

## FLORISTIC CONSERVATION VALUE, NESTED UNDERSTORY FLORAS, AND THE DEVELOPMENT OF SECOND-GROWTH FOREST

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*Abstract.* Nestedness analysis can reveal patterns of plant composition and diversity among forest patches. For nested floral assemblages, the plants occupying any one patch are a nested subset of the plants present in successively more speciose patches. Elimination of sensitive understory plants with human disturbance is one of several mechanisms hypothesized to generate nonrandom, nested floral distributions. Hypotheses explaining distributions of understory plants remain unsubstantiated across broad landscapes of varying forest types and disturbance histories. We sampled the vegetation of 51 floodplain and 55 upland forests across Illinois (USA) to examine how the diversity, composition, and nestedness of understory floras related to their overstory growth and structure (basal area), and their overall floristic conservation value (mean *C*).

We found that plant assemblages were nested with respect to site species richness, such that rare plants indicated diverse forests. Floras were also nested with respect to site mean *C* and basal area (BA). However, in an opposite pattern from what we had expected, floras of high-BA stands were nested subsets of those of low-BA stands. A set of early-successional plants restricted to low-BA stands, and more importantly, the absence of a set of true forest plants in high-BA stands, accounted for this pattern. Additionally, we observed a decrease in species richness with increasing BA. These results are consistent with the hypothesis that recovery of true forest plants does not occur concurrently with overstory regeneration following massive anthropogenic disturbance.

Nestedness by site mean *C* indicates that high conservation value (conservative) plants co-occur in highly diverse stands; these forests are assumed to be less disturbed historically. Because site mean *C* was uncorrelated with BA, BA-neutral disturbances such as livestock usage are suggested as accounting for between-site differences in mean *C*. When considered individually, conservative plants were actually more likely to be found in low-BA stands (uplands only). This suggests that floras of historically more open-canopied oak–hickory uplands are being degraded by canopy closure from increasing density of “mesophytic, nonpyrogenic” trees. It also indirectly suggests that recent moderate logging is uncorrelated with floristic conservation values.

*Key words:* anthropogenic disturbance; basal area; canopy cover; coefficient of conservatism; fire suppression; floristic quality assessment; herbaceous layer; livestock grazing; nestedness; overstory structure; temperate deciduous forest; true forest plants.

### INTRODUCTION

Nestedness is a characteristic of species distributions that can characterize patterns in the diversity and composition of ecological communities in both a quantitative and meaningful way. As such, it can overcome some limitations of more commonly used metrics. For example, species diversity or species abundance can be ambiguous and overly simplistic when trying to explore between community patterns (Worthen 1996, Jacquemyn et al. 2001a). Similarity indices that consider composition (i.e., Jaccard, Sorenson) reveal little about the specific species present when

comparing communities, despite the importance of such information (Crow et al. 2002).

Nestedness can be described as a patterned, ordered, or non-random occurrence of species across a group of islands or habitat “islands.” In an archipelago with a perfectly nested species assemblage, the species composition of any one island is a subset of the species present on every island richer in species than itself (Patterson and Atmar 1986). Thus, certain rare taxa are only present on the most speciose islands. Less rare taxa become absent on increasingly species-poor islands in a predictable sequence. Some regionally widespread generalists are present regardless of island richness.

Beyond islands, nested distributions have been found in a variety of different mainland habitats and systems (Patterson 1990, Cook and Quinn 1995, Boecklen 1997, Wright et al. 1998, Matthews 2004), and for numerous taxa (e.g., reptiles, birds, mammals, fish, amphibians,

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insects, and plants). Analysis of nested distributions may be useful as a conservation tool by identifying area-sensitive species, endemics, critical habitats, species indicative of diversity hotspots, as well as ecological mechanisms that order communities (Patterson 1987, Honnay et al. 1999b).

Area-dependent extinction (Patterson and Atmar 1986, Patterson 1987, Bolger et al. 1991), differential colonization (Patterson and Atmar 1986, Cook and Quinn 1995, Kadmon 1995, Butaye et al. 2001), and differential environmental tolerances among species (Blake 1991, Kodric-Brown and Brown 1993, Worthen et al. 1998, Honnay et al. 1999b) are capable of generating nested distributions. Each of these mechanisms is expected to lead to a different specific distribution. However, because these mechanisms are not mutually exclusive, their relative importance inspires considerable debate.

Recent studies have identified nested assemblages along habitat gradients other than species richness. This is not surprising considering the number of factors that determine whether a species will be present or absent in a given habitat patch. For example, anthropogenic disturbances are thought to have induced nested distributions of birds, where heavily disturbed, semi-urban forests contain species-poor avian faunas dominated by a few widespread generalists (Fernandez-Juricic 2002; for other examples see Fleishman et al. 2002).

Similarly, sensitive understory plants are eliminated from temperate forests by anthropogenic disturbances. The most often studied disturbance is logging (Reader 1987, Duffy and Meier 1992, Meier et al. 1995), where understory plant mortality could come directly from trampling, soil compaction, erosion, and slash fires (Bratton 1994), or indirectly by competition from fast-growing, early-successional species (Metzger and Schultz 1984, Roberts and Gilliam 1995), or alteration of factors such as light levels, soil temperature, through-fall precipitation, soil moisture deficits, soil nutrient availability, soil organic matter, leaf litter depth, or availability of pollinators (Anderson et al. 1969, Rogerson 1976, Black and Harden 1995, Nauertz et al. 2004). Agricultural use can have even greater residual effects on understory floras than logging alone (Flinn and Vellend 2005). While recolonization and recovery of original understory communities following massive disturbances should eventually occur, species composition may be affected for centuries after forest regrowth (Singleton et al. 2001, Dupouey et al. 2002).

For example, in Europe, stands protected for hundreds of years after clearing lack ancient forest plants, presumably because of their low dispersability, diaspore production, and growth rates (Hermy et al. 1999, McLachlan and Bazely 2001). Even the most ancient and protected of these forests seem to have gaps in diversity of these species, which are attributable to past human disturbance (Whitney and Foster 1988, Peterken

1992). More common forest specialists, or true forest plants (TFP), also show decreased diversity in second-growth forests (Peterken and Game 1984, Peet and Christensen 1988, Bratton et al. 1994, Meier et al. 1995, but see Metzger and Schultz 1984). However, even though it is well established that understory composition, diversity, and distributions are highly dependent on human disturbance (Christensen 1989, Drayton and Primack 1996), general patterns of species occurrence (e.g., nestedness) associated with disturbances or regeneration of forests have not been demonstrated (Roberts and Gilliam 2003, Whigham 2004).

In this paper, we use "true forest plants" (TFP) to refer to understory plants of closed-canopy forest interiors (Honnay et al. 2002); it is similar in usage to "forest interior plants" or "forest specialists" (Grashof-Bokdam and Geertsema 1998), and loosely analogous to "late-successional species." The European phrase, "ancient forest plants," refers to a subset of TFP restricted to ancient forests. When referring to overstory condition we use "old-growth" to refer to forests where historic timber removal is absent, or so minimal as to be undetectable. We use "secondary" or "second-growth" for intensely cut or cleared stands, which may or may not be primary (i.e., not post-agricultural; Marks and Gardescu 2001, but see Bellemare et al. 2002, and Flinn and Vellend 2005 for disparate usage). Old-growth in North America is primary and ancient.

