



Species traits as generalized predictors of forest community response to human disturbance

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ABSTRACT

During the past decade, substantial effort has been aimed at identifying a group of easily measured, widely applicable plant traits that could serve as a metric to predict temporal change in plant communities. Traits that transcend regional differences in species composition and ecological conditions through their consistent response to disturbance would give managers a simple tool for tracking ongoing and future forest change in response to human disturbance. Although a wide range of plant traits has been associated with human disturbance, consistent traits have not emerged in the literature. However, this may be due to differences in methodology among studies. Previously collected data from two eastern deciduous forest floras of North America (Iowa and Massachusetts) allowed us to evaluate whether such traits emerged, while controlling for methodological differences. We created a plot \times traits matrix for each site and ordinated them using principal components analysis (PCA) to identify disturbance gradients. We then assessed how well the traits most strongly associated with the disturbance gradients corresponded. The data sets shared only 4 of the 12 traits associated with disturbance and 6 of 12 traits associated with undisturbed sites. We did not find a consistent association between dispersal limitation and undisturbed sites or high dispersal capacity associated with disturbed sites. However, in both data sets degree of habitat specialization was an important variable on both ends of the disturbance gradient. Habitat generalists were associated with disturbance and habitat specialists were associated with more pristine sites in both data sets. These results agree with the findings of a wide range of site-specific studies, and we therefore propose that this variable is a promising candidate trait to provide a signal of forest community response to human disturbance. Our results should be particularly encouraging for managers because in many regions morphological trait data are not readily available, and compiling such data is a very time-intensive task and unlikely to be feasible for most managers to undertake. With a list of species and a published flora, upwards of several hundred species can quickly be coded for degree of habitat specialization and used to track the impact of current disturbance, to predict future impacts, and to target specific species for reintroduction or restoration.

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1. Introduction

During the past decade, substantial effort has been aimed at identifying a group of easily measured, widely applicable plant traits that could serve as a metric to track and predict temporal change in plant communities. A primary motive is the need for managers and ecologists to understand and plan for the effects of

human disturbances and global change on plant communities across a broad geographic range (Woodward and Cramer, 1996; McIntyre et al., 1999; Rusch et al., 2003). A key challenge to this effort is to identify plant traits that transcend regional differences in species composition and ecological conditions through their consistent response to disturbances. Managers could then develop indicators of vegetation change based on simplified patterns exhibited by traits (McIntyre et al., 1999; Moretti and Legg, 2006).

However, it has been a challenge to find such traits. An extensive literature on plant functional traits has identified a wide range of morphological traits that may mediate plant response to human disturbance. These range from traits with easy to intuit function such as capacity for dispersal to less intuitive traits such

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as leaf shape and structure (see review in Mabry et al., 2000). However, consistent traits associated with disturbance have not emerged. For example, several studies suggest that dispersal limitation is associated with the inability of some species to recolonize post-agricultural landscapes (Dzwonko and Loster, 1992; Matlack, 1994; Graae and Sunde, 2000; Dupré and Ehrlén, 2002; Verheyen et al., 2003), while other studies have found no evidence for this association (Mabry et al., 2000; Singleton et al., 2001; Wulf, 2004; Dambrine et al., 2007). Furthermore, the relationship between the morphology of propagules and actual dispersal is poor due to complexity in the processes that actually move seeds (Higgins et al., 2003).

This lack of consistency may be a result of differences in methodology among studies, however, rather than an indication that transcendent traits do not exist. Comparisons among sites have been confounded by differences in analytical methods, the methods and schemes used to classify traits, and by inclusion of different mixes of traits (McIntyre et al., 1999). Thus, we do not know whether dissimilar patterns have emerged due to different methods or due to fundamental ecological differences among regions.

Our objective in this study was to determine whether consistent plant traits were associated with human disturbance in two regionally distinct forest floras, with the larger goal of identifying traits that could be widely used by forest managers to track and predict future human impacts and mitigate against them. Both data sets were classified and analyzed identically to ensure that any intrinsic differences between the two data sets were not confounded by different methodologies.

Previously collected data from two eastern deciduous forest floras of North America provided an ideal opportunity test this idea. Our two regions, central Massachusetts and central Iowa, USA, are part of the temperate deciduous forest biome, but represent different formations within eastern North American Forests (Fig. 1; Barbour and Billings, 2000). Both regions have experienced intense human impacts, but the time period and type

of human disturbances have differed (Table 1). In Massachusetts and throughout New England, European settlement and deforestation were followed by a period of intensive agriculture (including both cultivation and pasture) that peaked around 1850. This was followed by widespread farm abandonment that has resulted in modern forests that are a mosaic of secondary forests interspersed with smaller areas used as woodlots but never cleared for agriculture (Gerhardt and Foster, 2002). In Iowa, timber harvesting, cattle grazing, and cultivation have been widespread since settlement began in the mid-1800s. Grazing, which peaked between 1924 and 1982, has had the greatest impact on the ground-layer vegetation of the remaining remnants (Whitney, 1994; Mabry, 2002). The impact of these disturbances on the forest herbaceous layer in both regions is increasingly a concern for conservation. This layer exhibits a long-term legacy of past disturbance, accounts for most of the forest biodiversity and is of critical functional significance in forest ecosystem processes, particularly, regeneration of canopy trees and nutrient cycling (Muller and Bormann, 1976; Roberts, 2004; Gilliam, 2008; Mabry et al., 2008). Long-term legacies of human impacts are likely much more widespread than previously realized and may extend over a millennia (Dambrine et al., 2007).

