Evidence for Flower Mediated Assembly in Spring Ephemeral Understory Communities

by

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ABSTRACT

EVIDENCE FOR POLLINATOR MEDIATED ASSEMBLY IN SPRING EPHEMERAL UNDERSTORY COMMUNITIES

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Plants with similar traits compete for resources. If related taxa share similar traits, phylogenetic relationships may predict competitive outcomes. Although plants compete for pollinators, flowers are rarely considered in community-assembly theory. I tested the hypothesis that plant communities are structured by competition for pollination. I inventoried communities at three spatial scales, measured seven flower traits, and tested the observed patterns against those generated by a null model to judge if community members were more or less similar in floral traits than expected by chance. I also measured the phylogenetic relatedness of community members to gauge trait-conservatism. Clustering of visually attractive traits suggests they promote facilitation of pollinators while over-dispersion of morphological traits suggests they partition pollinators in to avoid competition. Communities were phylogenetically even, but relatedness did not explain floral trait patterns. I suggest that flowers represent an ecological niche through which species can be sorted.

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CONTENTS

INTRODUCTION

Community ecology strives to discover general principles that explain patterns of biodiversity in the landscape, but few studies have been able to demonstrate that differences in ecological strategies among species influence coexistence patterns in communities (Gill *et al.* 2006). Although leaf and root traits, which impact the acquisition of limiting abiotic resources such as light and water, can structure plant communities (Tilman 1994, Cavender-Bares 2006), there is little precedent for considering flowers in this way (Sargent & Ackerly 2008). The persistence of many plant species depends on their ability to attract adequate pollination services from animal vectors (Harder & Aizen 2010) through their flowers. Communities of plant species can be linked in a network through their shared pollinators (Strauss & Irwin 2004, Lundgren & Olesen 2005, Oleasen *et al.* 2006), but the role that pollinator attraction plays in the assembly of these communities remains understudied (Heithaus 1974, Feinsinger 1987, Bosch *et al*. 1997, Moeller 2004, Sargent & Ackerly 2008, McEwan & Vamosi 2010).

The traits of a flower illustrate the ecological strategy, or pollination niche in which a plant has become evolutionary specialized in. Plants have evolved different visual cues, morphologies and scents to attract and guide effective pollinators to their flowers (Grant 1994, Caruso 2000, Harder & Johnson 2009). Though no species have identical flowers, unrelated taxa, with historically dissimilar traits, can converge on analogous floral phenotypes to specialize on the same subset of the pollinator community (Fenster *et al.* 2004). If pollinator-mediated selection can drive speciation of plants into a pollination niches (Johnson 2010) and plants share generalist pollinators (Ollerton 1996, Waser *et al*. 1996), we should see evidence of those niches within plant communities as well (Gould 2002, Lazaro *et al*. 2008).

Competition may exclude species that share pollinators from coexisting, but facilitation may draw them together into a community. Plants compete for pollination resources through two mechanisms, interference and exploitation. Interference competition occurs when pollinators deposit heterospecific pollen on the stigmas of neighbouring plants, reducing the receptivity of the stigmas to conspecific pollen (Zimmerman 1980). Exploitation occurs when superior floral competitors draw pollinators away from co-occurring species with attractive displays. However, highly attractive species can act either as a ‘magnet’ in the community, reducing the pollination success of neighbours (Laverty 1992), or as a ‘cornucopian’ species, facilitating pollination for less attractive community members that are present (Mosquin 1971). Facilitation occurs when at least one species attracts more pollinators and achieves higher fitness when co-flowering with plants that share pollinators than when flowering alone (Moeller 2004, Ghazoul 2006). Competition tends to structure communities of species with less similar traits than expected by

chance (trait evenness). Facilitation assembles species with more similar traits than expected by chance (trait clustering).