Simple measures of overstory structure and development such as basal area have been used to evaluate recent disturbance levels (i.e., logging intensity within the past 100–150 years), to monitor restoration, and to indicate potentially valuable forests in the region (Keddy and Drummond 1996, Norris and Farrar 2001). However, because compositional patterns of understory floras are not so easily measured and compared, patterns in second-growth floras are little known (Olivero and Hix 1998). Exploration of understory patterns and processes across broad landscapes, which include different forest types and successional stages has not occurred (but see Christensen and Peet 1984, Gilliam and Roberts 2003a). Indeed, studies on the herb layer in general, which have been both quantitative and geographically extensive are quite rare (but see Rogers 1981, 1982, Christensen and Peet 1984, Peterken and Game 1984, Rooney et al. 2004).

The midwestern United States presents an ideal landscape in which to study patterns of understory species distribution and recovery for several reasons. First, its forests are highly fragmented (and often discrete; Fig. 1). Second, as part of the Eastern Deciduous Forest Region of North America, it has considerable floristic overlap with a broad forested area (Braun 1950). Finally, it has a history of clearing and regrowth similar to temperate forests across eastern North America and Europe (Honnay et al. 2002, Christensen and Gilliam 2003). Illinois was once 38% forested and, by 1920, clearing and cutting had reduced coverage to 8.5%. Since then

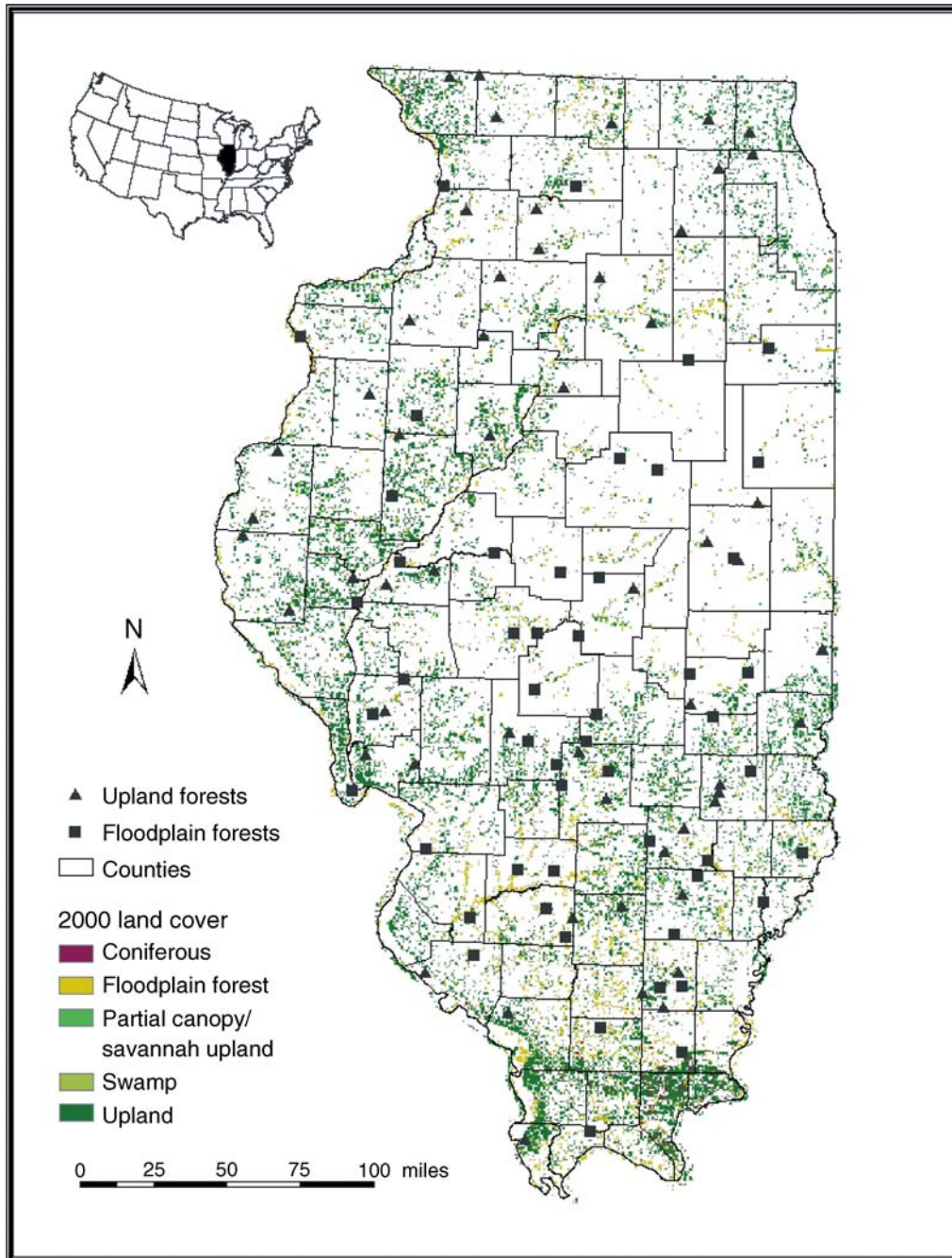


FIG. 1. Distribution of 106 randomly selected forest sites used in the analysis. Sites were sampled from 1998 to 2002. (SI conversion: 1 mile = 1.609 km.)

statewide forest coverage has increased to approximately 14% (Bretthauer and Edgington 2002). Remaining forests are almost without exception second-growth; a mere 0.07% of Illinois forestland is now old growth (Illinois Department of Energy and Natural Resources 1994). However, most stands are relatively mature, as only 3% of the state's forests are considered early successional (Trani et al. 2001).

Our study examines diversity and composition of understory plant communities across Illinois. We tested for nestedness of understory plant occurrences with respect to species richness, basal area (BA), and a measure of biological integrity/conservation value (mean *C*) among forest stands. The latter two tests represent a novel approach to studying nested patterns of plant distributions. We examine four questions:

1) Do understory species exhibit nested distributions with respect to stand BA? That is, are the floras of stands with lower BA nested subsets of the floras of stands with higher BA? We expect that stands with more developed overstories and/or less overstory disturbance (higher BA) will harbor a set of TFP that will be absent from lower-BA stands, causing a nested distribution.

2) Is understory species richness positively correlated with BA? That is, are more diverse understory floras associated with more developed and/or less disturbed overstories? We expect that higher-BA forests will harbor a richer complement of TFP causing greater species richness.

3) Do understory species exhibit nested distributions with respect to floristic conservation value of the site? That is, are the understory floras of low floristic conservation value sites (biologically degraded), nested subsets of high conservation value sites? Because of their inability to persist with anthropogenic disturbance, we expect that disturbance sensitive species will more often be absent from low conservation value forests, causing a nested distribution pattern.

4) Is the conservation value of the site positively correlated with BA? That is, are floras of high conservation value associated with more developed and/or less disturbed overstories? We expect lower-BA forests to have lower conservation values due to elimination of their disturbance sensitive plants by disturbances that decrease BA, such as logging.