Separate trait-based analyses of the Massachusetts and Iowa data sets demonstrated that fruit and seed characteristics, growth form, and degree of habitat specialization were among the most important categories of traits mediating response to human disturbance (Mabry et al., 2000; Mabry, 2002). However, prior to this combined analysis, the two studies were not directly comparable because methodologies differed.

We hypothesize that if traits transcend floristic differences across regions and can be used to track and predict the response of forest plant species to human disturbance, we should be able to identify similar associations between traits and disturbance in Iowa and Massachusetts despite differences in floras and specific details of human impacts. Our study adds a new dimension to prior work relating plant traits to human

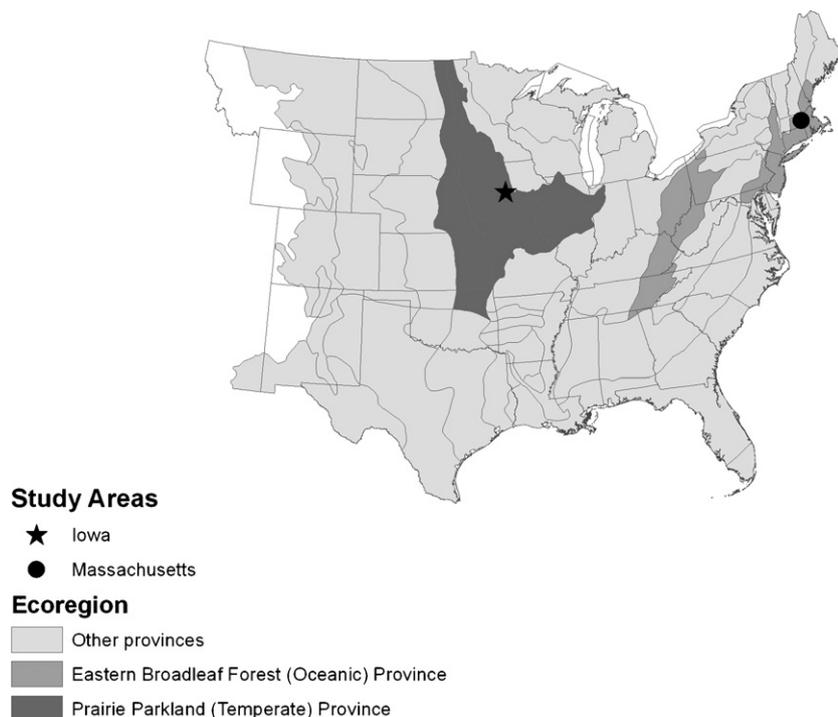


Fig. 1. North American forest ecoregions and study locations used in a comparative study of plant and trait response to human disturbance in two North American deciduous forest floras.

Table 1

Plot level disturbance and abiotic factors measured for two North American forest floras, and used to relate traits to environment/disturbance gradients.

Iowa	Massachusetts
Disturbance	Disturbance
Currently or recently grazed (past 10–15 years)	Primary woodland (not used for agriculture prior to 1830)
Ungrazed for 50+ years	Secondary woodland (pastured or cultivated prior to 1830)
Abiotic factors	Abiotic factors
Slope (%)	Slope (%)
Exposure	Exposure
NE, 346–360, 1–105 (least solar)	NE, 346–360, 1–105 (least solar)
286–345, 106–105	286–345, 106–105
SW, 166–285 (most solar)	SW, 166–285 (most solar)
Landscape position	Landscape position
Level upland, upper slope	Ridgecrest, terrace, upper slope
Midslope	Midslope
Low slope	Low slope
Soil nutrients: percent phosphorous, potassium, nitrogen	Soil bulk density (O and M horizon) (g/cm³)
Soil percent organic matter	Soil percent sand and fines (silt and clay combined)
Soil pH	Soil percent organic matter (O and M horizon)
	Soil pH (O and M horizon)

disturbance because we use identical traits and analytic methods, which removes these as confounding factors in the cross regional comparison and allows us to pinpoint consistent patterns. We also focus on identifying a simple indicator that could be adapted by forest managers.

