecological Archives* E085-100-A2.

APPENDIX C

Tables showing forest-herb community data are available in ESA's Electronic Data Archive: *Ecological Archives* E085-100-A3.

APPENDIX D

Tables showing genetic data for *Trillium grandiflorum* are available in ESA's Electronic Data Archive: *Ecological Archives* E085-100-A4.

APPENDIX E

A table showing summary measures of species diversity and divergence, genetic diversity and divergence, landscape attributes, and environmental conditions in all sampled stands is available in ESA's Electronic Data Archive: *Ecological Archives* E085-100-A5.

APPENDIX F

A table showing correlations and partial correlations between species diversity and genetic diversity, and between community divergence and genetic divergence, is available in ESA's Electronic Data Archive: *Ecological Archives* E085-100-A6.