#### METHODS

Data were collected as part of the Illinois Critical Trends Assessment Program (CTAP) (Illinois Department of Natural Resources 2001). A total of 106 forests (51 floodplain [alluvial] and 55 upland [non-alluvial]), sampled from the years 1998–2002 were randomly chosen from the CTAP database for the analysis (Fig. 1). All forests were second-growth with >75% canopy cover and were >8 ha in size. Sites were visited across Illinois from south to north, from 15 May through 30 June. Sampling was confined to as homogeneous areas of forest with respect to aspect, hydrology, topography, and forest type as possible. All sampling was done at least 50 m from the forest edge. We recorded all vascular plants within 30 0.25-m<sup>2</sup> (0.5 × 0.5 m) quadrats, distributed evenly along three randomly selected 50-m transects (10 quadrats per transect). Tree diameter at breast height (dbh) was measured on all stems greater than 5 cm dbh in a 10 × 50 m plot along each transect. While this sampling area is below the minimum area threshold suggested to characterize understory communities, this requirement is very rarely met (McCarthy 2003), suggesting that our data are at least comparable to previous studies.

Sampling method affects the results of nested analysis, suggesting that standardized sampling, such as that utilized here is preferred (Cam et al. 2000, Fischer and Lindenmayer 2002). Size of forest patch was unrelated

to measured variables (BA by forest patch size,  $r = 0.14$ ,  $df = 105$ ,  $P = 0.16$ ; mean  $C$  of the sampled area by forest patch size,  $r = 0.06$ ,  $df = 105$ ,  $P = 0.53$ ; species richness within the sampled area by forest patch size,  $r = 0.003$ ,  $df = 105$ ,  $P = 0.98$ ), suggesting minimal area effects for the region's forests (see also Levenson 1981, Simberloff and Gotelli 1984, Dunn and Loehle 1988, Pearson et al. 1998). Whereas some studies have excluded non-forest species, we recorded all plants encountered. Detailed CTAP methodology is explained elsewhere (Carroll et al. 2002). Botanical nomenclature follows Mohlenbrock (1986).

#### Basal area and site effects

Basal area (m<sup>2</sup>/ha) is a measure of overstory development or structure, which increases with stand age and stem density (Oliver and Larson 1996, Gilliam and Roberts 2003b, Kraft et al. 2004). It can also be influenced by site factors such as aspect, slope, hydrology, edaphic characters, latitude, and tree composition (Daniel et al. 1979, Ek 1982). Growth models that could be used to control for site influences on BA are lacking for uneven aged, mixed species hardwoods (Held and Winstead 1975). Consequently, several checks were made to insure that site factors were relatively insignificant when comparing BA values across our sites.

First, differences in tree productivity from nutrient deficits can be assumed to be insignificant because of the high uniform fertility of Illinois soils (>95% Alfisols or Mollisols; Fehrenbacher et al. 1984, Iverson 1991, Woolery et al. 2002; J. Dawson, *personal communication*). Indeed, we sampled no stands with exposed rock (i.e., thin-soiled barrens, glades), which is the character that explains 74% of all variability in BA among regional reference stands (Spetich et al. 1997).

Second, as expected in non-mountainous regions (Aber et al. 1978, Abella et al. 2004), we found no relationship between slope and BA ( $r = 0.09$ ,  $df = 105$ ,  $P > 0.05$ ). Nor was there a relationship between aspect (deviation from SW exposure) and BA ( $r = 0.11$ ,  $df = 105$ ,  $P > 0.05$ ). Although it is known that variance in overstory composition can yield different BA values (Hillebrand et al. 1992), we found no association between BA and latitude or longitude (linear regression,  $\alpha = 0.05$ ), natural division or forest type (i.e., dry-mesic upland, wet floodplain) (ANOVA,  $\alpha = 0.05$ ), suggesting that tree composition was homogenous enough (Braun 1950, Schwegman et al. 1973), to contribute little variance to BA.

As a final test, we analyzed BA data from 1567 randomly placed USDA Forest Service, Forest Inventory Analysis (FIA) sample sites in Illinois (pine plantations excluded; data *available online*).<sup>4</sup> Multiple regression analysis showed the best predictor of BA to be stand density followed by estimated stand age, while

<sup>4</sup> (<http://fia.fs.fed.us/>)

latitude, slope, and aspect were all nonsignificant predictors ( $BA = 34.24 + [0.03 \times \text{tree density}] + [0.49 \times \text{stand age}]$ ,  $df = 1562$ ,  $r = 0.54$ ,  $P < 0.001$ ). Significant predictor variables were consistent across the five most common USDA Forest Service forest cover types tested.

#### *Basal area and logging*

Forest management, such as stocking, timber harvesting, and small-pole thinning, also influences BA. Clearing obviously decreases stand age, while thinning decreases density and stocking increases it. This study is primarily concerned with those larger anthropogenic disturbance events that both directly affect understory floras, and significantly depress BA (see Smith 1962:107, Aber et al. 1978, Young 1982:217). For example, full BA recovery does not occur for at least 60–70 years following moderate logging, or at least 150 years following a complete cut in Illinois (Fralish 1994). Timber stocking, thinning of small pole timber, and natural canopy disturbances (e.g., blow downs), which have limited effects on understory floras, are assumed to be randomly distributed across the data set. For second-growth stands, BA is therefore considered to be a result of stand age, stand density, and the severity of or time since tree harvesting (Oliver and Larson 1996). We performed all analyses using mean tree dbh of stands (data not shown), as a second measure of overstory structure and development, and since these results were nearly identical to those for BA, it is assumed to be a consistent and robust metric for this study.

#### *Site histories*

Historic aerial photos (1937–1940) were available for 51 of 106 forest sites analyzed, and these were searched for evidence of historic crop farming (i.e., till rows). Additionally, land owners were interviewed and on-site indicators of historic agricultural use such as stand edges or fence rows were noted (Egan and Howell 2001). While indications of farming were not found in the forests analyzed, they cannot be ruled out because of the incomplete photo and land owner record. Nonetheless, the available evidence suggests that clearing for pasture and logging dominated the historic use of Illinois forestland, rather than crop farming, which is most productive on former grasslands (Fig. 7.2 in Mankin and Warner 1997, Iverson 1988). While post-tillage forests occur in the region, outside of small patches associated with the earliest settlement outposts, they tend to be young, easily discernable (Iverson 1988, 1991), and as such, probably comprised few if any of the sites analyzed.