2. Study areas

Our study includes two floristically distinct components of the North American eastern deciduous forest (Fig. 1). Central Massachusetts is a mixed deciduous forest characterized by a transition between hardwoods and white pine-eastern hemlock. The forest canopy is characterized by *Pinus strobus*, *Tsuga canadensis*, *Acer rubrum*, *Betula lenta*, *Betula alleghaniensis*, *Fagus grandifolia*, and *Quercus rubra* (Gerhardt and Foster, 2002). Central Iowa is located in the transition between the central prairies and plains and the eastern deciduous forest. *Acer nigrum*, *Carya ovata*, *Quercus alba*, *Q. macrocarpa*, *Q. rubra*, *Q. velutina* and *Tilia americana* dominate the upland forests (van der Linden and Farrar, 1993).

We used plant species data from previously conducted studies (Mabry, 2000; Gerhardt and Foster, 2002). In each study, data included measures of canopy trees, understory trees, shrubs, and all vascular non-woody understory or ground-layer species. In both Iowa and Massachusetts, species were sampled in 20 m × 20 m plots. In central Iowa, plots ($n = 103$) were located in remnant forests that could be separated into two levels of grazing intensity: ungrazed for at least 50 years vs. currently grazed or grazed within the past 15 years (Mabry, 2002). In central Massachusetts, the plots ($n = 76$) were located in the township of Petersham and could be divided into two types of land use: secondary forests that developed on abandoned agricultural land and primary forests that may have been selectively logged during the period of intensive agriculture, but had never been converted to pasture or row crops (Gerhardt and Foster, 2002). Similar abiotic data were also collected for the Iowa and Massachusetts plots (Table 1).

3. Methods

3.1. Trait selection

We classified all species in the two data sets with respect to 17 traits (54 trait states when expanded to binary form). The 17 traits included eight related to reproduction, six related to vegetative structure and three related to habitat (Table 2). This array of traits was chosen because each had previously been shown to have some relationship to disturbance (reviewed in Mabry et al., 2000). Due to the large number of species and the difficulty in measuring physiological traits, we were limited to reproductive and vegetative traits that could be scored from published sources and herbarium specimens (Barkely, 1986; Gleason and Cronquist, 1991).

Table 2

Attributes compiled for three North American deciduous woodland floras.

Reproductive traits	Vegetative traits	Habitat traits
Diaspore dispersal	Vegetative spread	Historic range
Wind	None ^a	Native
Animal internal	Low ^b	Non-native
Animal external	High ^c	
Passive		Habitat preference 1
Ants	Life form	Habitat specialist – rich/mesic sites
Cache	Annual/biennial	Habitat generalist – rich/mesic or dry sites
	Perennial herb	
Flower structure	Graminoid	Habitat preference 2
Flowers perfect	Pteridophyte	Habitat specialist – sites in deep shade
		Habitat generalist – sites in deep shade or open
Flowers imperfect	Woody understory	
	Canopy tree	
Flower arrangement	Spring ephemeral	
Borne singly		
Inflorescence	Leaf arrangement	
	Alternate	
Pollination	Opposite	
Wind	Whorled	
Animals	Basal	
Fruit type 1	Leaf structure	
Fruit fleshy	Simple	
Fruit dry	Compound	
Fruit type 2	Leaf margins	
Fruit dehiscent	Entire	
Fruit indehiscent	Serrate	
	Lobed/dissected	
Seed size	Height	
<1 mm	<0.5	
1.1–2 mm	0.6–1.5	
2.1–3 mm	1.6–5	
3.1–5 mm	5–20	
5.1–10 mm	>20	
>10 mm		
Seeds per fruit		
1–3		
4–20		
20+		
Diaspores per plant		
<25		
25–100		
100–1000		
>1000		

^a No vegetative spread = caudex or crown present; if woody, sprouting from base present.

^b Low vegetative spread = root a tuber, corm or stocky rhizome, or tillers form.

^c High vegetative spread = spreading or long creeping rhizomes or stolons present.

We also categorized each species by three habitat attributes because an association between aspects of habitat and human disturbance has been previously demonstrated for both study regions (Mabry et al., 2000; Mabry, 2002). Species were classified by whether they were present in the region prior to Euro-American settlement or not (native vs. non-native). We also classified species by two aspects of habitat specialization, which refers to the need or preference some organisms exhibit for specific environmental conditions in which to live. We contrast specialists for deeply shaded sites with generalists that occur in both deep shade and more open forests (i.e. which show no such preference). We also contrast specialists on sites with rich, mesic soils with generalists that are found in both rich, mesic and drier sites (Table 2). Note that habitat specialization is not circular with human disturbance. For example, in the Midwest, USA, some forest plant species occur in open dry forests and savannas as well as closed canopy and moist forests, all of which are considered non-degraded native plant communities (Brudvig and Mabry, 2008). Habitat traits were obtained from the description of species' habitats in published floras, primarily Gleason and Cronquist (1991), but also Flora of the Great Plains (Barkely, 1986) if a species was not included in the former flora.