#### *Floristic conservation value*

The floral conservation value of each site was assessed using floristic quality assessment (we use “floristic quality” synonymously with “floristic conservation value”; Swink and Wilhelm 1994). Floristic quality assessment utilizes “coefficient of conservatism” ( $C$ )

values, ranging from 0 to 10 that have been assigned to each plant species in Illinois (Taft et al. 1997). Highly conservative plants (7–10) are only found in minimally degraded natural areas, and species that persist in or readily invade degraded areas are given lower numbers, with nonnatives receiving values of zero in this study. A species conservatism is not related to the range or type of habitats in which it occurs, it simply measures propensity of a plant to occur in human-disturbed habitats. Floristic conservation value for each site was calculated as the mean coefficient of conservatism (mean  $C$ ) for all species recorded, including nonnatives. Mean  $C$  has been shown to be a successful metric of anthropogenic habitat disturbance (i.e., a measure of the degree to which a habitat is a biologically undegraded remnant, and therefore representative of historic composition; Wilhelm and Masters 1994, Francis et al. 2000, Lopez and Fennessy 2002, Mushet et al. 2002, DeKeyser et al. 2003, Matthews 2003, Cohen et al. 2004).

#### *Analysis*

Relationships among site variables (species richness, stand-level BA, and mean  $C$ ) were investigated using Pearson correlation coefficients. Patterns of individual species distribution with respect to site species richness, BA, and mean  $C$  were investigated using Wilcoxon two-sample rank tests (Mann-Whitney  $U$  tests). Tests were performed separately for floodplain and upland forests, and only species that occurred in at least three sites were included (115 species in floodplains and 132 in uplands). Sites were rank ordered by decreasing species richness, and a Wilcoxon test was used to determine the degree to which an individual species presence among sites was ordered along this ranked sequence (Siegel 1956, Schoener and Schoener 1983). The sample statistic produced by the test is approximately normally distributed, and deviation from a random distribution of presences and absences among sites can be determined using the standard normal variate,  $z$  (Siegel 1956). Species with significant positive  $z$  scores ( $\alpha = 0.05$ ) are more likely to occur in species rich sites and contribute to the nested distribution of the species assemblage as a whole, whereas species with significantly negative  $z$  scores are more likely to occur in sites of low species richness. Because we made no assumption about the direction of species departures from random distributions, we use a two-tailed test for significance. Sites were re-ranked by mean  $C$  and BA, and data were reanalyzed to assess the influence of these site variables on patterns of species distribution. Because the calculated value of mean  $C$  for a site is dependent upon the  $C$ -value of the individual species being tested, a bias is introduced. Highly conservative species increase the mean  $C$  of any site at which they occur, and thus are more likely to be found significantly ordered with respect to mean  $C$ . To eliminate this bias a species was excluded from the

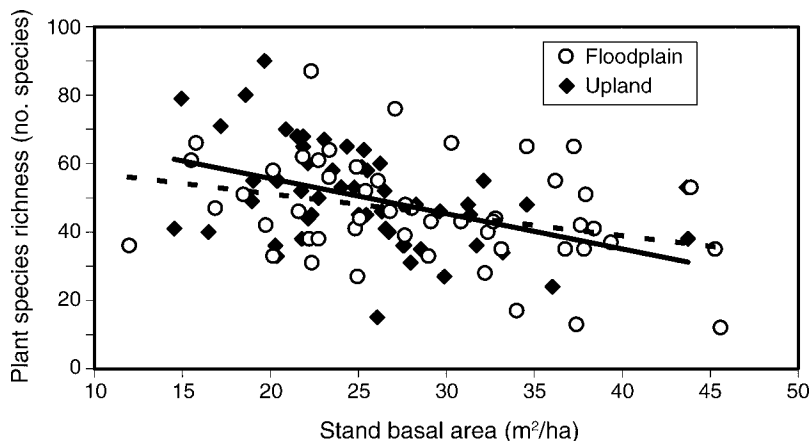


FIG. 2. Relationship between understory plant species richness and stand-level tree basal area in Illinois floodplain forests (dashed line,  $r = -0.34$ ,  $P < 0.05$ ) and upland forests (solid line,  $r = -0.42$ ,  $P < 0.01$ ).

calculations of mean  $C$  for all sites *before* performing the Wilcoxon test for that species.

Spearman rank correlation coefficients were used to investigate the relationship between individual species'  $C$  values and species nestedness scores (Wilcoxon  $z$  scores) in order to determine whether conservative species were more likely to be nonrandomly associated with sites of high species richness, floristic conservation value, or BA (Matthews 2004). Analyses were performed using Statistix version 2 (Analytical Software, Tallahassee, Florida, USA).

The natural logarithms of the tail probabilities of Wilcoxon tests for individual species were combined using Fisher's method (Sokal and Rohlf 1995) to obtain measures of nestedness of the overall species assemblages in floodplain and upland forests with respect to species richness, BA, and mean  $C$  (Kadmon 1995, Hecnar and M'Closkey 1997, Matthews 2004).

As a second measure of the nestedness of the entire species assemblages for floodplain and upland forests, we employed the Nestedness Temperature Calculator computer program (Atmar and Patterson 1995). Unlike the method described above, the "temperature" ( $T$ ) metric measures nestedness of a species-by-site matrix without respect to external site variables such as area or species richness. Temperature is analogous to the concept of disorder in a system, and varies from  $0^\circ$  for a completely ordered matrix to  $100^\circ$  for a completely random matrix (Atmar and Patterson 1993). The program reorganizes rows and columns of the species-site matrix in order to arrange it into a state of maximum nestedness. Generally, species-rich sites are ordered in the topmost rows of the matrix, and frequently occurring species are ordered in the leftmost columns. The program calculates the temperature of the maximally packed matrix by measuring the level of unexpectedness, or deviation from a perfectly nested matrix, by measuring unexpected species presences and absences. The temperatures of the observed matrices (floodplain and

upland) were compared to expected temperatures based on Monte Carlo simulations ( $n = 500$ ) in order to determine the probability of randomly producing a matrix more nested (lower temperature) than the observed matrix (Atmar and Patterson 1993, 1995).

## RESULTS

In both floodplain and upland forests, species richness was significantly negatively correlated with BA (Fig. 2). Site floristic conservation value (mean  $C$ ) was not significantly correlated with stand-level BA in either floodplains ( $r = 0.10$ ,  $P = 0.49$ ) or uplands ( $r = 0.04$ ,  $P = 0.80$ ). Mean  $C$  was unrelated to species richness in floodplains ( $r = 0.07$ ,  $P = 0.63$ ), but showed a weak positive correlation with species richness in uplands ( $r = 0.25$ ,  $P = 0.07$ ).

A total of 38 species (33%) of floodplains and 36 species (27%) of uplands were significantly ( $P < 0.025$ ) nonrandomly distributed with respect to site species richness, with positive Wilcoxon  $z$  scores indicating that they occurred more often in species rich sites (Table 1). Three species in floodplains and one in uplands had significantly negative  $z$  scores, indicating that these species were associated with sites of low species richness. Conservative species were more likely than non-conservative species to be positively ordered with respect to site species richness, as indicated by a significant correlation between individual species Wilcoxon  $z$  score and species  $C$  values in both floodplains and uplands (Table 2). This means that conservative species were more often found in relatively species rich sites. Combining the tail probabilities via Fisher's method for all individual species in each forest type revealed that the species assemblages in both floodplain forests and upland forests were significantly nested with respect to species richness ( $\chi^2 = 669$ ,  $df = 230$ ,  $P < 0.0001$  and  $\chi^2 = 710$ ,  $df = 264$ ,  $P < 0.0001$ , respectively). Likewise, the temperature analysis of the understory species assemblages indicated that floodplain and upland forests were

TABLE 1. Species of forest sites significantly ( $P < 0.025$ ) positively or negatively ordered among sites with respect to the site variables stand-level tree basal area ( $m^2/ha$ ), species richness, and site conservation value (mean  $C$ ).