3.2. Data analysis

To determine whether similar traits are associated with human-caused disturbance in the two data sets, we created a matrix of plots \times traits. This was done by multiplying a species \times traits matrix by a plots \times species matrix to create a new matrix of plots \times traits. In the resulting matrix, data were the presence/absence of traits in the plots. Ordinations of the plot \times trait matrices were then conducted with principal components analysis (PCA), which is effective for reducing the dimensionality of morphological trait matrices (McCune and Grace, 2002). We chose to use Pearson correlation coefficients in the cross-products matrix to ensure that all variables contributed equally to the solution. Using the resulting PCA axis scores for each plot, we analyzed the relationship between plot scores and environment and disturbance factors measured for each plot. This allowed us to validate previous results that revealed disturbance as a significant gradient in the vegetation (Mabry et al., 2000; Mabry, 2002). Relationships were assessed using Pearson correlation for continuous factors, and one-way analysis of variance (ANOVA) for categorical factors. In the ANOVAs, PCA scores were the response variables, and environment/disturbance factors were the independent variables (fixed effects).

To examine the traits with the disturbance gradient, we identified the 12 traits (~20% of traits) that had the highest loadings on both the positive and negative portion of PCA axis, which were associated undisturbed and disturbed plots respectively. To examine the possibility that picking the traits with the highest axis scores irrespective of sign skewed the traits towards the positive or negative end of the PCA axes, we also examined traits with the highest axes scores irrespective of sign. This resulted in only 1–2 more traits on the positive end of the gradient. We concluded that trait scores were not highly skewed and retained our use of 12 traits on each end of the axis to make comparison clearer.

We used multi-response permutation procedure (MRPP) to test for differences in trait abundance between the two matrices. The MRPP provided a non-parametric test of the null hypothesis that there is no difference in trait composition between the matrices (McCune and Grace, 2002). We selected Euclidean distance as our distance measure following the recommendations of Zimmerman et al. (1985).

4. Results

The Iowa and Massachusetts data had 64% of plant families and 23% of species in common. A list of the most common species in each data set is provided in Appendix A. The first two axes of the PCA explained 54% and 63% of the variation in the plot \times trait matrix in Iowa and Massachusetts, respectively (Iowa: PCA 1 = 42%, PCA 2 = 12%; Massachusetts: PCA 1 = 63%, PCA 2 = 8%). As expected based on previous separate analyses of the data, we identified a gradient of human disturbance in each data set. In each, PCA 1 was significantly associated with abiotic variables and PCA 2 with the respective regional human disturbance, i.e. cattle grazing in Iowa ($F = 16.0$, $p = 0.0001$) and past land use in Massachusetts ($F = 8.9$, $p = 0.004$; Fig. 2).

Because we were interested specifically in plant community response to human disturbance across regions, we focused on the association between traits and the disturbance gradients identified. At the undisturbed ends of the gradients, Iowa and Massachusetts shared 6 of 12 traits (50%), while at the disturbed end of the gradient the two data sets shared only 4 of 12 traits (33%) (Table 3). Results of the MRPP also suggested that, overall, the two matrices differed in trait abundance ($A = 0.31$, $p \leq 0.0001$).

In both Iowa and Massachusetts, ferns were associated with the undisturbed end of the gradient (axis 2), along with basal

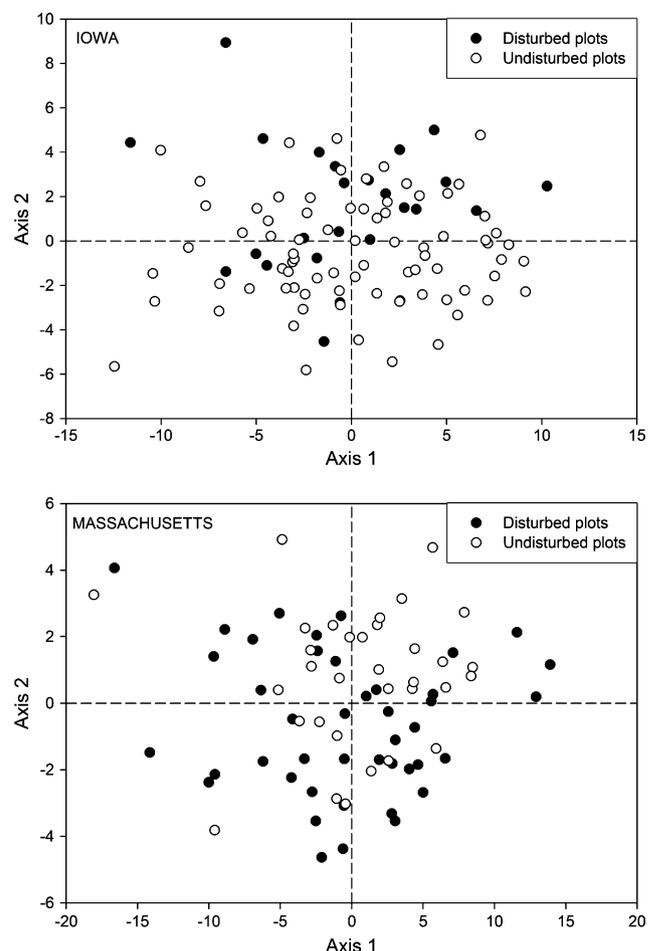


Fig. 2. PCA ordination of two North American deciduous forest floras. The first two axes explained 54% and 63% of the variation in the plot \times trait matrix in Iowa and Massachusetts, respectively (Iowa: PCA 1 = 42%, PCA 2 = 12%; Massachusetts: PCA 1 = 63%, PCA 2 = 8%). In both data sets, PCA 1 represented an abiotic gradient and PCA 2 a human disturbance gradient (cattle grazing in Iowa and past land use in Massachusetts).

Table 3

Traits most strongly associated with the negative portion of PCA axis 2 (undisturbed) and the positive portion of PCA axis 2 (disturbed). Characters in bold occur in both floras in association with the same portion of the gradient (e.g. undisturbed or disturbed).

Iowa		Massachusetts	
Undisturbed		Undisturbed	
Diaspore dispersal ants	-0.2983	Seed size 2.1–3 mm	0.2252
Spring ephemeral	-0.2744	Phyllotaxy whorled	0.1519
Fruits dehiscent	-0.2676	Habitat specialist – rich/mesic	0.1445
Seeds/fruit 4–20	-0.2527	Vegetative spread low	0.1358
Height < 0.5 dm	-0.2521	Phyllotaxy basal	0.135
Habitat specialist – rich/mesic	-0.2444	Perennial herb	0.1145
Habitat specialist – shade	-0.2123	Flowers solitary	0.1012
Phyllotaxy basal	-0.1861	Height 0.6–1.5 dm	0.0911
Fern	-0.1646	Seeds/fruit 4–20	0.0866
Flowers solitary	-0.1562	Fruits dehiscent	0.0815
Vegetative spread high	-0.1177	Fern	0.0793
Leaves lobed or dissected	-0.1156	Leaves compound	0.0781
Disturbed		Disturbed	
Flowers in inflorescence	0.0981	Seed size 5.1–10 mm	-0.069
Fruit indehiscent	0.1039	Diaspores/plant 1000+	-0.083
Seeds/fruit 1–3	0.1062	Phyllotaxy alternate	-0.0843
Vegetative spread none	0.1124	Height 5–20 m	-0.148
Graminoid	0.1128	Flower imperfect	-0.1653
Height 0.6–1.5 dm	0.1432	Pollination wind	-0.1883
Pollination wind	0.1479	Habitat generalist – rich/mesic or dry	-0.1911
Habitat generalist – shade or open	0.1888	Height > 20 m	-0.3424
Annual/biennial	0.1927	Seed size > 10 mm	-0.3439
Habitat generalist – rich/mesic or dry	0.1964	Seeds cached	-0.3439
Non-native	0.1974	Vegetative spread none	-0.3555
Diaspore dispersal animal external	0.1992	Canopy tree	-0.3644

phyllotaxy, solitary flowers, and dehiscent fruits with 4–20 seeds (Table 3). No single life form was associated with disturbance in both data sets. In Iowa, disturbance was associated with graminoids, annuals/biennials and non-native species, whereas in Massachusetts it was associated with canopy trees and traits such as high reproductive output, and large seeds that are cached by animals. In both data sets disturbance was also associated with wind pollination, lack of vegetative spread and indehiscent fruits (Table 3).

In both Iowa and New England, habitat was an important variable on both ends of the disturbance gradient. In both, specialists on rich/mesic sites were associated with the undisturbed portion of the gradient, whereas generalists occurring on both dry and rich/mesic habitats were associated with the disturbed portion of the gradient (Table 3).

Axis 1 in Iowa was a gradient of low to high soil organic matter, high to low phosphorous and high to low slope. In Massachusetts this axis was a gradient of low to high O (organic) horizon soil pH and of high to low bulk density of the M (mineral) soil horizon. In both data sets the axes were separated by life form groups, with perennial herbs separated from annuals/biennials and non-native species (data not shown).

5. Discussion

Our goal was to assess whether consistent plant traits were associated with human disturbance in two regionally distinct forest floras of North America. If so, it would be feasible for managers to use easily measured, widely applicable traits to track and predict changes in forest communities in response to human disturbance. This is a particularly critical need, given the chronic disturbances increasingly imposed by humans (Gilliam, 2008).