Variable and ordering	Floodplains	Uplands
Basal area		
Positive	<i>Rudbeckia laciniata</i>	<i>Hydrophyllum virginianum</i>
Negative	<i>Aster pilosus</i> , <i>Carex jamesii</i> , <i>Carex radiata</i> , <i>Circaea lutetiana</i> , <i>Eupatorium rugosum</i> , <i>Menispermum canadense</i> , <i>Parthenocissus quinquefolia</i> , <i>Polygonum hydropiper</i> , <i>Stellaria media</i> , <i>Symphoricarpos orbiculatus</i>	<i>Carex hirsutella</i> , <i>Carex oligocarpa</i> , <i>Eupatorium rugosum</i> , <i>Galium circaezans</i> , <i>Impatiens capensis/pallida</i> , <i>Oxalis dillenii/stricta</i> , <i>Solidago ulmifolia</i>
Richness		
Positive	<i>Agrimonia parviflora</i> , <i>Arisaema triphyllum</i> , <i>Asplenium platyneuron</i> , <i>Botrychium virginianum</i> , <i>Campanula americana</i> , <i>Carex blanda</i> , <i>Carex radiata</i> , <i>Circaea lutetiana</i> , <i>Corylus americana</i> , <i>Dioscorea quaternata/villosa</i> , <i>Elymus villosus</i> , <i>Eupatorium rugosum</i> , <i>Festuca obtusa</i> , <i>Galium aparine</i> , <i>Galium circaezans</i> , <i>Geum canadense</i> , <i>Hydrophyllum virginianum</i> , <i>Impatiens capensis/pallida</i> , <i>Lonicera japonica</i> , <i>Lysimachia nummularia</i> , <i>Panicum clandestinum</i> , <i>Parthenocissus quinquefolia</i> , <i>Phlox divaricata</i> , <i>Phryma leptostachya</i> , <i>Poa sylvestris</i> , <i>Podophyllum peltatum</i> , <i>Polygonum scandens</i> , <i>Polygonum virginianum</i> , <i>Potentilla simplex</i> , <i>Rosa multiflora</i> , <i>Sanicula gregaria</i> , <i>Smilacina racemosa</i> , <i>Solidago ulmifolia</i> , <i>Symphoricarpos orbiculatus</i> , <i>Trillium recurvatum</i> , <i>Viola pubescens</i> , <i>Viola sororia</i> , <i>Viola striata</i>	<i>Arisaema triphyllum</i> , <i>Aster lateriflorus</i> , <i>Aster pilosus</i> , <i>Botrychium virginianum</i> , <i>Carex blanda</i> , <i>Carex cephalophora</i> , <i>Carex hirsutella</i> , <i>Carex hirtifolia</i> , <i>Carex oligocarpa</i> , <i>Carex pennsylvanica</i> , <i>Carex radiata</i> , <i>Carex rosea</i> , <i>Cystopteris protrusa</i> , <i>Desmodium glutinosum</i> , <i>Dioscorea quaternata/villosa</i> , <i>Ellisia nyctelea</i> , <i>Eupatorium purpureum</i> , <i>Eupatorium rugosum</i> , <i>Festuca obtusa</i> , <i>Galium circaezans</i> , <i>Geum canadense</i> , <i>Leersia virginica</i> , <i>Phlox divaricata</i> , <i>Poa sylvestris</i> , <i>Polystichum acrostichoides</i> , <i>Rubus allegheniensis</i> , <i>Sanicula gregaria</i> , <i>Smilax hispida</i> , <i>Solidago ulmifolia</i> , <i>Thalictrum thalictroides</i> , <i>Triodanis perfoliata</i> , <i>Verbesina alternifolia</i> , <i>Viola pubescens</i> , <i>Viola sororia</i> , <i>Vitis aestivalis</i>
Negative	<i>Polygonum pennsylvanica</i> , <i>Ranunculus abortivus</i> , <i>Sicyos angulatus</i>	<i>Campsis radicans</i>
Mean $C$		
Positive	<i>Arisaema dracontium</i> , <i>Campsis radicans</i> , <i>Lindera benzoin</i> , <i>Lonicera japonica</i> , <i>Menispermum canadense</i> , <i>Parthenocissus quinquefolia</i> , <i>Polygonatum commutatum</i> , <i>Toxicodendron radicans</i>	<i>Adiantum pedatum</i> , <i>Arisaema triphyllum</i> , <i>Aster pilosus</i> , <i>Cystopteris protrusa</i> , <i>Dioscorea quaternata/villosa</i> , <i>Galium circaezans</i> , <i>Galium concinnum</i> , <i>Laportea canadensis</i> , <i>Lindera benzoin</i> , <i>Phlox divaricata</i> , <i>Phryma leptostachya</i> , <i>Polystichum acrostichoides</i> , <i>Sanguinaria canadensis</i> , <i>Sanicula gregaria</i> , <i>Smilacina racemosa</i> , <i>Solidago ulmifolia</i> , <i>Uvularia grandiflora</i> , <i>Verbesina alternifolia</i> , <i>Viola triloba</i>
Negative	<i>Alliaria petiolata</i> , <i>Cryptotaenia canadensis</i> , <i>Eupatorium rugosum</i> , <i>Eupatorium serotinum</i> , <i>Hackelia virginiana</i> , <i>Leersia virginica</i> , <i>Ranunculus abortivus</i> , <i>Rosa multiflora</i> , <i>Stachys tenuifolia</i> , <i>Urtica dioica</i>	<i>Allium canadense</i> , <i>Cornus drummondii</i> , <i>Rhamnus cathartica</i> , <i>Smilax hispida</i> , <i>Taraxacum officinale</i> , <i>Toxicodendron radicans</i> , <i>Trillium recurvatum</i>

Note: Nomenclature follows Mohlenbrock (1986).

significantly nested ( $T = 32.8^\circ$ ,  $P < 0.0001$  and  $T = 33.2^\circ$ ,  $P < 0.0001$ , respectively).

In floodplain forests, only one species was significantly positively ordered along the sequence of sites

ranked by BA (Table 1). Ten species were significantly negatively ordered, indicating that sites with low BA were more likely to support these 10 species. Likewise, in upland forests, only a single species was significantly

TABLE 2. Spearman rank correlations ( $r_s$ ) among species variables in floodplain forests (above diagonal, in bold type) and upland forests (lightface type).

	$C$	Basal area $z$	Mean $C_z$	Richness $z$
$C$		<b>-0.02</b>	<b>0.33***</b>	<b>0.20*</b>
Basal area $z$	-0.17*		<b>0.05</b>	<b>-0.40***</b>
Mean $C_z$	0.42***	-0.13		<b>0.20*</b>
Richness $z$	0.21*	-0.49***	0.28***	

Note: Variables include individual species coefficient of conservatism scores ( $C$ ), and species  $z$  scores with respect to site variables basal area ( $m^2/ha$ ; basal area  $Z$ ), mean coefficient of conservatism (mean  $C_z$ ), and species richness (richness  $z$ ).

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

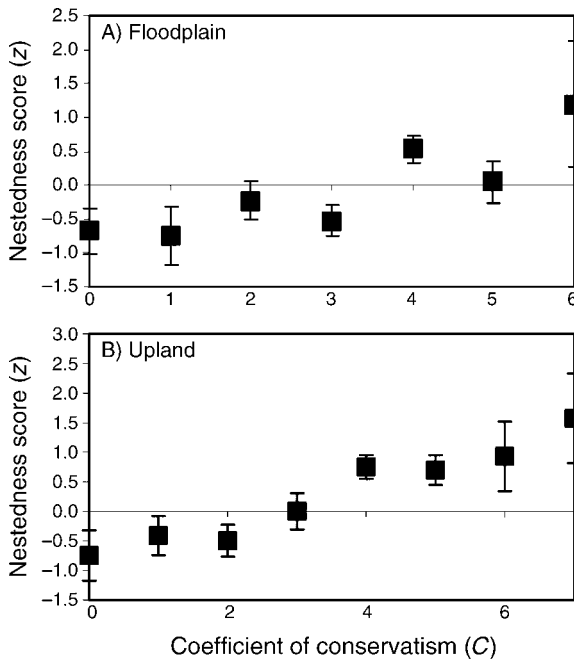


FIG. 3. Individual species Wilcoxon  $z$  score (mean  $\pm$  SE) vs. species coefficient of conservatism ( $C$ ) for understory plants in (A) floodplain forests and (B) upland forests. Species  $z$  score was obtained from Wilcoxon two-sample rank tests to determine whether the species distribution among sites was significantly nonrandom with respect to site floristic quality (estimated as mean  $C$  of all species except the target species). Positive values on the  $y$ -axis indicate that a species is more likely to occur in sites of high floristic quality, whereas negative values indicate that a species is more likely to occur in sites of low floristic quality. Data points are means for all species within a coefficient of conservatism category.

positively ordered with respect to BA, whereas seven species were significantly negatively ordered (Table 1). Individual species  $z$  scores for BA were unrelated to species  $C$  values in floodplains, but were negatively correlated to  $C$  values in uplands (Table 2), indicating that conservative species tended to occur in upland forests of lower BA. Combining the results for all individual species in each forest type revealed that the species assemblages in both floodplain forests and upland forests were significantly “negatively” nested with respect to BA ( $\chi^2 = 365$ ,  $df = 230$ ,  $P < 0.0001$  and  $\chi^2 = 422$ ,  $df = 264$ ,  $P < 0.0001$ , respectively). Therefore, floras of sites with high BA tended to be subsets of floras of sites with low BA.

In floodplain forests, eight species were significantly positively ordered along the sequence of sites ranked by mean  $C$  and 10 species were significantly negatively ordered; and in upland forests, 19 species were significantly positively ordered and seven species were significantly negatively ordered (Table 1). In both floodplains and uplands, conservative species were more likely than nonconservative species to be associated with sites of high floristic conservation value (Table 2, Fig. 3). This indicates that conservative species are more likely

to occur at sites that harbor other conservative species. The overall species assemblage was significantly nested with respect to mean  $C$  in upland forests but not in floodplain forests ( $\chi^2 = 394$ ,  $df = 264$ ,  $P < 0.0001$  and  $\chi^2 = 257$ ,  $df = 230$ ,  $P = 0.11$ , respectively), indicating that for upland forests, floras of low conservation value sites are subsets of floras of higher conservation value sites.

## DISCUSSION

### *Nestedness by species richness*

As with many systems studied, we found understory species to exhibit a highly nested distribution pattern with respect to species richness (for exceptions see Guegan and Huguéy 1994, Worthen 1996). In this positively nested system, the presence of a rare plant indicates a forest with high plant diversity. For these forests—where species poor sites had subsets of the plants of species rich sites—a predictable series of species presences and absences suggests that some environmental gradient defines not only species richness, but also species composition. Most of the discussion that follows is dedicated to describing the likely causes and mechanisms responsible for our observed nested patterns.

Honnay et al. (1999b) found a nested pattern for understory floras in Europe. After eliminating several other factors, they suggested that anthropogenic disturbance and habitat diversity (indicating available niches) within the forests best explained the pattern. Finding a nested distribution directly along a geographical, environmental, or disturbance gradient would more specifically implicate a mechanism responsible for the pattern. In the present study, floras were found to also be nested with respect to stand basal area (BA) and site floristic conservation value (mean  $C$ ). Furthermore, when species were considered individually, conservative plants tended to associate with species rich sites of high conservation value; whereas in upland forests, conservative species were actually more likely to be associated with low BA.

### *Nestedness by basal area*

The nested distribution of plants with respect to stand BA occurred in an opposite pattern from what we had predicted. Floras of higher-BA stands were subsets of the species found in low-BA stands. Therefore, the presence of a set of species specific to low-BA stands accounted for their higher richness (see also Roberts and Gilliam 1995, Graae and Heskjaer 1997). Conversely, and more importantly, there was no set of species specific to high-BA stands (see also Hoehne 1981), as previous work has suggested that later-successional, less-disturbed, or older forests would be expected to have (Peterken and Game 1984, Bratton et al. 1994, Matlack 1994).

Interpreting the individual species contributing to a nested pattern can be highly informative (Simberloff and Martin 1991, Kadmon 1995, Honnay et al. 1999b). In

this case, the “low-basal-area species” driving the nested pattern (Table 1: basal area, negative ordering) generally fall into two categories according to regional floras (Mohlenbrock 1986, Swink and Wilhelm 1994). They are either widespread forest generalists (e.g., *Carex jamesii* Schwein, *Circaea lutetiana* ssp. *canadensis* (L.) Asc. & Mag., *Eupatorium rugosum* Houtt., *Parthenocissus quinquefolia* (L.) Planch), or, they are species of disturbed or open woodlands. This second group suggests a dynamic where understory plants associated with low-BA forest are either remnants of a recently disturbed past (early-successional weeds; *Aster pilosus* Willd., *Oxalis* spp. L., *Polygonum hydropiper* L., *Stellaria media* (L) Vill), or they are species of more stable, open-canopy woodlands (savanna, oak-hickory; e.g., *Carex hirsutella* Mack., *Solidago ulmifolia* Muhl.). In either case, they were absent from understory communities in high-BA forests, causing these forests to be less diverse.

The absence of a patterned occurrence of TFP in high-BA stands may be attributable to two interpretations (see *Understory degradation and logging* and *Understory degradation and recolonization* for a discussion of these). Regardless of the mechanism responsible, insofar as overstory regrowth (i.e., basal area) did not parallel increased occurrence of TFP and species richness, our results are consistent with the hypothesis that the turnover of temperate forests (the cycle of clearing and then regrowth) happens faster than the rate at which understory communities recover from disturbance. Forest strata can be linked to each other via their disturbance and management histories (Gilliam et al. 1995), and due to the highly disturbed nature of modern forests, forest strata are now said to be decoupled from each other (Matlack and Monde 2004). Though previously documented in North America, decoupled forest strata have not been shown to occur over such a large area (Grigal and Arneman 1970, Rogers 1980, Carleton and Maycock 1981, Bergeron and Bouchard 1983, Gilliam et al. 1995, Roberts and Gilliam 1995, Sagers and Lyon 1997; see review in Gilliam and Roberts 2003b).