We did not find expected patterns in mechanistic traits. Specifically, there was no consistent association between limited dispersal and undisturbed sites (Dzwonko and Loster,

1992; Matlack, 1994; Graae and Sunde, 2000; Dupré and Ehrlén, 2002) or high dispersal capacity and disturbed sites (Matlack, 1994; Graae and Sunde, 2000; McLachlan and Bazely, 2001). The mechanistic traits associated with disturbance in both data sets included wind pollination, indehiscent fruits and lack of vegetative spread. These traits are shared by graminoids, annuals/biennials, and canopy trees, which are life forms that were well represented in disturbed sites in both data sets. Thus, it is likely that the association between these traits and disturbance was due to their correlation with major life form groups, rather than a functional response to disturbance. Similarly, the association between undisturbed sites and basal phyllotaxy probably reflects the presence of ferns in these areas. The association between undisturbed sites, solitary flowers, and dehiscent fruits with 4–20 seeds suggests low reproductive output, which is consistent with other studies (Matlack, 1994; Dupré and Ehrlén, 2002; Mabry, 2004). However, other traits that have also been associated with low dispersal capacity – lack of vegetative spread, few seeds/fruit, large seeds – were associated with disturbance for at least one of our two study areas. In his model of the response of forest herbaceous species to disturbance, Roberts (2004) points out that propagule availability is one of seven major factors that mediate response to disturbance, and that species will respond very differently to these eight factors depending on their life history traits. Thus, it may not be surprising to observe a lack of consistency in dispersal related traits across floras that include many varying abiotic factors, features of disturbance and species with different constellations of traits.

In contrast, we found a consistent association between habitat generalists and disturbance and habitat specialists with more pristine sites in Iowa and Massachusetts. A small data set of 13 plots from North Carolina allowed us to evaluate whether the same pattern was present in a third North American floristic province, the Appalachian region. This data set consisted of 224 plant species sampled from plots located on four undisturbed, six logged and

three abandoned agricultural sites. Species were classified into habitat characters identically to our other two data sets. A one-way analysis of variance with disturbance type as the grouping factor and habitat specialization as the response variable indicated the same association between disturbance and habitat in this data set. Undisturbed plots had an average of 12.9 species specializing on rich moist sites, while plots on former agricultural land had an average of only 6.8 specialist species. Logged sites were intermediate with 8.8 species (treatment MS = 36.0; $F = 3.8$; $p = 0.06$).

We thus propose that degree of habitat specialization is a promising candidate as a general attribute for predicting plant response to human disturbance. This is especially encouraging given the wide disparity in the details of the past human disturbances experienced in these regions, and suggests that degree of habitat specialization can transcend both differences in floristic composition and site-specific details of the disturbance.

We believe our results are particularly encouraging for managers because in many regions morphological trait data are not readily available, and compiling such data is a very time-intensive task and unlikely to be feasible for most managers to undertake. In contrast, with a list of species and a published flora, upwards of several hundred species can be coded for degree of habitat specialization in a matter of hours, and can then be used by managers, for example, to track the impact of current disturbance, to predict future impacts, and to target specific species for reintroduction or restoration.

The association of habitat specialization with disturbance as a key trait in our comparative study of two regional floras validates the findings of a number of site-specific studies that have found similar patterns, and reinforces the generality of this attribute. In a long-term retrospective study from a forest preserve near the city of Boston, USA, approximately 80 miles east of our Massachusetts study region, species with a habitat preference for rich, mesic forested sites were most likely to be extirpated from areas disturbed by human activity, particularly trails and foot traffic (Drayton and Primack, 1996). In another long-term retrospective study from Wisconsin, a state adjoining our Iowa study region, areas with high deer density experienced significant homogenization of the ground-layer flora, largely because habitat specialist species were replaced by habitat generalists (Rooney et al., 2004).

Similar patterns have also been found in many studies investigating the impact of human activities on European forests. For example, degree of habitat specialization was useful for distinguishing disturbed and undisturbed areas in European forests (Dupré and Ehrlén, 2002; Godefroid and Koedam, 2003; Hérault and Honnay, 2007; Guirado et al., 2006). In an exemplary instance of species' habitat preference driving patterns of response to human disturbance, Dambrine et al. (2007) found a strong positive correlation between proximity to Roman settlements and species richness and frequency of nitrogen demanding species. They concluded that the long time span and relatively limited spatial scale of their study precluded dispersal limitation as an explanation. Rather, it was the effect of fertilization on the mineralization of soil organic matter in their nutrient limited system that explained the increased frequency of nutrient demanding species near past settlements (Dambrine et al., 2007).

In proposing to use degree of habitat specialization as a metric for response to human disturbance, it is important to emphasize that this attribute is not confounded with the very disturbances we are trying to track. Non-degraded native plant communities may be composed of species of both narrow and wide habitat breadth. A good example is the case of native

Midwestern savannas (Brudvig and Mabry, 2008). These woodlands have highly diverse ground-layer floras, including mixtures of xeric and mesic species, in different microsites resulting from variation in light, soil properties and a mixture of areas burned and protected from fire (Bray, 1960; Leach and Givnish, 1999).