The relationship between overstory regrowth following a disturbance and understory diversity has been found to be unpredictable and varied (McCarthy 2003; Table 13.1 in Roberts and Gilliam 2003). However, the pattern of understory composition and overstory regrowth has been consistent with our results. Early-successional or open-canopy species are lost as overstories regrow, while TFP do not seem to increase their numbers (though some may increase in abundance or cover; Hoehne 1981, Gilliam et al. 1995, Ford et al. 2000, Kraft et al. 2004). When considering this relationship, previous studies have tended to focus on stand age, while fewer studies focus on BA. Our study illustrates that BA can be an especially informative metric for studying modern forested landscapes because of their complex histories. This is because BA both increases

with age (at least up to the old-growth stage) and decreases with logging (see *Methods*) (Ginrich 1967, Curtis 1970, Levenson 1981, Caspersen 2004). In our analysis, for example, determining meaningful ages for multispecies stands of such diverse land-use histories would not have been possible.

We acknowledge, however, that a drawback to using BA is that it is difficult to separate the effects of stand age from disturbance history from structure (e.g., tree density, mean dbh). Across our sites, mean dbh and BA had nearly identical results (e.g., nestedness, mean dbh by understory richness [ $r = -0.35$ ,  $df = 105$ ,  $P < 0.05$ ]). Tree density and BA on the other hand, had dissimilar relationships with respect to the understory (see also Levenson 1981; i.e., tree density was positively related to understory richness, [ $r = 0.21$ ,  $df = 105$ ,  $P < 0.05$ ], while basal area negatively correlated to richness [Fig. 2]). Due to the complexity of overstory structure among forests, the generality of these overstory trends is unclear.

Many factors interact with overstory structure to determine species occurrence in regenerating second growth (Hoehne 1981, Gilliam and Turrill 1993, Neufeld and Young 2003). Perhaps the most important characteristics of overstory structure to directly affect understory plants are canopy cover and light availability (Hoehne 1981, Gilliam and Turrill 1993). While the relationship between stand age, density, light availability, and understory diversity is not completely monotonic (Brown and Parker 1994, Ford et al. 2000, Neufeld and Young 2003), canopy cover generally increases with BA (Barbour 1987), meaning that shading out of certain species was probably responsible for our observed declines in diversity with increasing BA (Brewer 1980, Metzger and Schultz 1984, Jenkins and Parker 2000, Charbonneau and Fahrig 2004). However, effects from canopy cover should not be overemphasized. If light were the overriding limiting resource for understory herbs, their greatest diversity and cover would occur in mid-successional stands, which it does not (Neufeld and Young 2003).

#### *Understory degradation and logging*

Logging can eliminate sensitive TFP by directly disturbing understory plants and soil (see *Introduction*) (Kraft et al. 2004). Surviving taxa may continue to decline long after a major logging episode because of competition from dense, weedy regrowth (Elliot et al. 1997). However, surviving populations can begin to increase in abundance again once forests reach a threshold of post-disturbance maturity (e.g., >90 yr old). Recovery may vary with stand area, stand age at disturbance, habitat connectivity, overstory composition, slope, aspect, moisture regime, and proximity to roads or weedy, young forests (Ford et al. 2000), but it is the degree of disturbance which appears to be most important in influencing species changes (Parker and Swank 1982). Therefore, we hypothesized that because the severity and time since logging over the past 100–150

years strongly correlates with BA, we would find diversity and floristic quality to positively correlate with BA values.

While this was a patterned occurrence of early-successional plants in low-BA forests, we found no overall connection between overstory disturbance (via basal area) and understory floral degradation in our results (i.e., mean *C* and BA uncorrelated, no nestedness of TFP with BA). Numerous factors may account for this finding. The first and most likely is that BA, as an indirect measure of logging, can only account for recent overstory disturbance. These forests can be assumed to have histories of logging, clearing, and other disturbances, such that isolating any single one disturbance type was not possible using our methodology.

Effects from logging and clearing on understory floras can be varied and complex. Effects range from minimal in select cuts, to extensive in clear-cuts (Collins and Pickett 1988, Marquis and Johnson 1989, Hughes and Fahey 1991). Damage to TFP diversity can also be minimized depending on the tree harvesting technique (Metzger and Schultz 1984, Reader 1987, Reader and Bricker 1992, Graae and Heskjaer 1997). Clearing followed by tillage and crop farming however, is assumed to completely eliminate TFP. Thus, care must be taken when interpreting our results, because mature post-agricultural forests cannot be separated from mature post-logging forests if they have similar BA values, even though these two forests could be expected to have different understory floras (Huebner et al. 1995, Jenkins and Parker 2000, Flinn and Vellend 2005). In this way, historically farmed forests could bias our interpretations. However, we suggest historic crop farming effects, if present, were minimal compared to those identified in eastern North America and Europe (see *Site histories*) (Vellend 2005).

#### *Understory degradation and recolonization*

A second explanation for the lack of expected TFP and low diversity in mature second growth involves barriers to their recolonization, as opposed to a mechanism for their extirpation (i.e., logging or clearing). Second growth may be unsuitable habitat, as environmental conditions specific to old growth that can take 300–400 years to develop may limit establishment of some herbs (Huebner et al. 1995, Honnay et al. 1999a, Verheyen et al. 1999, Verheyen and Hermy 2001, Dupouey et al. 2002, McCarthy 2003). For example, patchy overstory and mid-story structure, gap-phase succession, tip-up mounds, “nurse logs,” and other microclimatic and micro-site conditions create specific habitats (Oliver 1981), while altered tree composition of second growth may present altered properties of litter and soil (shade, pH, nutrient levels, fungal and microbial communities; Hicks 1980, Crozier and Boerner 1984, Whitney and Foster 1988, Graae and Heskjaer 1997). However, the importance of such environmental barriers to recolonization have been increasingly questioned

(Ehrlén and Eriksson 2000, Bellemare et al. 2002, Butaye et al. 2002, Honnay et al. 2002; but see Vellend 2004, Verheyen and Hermy 2004).

A second barrier is isolation from seed sources and the poor dispersability of TFP (Hermy 1994). For example, recolonization of sensitive herbs into mature second growth is extremely slow even if there is a rich old-growth seed source abutting the stand (Matlack 1994, Brunet and von Oheimb 1998, Singleton et al. 2001). The relative absence of old growth and ancient forest seed sources across the landscape further limits recolonization (Whitney and Foster 1988, Duffy and Meier 1992, Meier et al. 1995, Bellemare et al. 2002, Honnay et al. 2002, Vellend 2003). Therefore, isolation contributes to nestedness in forests (but see Hermy 1994, Grashof-Bokdam 1997, Butaye et al. 2001, Jacquemyn et al. 2001a, b).