Our findings do not negate the results of single-site studies, but suggest that to scale up or extrapolate regionally it may be important to look at more integrative plant attributes. Habitat specialization may have emerged as a consistent trait in our study because it synthesizes physiological and morphological traits that fail to reveal meaningful patterns when treated individually. For example, we found that ant seed dispersal was associated with undisturbed sites in Iowa, while low vegetation spread was associated with undisturbed sites in Massachusetts. Other site-specific studies have linked both traits with less disturbed areas (Grime, 1979; Matlack, 1994; Mabry, 2002). However, we would not have found a consistent pattern between our two regions had we not grouped species by habitat specificity: 12 of 16 (75%) of ant dispersed species in Iowa were mesic habitat specialists, and 44 of 68 (65%) of species with low vegetative spread in Massachusetts were mesic habitat specialists. Similarly, degree of patch isolation due to disturbance had a greater negative effect on forests specialist vs. generalist species in Sweden, possibly because these species also tended to exhibit similar morphological traits, i.e., colonial perennials that produce few seeds (Dupré and Ehrlén, 2002).

Despite our conclusions about the value of a more synthetic trait for comparative studies, we recognize that site-specific studies focused on understanding the relationship of specific mechanistic traits to disturbance have often helped pinpoint specific mechanisms of change (Dzwonko and Loster, 1992; Matlack, 1994; Graae and Sunde, 2000; Kirkman et al., 2004; Mayfield et al., 2006). In contrast, habitat traits may not necessarily reveal such mechanisms, but only patterns of change. We believe the two approaches have different but complementary aims: one to identify site-specific mechanisms of change, the second to track and predict change over broad spatial scales and floristically dissimilar floras.

Taking into account phylogenetic relationships among species may increase our chances of finding mechanistic traits that are generalizable across floras (Herrera, 1992). For example, a study in Iowa using taxonomically paired species showed that less common species had larger seeds than closely related common species (Mabry, 2004). However, without the paired design that allowed species' relatedness to be factored out, these patterns would not have been evident. For instance, if an uncommon *Viola* was compared to a common and much larger seeded *Podophyllum*, the relationship between seed size and abundance would be obscured because species in the Berberidaceae have larger seeds than species in the Violaceae. Comparative analyses often do not reveal this type of distinction unless the additional step is taken to include phylogeny. However, these analyses are unlikely to be feasible for managers because they require substantial training to conduct and interpret and are time consuming to perform.

Despite the evidence for a direct legacy of disturbance found on axis 2 in both data sets, it is important to note that much of the variation in the trait data was associated with abiotic variables on axis 1. Human disturbances have a well-documented impact on many of the variables associated with axis 1, including bulk density, pH and organic matter (Compton and Boone, 2000; Fraterrigo et al., 2005). This raises the possibility that there is a more complex soil–human disturbance interaction occurring along this axis. The original Iowa and Massachusetts

studies were not designed to address the impact of disturbance on soil properties and the possibility that there are trait-disturbance associations mediated by soils is worthy of further investigation.

6. Conclusion

Our results suggest that the degree of habitat specialization is a good candidate for a simple metric to track the impact of past and ongoing human disturbance and as a general predictor of change in response to future human disturbance. We have confidence in our results because potential confounding factors were controlled by our use of an identical trait classification scheme and analytical methods in the comparison, and because our comparative approach validated the results of

site-specific studies from both the United States and Europe. We believe our results can be readily applied by managers because habitat specialization is a relatively quick and simple way to classify plant species. It therefore has the potential to identify groups of species most likely to decline as human disturbances intensify and to target species for conservation and restoration.

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Appendix A

Canopy trees, herbaceous species and shrubs with the highest frequency of occurrence in two eastern United States deciduous forest data sets. No. = frequency of occurrence out of 103 plots in central Iowa and 76 plots in Massachusetts.

Central Iowa				Massachusetts			
Latin name	Common name	Family	No.	Latin name	Common name	Family	No.
Canopy trees				Canopy trees			
<i>Acer nigrum</i>	Black maple	Aceraceae	41	<i>Acer rubrum</i>	Red maple	Aceraceae	76
<i>Carya cordiformis</i>	Bitternut hickory	Juglandaceae	41	<i>Betula alleghaniensis</i>	Yellow birch	Betulaceae	41
<i>Carya ovata</i>	Shagbark hickory	Juglandaceae	72	<i>Betula lenta</i>	Black birch	Betulaceae	49
<i>Celtis occidentalis</i>	Hackberry	Ulmaceae	57	<i>Castanea dentata</i>	American chestnut	Fagaceae	37
<i>Ostrya virginiana</i>	Ironwood	Betulaceae	74	<i>Pinus strobus</i>	White pine	Pinaceae	71
<i>Quercus alba</i>	White oak	Fagaceae	59	<i>Prunus serotina</i>	Black cherry	Rosaceae	49
<i>Quercus rubra</i>	Red oak	Fagaceae	50	<i>Quercus alba</i>	White oak	Fagaceae	47
<i>Tilia americana</i>	Basswood	Tiliaceae	67	<i>Quercus rubra</i>	Red oak	Fagaceae	72
<i>Ulmus americana</i>	American elm	Ulmaceae	76	<i>Quercus velutina</i>	Black oak	Fagaceae	35
<i>Ulmus rubra</i>	Slippery elm	Ulmaceae	60	<i>Tsuga canadensis</i>	Eastern hemlock	Pinaceae	63
Herbaceous species				Herbaceous species			
<i>Carex blanda</i>	Eastern woodland sedge	Cyperaceae	93	<i>Aralia nudicaulis</i>	Wild sarsaparilla	Araliaceae	64
<i>Carex radiata</i>	Eastern star sedge	Cyperaceae	78	<i>Brachyelytrum erectum</i>	Bearded shorthusk	Poaceae	28
<i>Circaea lutetiana</i>	Enchanter's nightshade	Onagraceae	92	<i>Carex pensylvanica</i>	Pennsylvania sedge	Cyperaceae	36
<i>Claytonia virginica</i>	Spring beauty	Portulacaceae	70	<i>Clintonia borealis</i>	Blue bead lily	Liliaceae	31
<i>Cryptotaenia canadensis</i>	Honewort	Apiaceae	68	<i>Coptis trifolia</i>	Goldthread	Ranunculaceae	32
<i>Desmodium glutinosum</i>	Cluster leaf tick trefoil	Fabaceae	72	<i>Dennstaedtia punctilobula</i>	Hayscented fern	Dennstaedtiaceae	55
<i>Dicentra cucullaria</i>	Dutchman's breeches	Fumariaceae	80	<i>Dryopteris intermedia</i>	Intermediate fern	Dryopteridaceae	38
<i>Erythronium albidum</i>	White trout lily	Liliaceae	69	<i>Eurybia divaricata</i> ^a	White wood aster	Asteraceae	27
<i>Festuca subverticillata</i>	Nodding fescue	Poaceae	87	<i>Gaultheria procumbens</i>	Wintergreen	Ericaceae	51
<i>Galium aparine</i>	Cleavers	Rubiaceae	93	<i>Lycopodium clavatum</i>	Running clubmoss	Lycopodiaceae	24
<i>Galium concinnum</i>	Shining bedstraw	Rubiaceae	80	<i>Lycopodium dendroideum</i>	Tree groundpine	Lycopodiaceae	58
<i>Geum Canadensis</i>	White avens	Rosaceae	90	<i>Maianthemum canadense</i>	Canada mayflower	Liliaceae	67
<i>Osmorhiza claytonii</i>	Bland sweet cicely	Apiaceae	67	<i>Medeola virginiana</i>	Indian cucumber	Liliaceae	57
<i>Phlox divaricata</i>	Forest phlox	Polemoniaceae	72	<i>Mitchella repens</i>	Partridgeberry	Rubiaceae	72
<i>Phryma leptostachya</i>	Lopseed	Verbenaceae	87	<i>Monotropa uniflora</i>	Indianpipe	Monotropaceae	59
<i>Polygonatum biflorum</i>	Solomon's seal	Liliaceae	81	<i>Osmunda cinnamomea</i>	Cinnamon fern	Osmundaceae	44
<i>Ranunculus abortivus</i>	Small-flowered crowfoot	Ranunculaceae	90	<i>Pteridium aquilinum</i>	Brackenfern	Dennstaedtiaceae	36
<i>Sanicula odorata</i>	Cluster-sanicle	Apiaceae	99	<i>Thelypteris noveboracensis</i>	New York fern	Thelypteridaceae	43
<i>Viola pubescens</i>	Yellow forest violet	Violaceae	77	<i>Trientalis borealis</i>	Star flower	Primulaceae	72
<i>Viola sororia</i>	Dooryard violet	Violaceae	98	<i>Uvularia sessilifolia</i>	Sessileleaf bellwort	Liliaceae	53
Shrubs				Shrubs			
<i>Parthenocissus quinquefolia</i>	Virginia creeper	Vitaceae	102	<i>Amelanchier</i> sp.	Serviceberry	Rosaceae	43
<i>Ribes missouriense</i>	Gooseberry	Grossulariaceae	98	<i>Vaccinium angustifolium</i>	Low bush blueberry	Ericaceae	60
<i>Smilax tamnoides</i>	Bristly greenbrier	Smilacaceae	92	<i>Vaccinium corymbosum</i>	Highbush blueberry	Ericaceae	49
<i>Toxicodendron radicans</i>	Poison ivy	Anacardiaceae	79	<i>Viburnum nudum</i>	Possumhaw	Caprifoliaceae	53

^a Formerly *Aster divaricata*.

References

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