While some sensitive taxa such as *Trillium* spp. have recently been shown to be more vagile than previously assumed (Zettler et al. 2001, Vellend et al. 2003, Myers et al. 2004), deviations from slow incremental migration are rare (Matlack 1994, 2005, Cain et al. 1998). Furthermore, some studies have suggested isolation effects could be mitigated in floodplain forests (Bratton et al. 1994, Oliver and Larson 1996, Honnay et al. 2001), because they are more contiguous and more likely to receive seed via flooding (Jacquemyn et al. 2001b), or because they can act as refugia (Bratton et al. 1994). Our data, however, do not support this hypothesis as similar patterns were found for floodplain and upland forest diversity (Fig. 2). Taken as a whole, these studies suggest that isolation is likely to inhibit recovery of TFP diversity for centuries (Peterken 1977, Cain et al. 1998, Jacquemyn et al. 2001a, Honnay et al. 2002, Vellend 2004, Matlack and Monde 2004).

#### *Understory degradation and canopy closure*

Hypotheses regarding forest understory dynamics discussed thus far are based on studies conducted in formerly contiguous, closed-canopy ecosystems (but see Vera 2000). These assume that floras are degraded with forest clearing, and that subsequent BA increases mark an overstory recovery. However, we found no significant overall correlation between BA and floristic conservation value (mean *C*), nor did we find a patterned occurrence of TFP associated with high BA.

Therefore, rather than representing a recovery, high BA values for many upland forests may be indicative of a forest degradation. For forests that were historically more open, increasing BA due to a lack of natural disturbances (primarily fire in this region and, to a lesser extent, large herbivores) would lead to a nested pattern if the species intolerant of deep shade and full canopy closure (e.g., *Carex hirsutella*, *Solidago ulmifolia*), drop out of the assemblage as BA increases. In a matrix of open forest, many of the shade tolerant TFP would be locally absent from the potential species pool, and could not rapidly replace plants eliminated from shading.

This is likely the case in Illinois, where most forestland was historically ecotonal and characterized by a patchwork of grasslands, open, and closed canopy woodlands (Anderson 1991). Almost all forest patches of the type used in this study were historically forested (Iverson 1988), but fire suppression and timbering has caused overall tree density to dramatically increase, while average tree size has decreased—as compared to presettlement conditions. This has closed canopies and increased BA of historically open-canopy forests (Ebinger and McClain 1991, Fralish et al. 1991, Abrams 1992, 2005). While TFP did dominate deep-shade “rich mesic forest,” communities characteristic of more open woodlands (less shade tolerant, more fire tolerant) would have made up the majority of the forest matrix, suggesting that a guild of rich mesic species would not be present in some wooded areas (Whitford 1949).

Closed-canopy floras might replace open-canopy understory communities eliminated by shade in 50–100 years (Fralish 1997). There is no evidence however that any such species replacement has occurred after invasion from “mesophytic, nonpyrogenic trees,” even with adjacent propagule sources (Fralish 1997). For example, a long protected oak–hickory forest in New Jersey (USA) lost much of its original understory community and diversity after 30 years of fire suppression caused canopy closure and competition from shade tolerant competitors (Davison and Forman 1982). This phenomena may apply across open woodlands of east and central North America (e.g., oak–hickory, oak–pine; Fralish et al. 1991, Anderson et al. 1999, Abrams 2005).

#### *Nestedness by floristic conservation value*

As expected, floras were nested with respect to floristic conservation value of sites (though not significantly in floodplain forests), indicating that the more conservative a species was the more likely it was to be found in a forest of high conservation value. Overall, mean *C* accurately identifies stands with co-occurring conservative plants (Table 2, Fig. 3), which may be assumed to be less biologically degraded. When considered individually, conservative species tended to associate with species rich sites of high conservation value (Table 2), suggesting a group of relatively undisturbed forests with high diversity and conservation value. Although the “negatively” nested species with respect to BA seemed to be related to an identifiable environmental mechanism (i.e., canopy openness), such a trend in the species nested with respect to mean *C* and richness was not apparent to the authors (Table 1).

However, conservative species were slightly more likely to be associated with low BA in upland forests (Table 2). This further suggests that historically open-canopied uplands require more intensive management (as with periodic fire) to maintain their understory communities of high conservation value. For example, a primary oak–hickory forest in southern Wisconsin (USA) lost its conservative open-woodland herbs and

diversity over a 110-yr period of increasing BA and tree density because of fire suppression and canopy closure (Cottam 1949).

Previous studies have shown a positive correlation between overstory maturity or disturbance, and mean *C* (Francis et al. 2000). However, because mean *C* and BA were uncorrelated across all sites, overstory structure alone cannot account for floral degradations in our study. Because paired grazed and ungrazed stands have been shown not to differ in BA (Dennis 1997, Mabry 2002), we suggest that livestock use (cattle and hogs), which would allow mean *C* and BA to vary independently of one another, has caused nested floral distributions with respect to site mean *C*. Slow-growing “conservative” species cannot tolerate repeated browsing (known as grazing decreasees; Anderson 1994, McGraw 2005), and cattle avoid certain understory plants (grazing increasees), while certain plants are more resistant to trampling and grubbing than others (Cawley 1960). Livestock use could act as a filter to remove grazing intolerant plants from intensely grazed/pastured forests, and a gradient in grazing intensity would lead to a nested distribution of understory plants with only the most tolerant plants occurring in heavily grazed forests.

Despite the near ubiquity of this land use (at least 90% of forests in midwestern North America; Whitney 1994, Mabry 2002), the legacy of grazing on understory floras vs. other disturbances is poorly understood (Stover and Marks 1998). Previous studies have shown that grazing can cause shifts in understory floral composition similar to those present in our low conservation quality sites (Dambach 1944, Dennis 1997, Mabry 2002). However, past studies have not been able to distinguish compositional differences associated with grazing, vs. other disturbances (Stover and Marks 1998). Unlike relatively discrete anthropogenic disturbances such as timbering and farming, grazing effects are spatially and historically variable (e.g., numbers of animals, type of animals, timing of grazing, length of grazing, time since grazing, planting of pasture grasses, openness of pasture or grazed forest; Marks and Gardescu 2001), while there are also probably inherent environmental differences between areas chosen to be grazed that cannot be controlled for (e.g., forest slope, rocky soil, swampy areas). Additionally, as the prevalence of livestock grazing continues to decline (Whitney and Somerlot 1985), recent evidence suggests that deer overabundance will also contribute to regional floral patterns (Rooney et al. 2004).

A critical challenge to future studies attempting to explain floral distributions and patterns across the north-temperate forest zone will be to better relativize and quantify complex disturbance histories of livestock use and clearing (Vera 2000, Watkinson et al. 2001). Care must be taken to avoid oversimplifications such as grazed vs. ungrazed, agricultural vs. non-agricultural, primary vs. secondary, and old-growth vs. second-growth. Future analysis must also consider that effects

on understory floras from factors such as forest age, geography (patch size, isolation, soil), and/or anthropogenic disturbance (clearing, logging, livestock, plowing) probably vary between forest types (i.e., open vs. closed canopy, floodplain vs. upland, mesic vs. xeric; Bratton et al. 2004).

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