By studying trait patterns among co-existing species we can identify the ecological mechanisms most influential to the assembly of that community. Environmental filtering sorts the regional species pool into communities of taxa with similar traits that allow them to thrive in their shared habitat and climate (Kraft & Ackerly 2010). Environmental filtering may sort species in and out of broad-scale communities, such as regional species pools, or habitats. Patterns of traits associated with environmental gradients may only be observed if the community is considered from a site-level perspective. Within an environment, at smaller spatial scales, competitive interactions can cause predictable community structure as well by excluding species with similar traits (Gause 1932, Diamond 1975, Tilman 1994, Tilman *et al*. 1997). Plants typically interact over short distances for resources, so competition may only be important in understanding fine-scale patterns of community composition. Therefore, traits associated with resource acquisition may only be important in understanding local scale patterns of diversity and abundance. These two mechanisms, competition and environmental sorting, can operate simultaneously at different scales (Gilbert & Lechowicz 2004), or on different subsets of the community (Bell 2001, Holyoak & Loreau 2006, Kembel 2009). Because pollinators are motile, plants may compete for these resources across larger distances than they would for abiotic resources (Chittka *et al*. 1999, Zurbuchen *et al*. 2010). Therefore, interactions mediated by floral traits may be as equally important as environmental filtering at larger scales in some plant communities (Cavender-Bares *et al*. 2006, Swenson *et al*. 2006, Kembel & Hubbell 2006). Because co-flowering plants can also locally compete and facilitate each other's pollination, floral traits may be important in community assembly at smaller scales as well.

The extent to which competition or facilitation occurs between species may be influenced by their phylogenetic relationships (Webb *et al.* 2002, Ackerly 2003, Vamosi *et al.* 2009). Because species share a common ancestry, traits are typically conserved among close relatives, and relatedness may be used to represent ecological similarity (Prinzing *et al*. 2001, Webb *et al*. 2002, Kembel & Hubbell 2006, Vamosi *et al*. 2009). However, traits may also converge among distant relatives, or be randomly distributed among related taxa (Ackerly *et al.* 2006, Cavender-Bares *et al.* 2006). The phylogenetic distribution of these traits will dictate which species get filtered into a community by the environment, or competitively excluded from the community by species with similar traits (Lovette & Hochachka 2006, Cavender-Bares *et al*. 2009). If traits are conserved among closely related species, then competition will likely produce a community of

more distantly related, and therefore more functionally dissimilar species. If facilitation is occurring and traits are conserved, communities will be composed of close relatives.

Using a community of early blooming wild-flowers native to eastern North America, I tested the hypothesis that traits used to attract pollinators are ecological niches through which plant species can be assembled into communities (Strauss & Irwin 2004, Sargent & Ackerly 2008). Spring ephemerals are an ideal community to investigate pollinator-mediated community assembly for two reasons. First, pollination may be a limiting stage in the life cycle of these plants, and so the influence of pollination on community structure may be more pronounced. In flowering early they risk freezing temperatures that can damage flowers and prevent pollinators from foraging. The flowers of many species are also short-lived, and may not coincide with ideal weather for pollination; in some years the earliest species may bloom for less than a week and individuals may only bloom for one day (Schemske *et al.* 1978). Second, because spring ephemerals are generalists (Schemske *et al.* 1978, Motten 1986) there is potential for them to share pollinator resources. This increases the likelihood that spring ephemeral communities interact with each other through either competition for or facilitation of pollination.

I inventoried plant communities at three spatial scales and compared levels of trait similarity among sets of observed co-occurring species with randomly constructed null communities. The objectives of this study were to (1) identify floral traits that are significantly more or less similar among species that co-occur; (2) measure the evolutionary relatedness of community members along with the level of floral-trait conservation among them; (3) determine if evenness of floral traits in a community suggests that competition for pollination is important for driving community assembly or if trait clustering suggests that facilitation of pollination is structuring the community.

METHODS

Study System

This study focused on spring ephemerals plant, an assemblage of early flowering woodland forbs, native to the forests in Eastern North America (Table 1). All species in this assemblage have a relatively brief flowering season, relying on a narrow window of pollinator availability in the spring for sexual reproduction. Except for hummingbird-pollinated *Aquilegia canadensis*, all species are insect-pollinated and offer either pollen or nectar as a reward. All spring ephemerals except *Dicentra canadensis* and *D. cucullari* are self-compatible. Some of the earliest flowering species like *Sanguinaria canadensis* and *Thalictrum thalictorides* are facultatively autogamous (Voss 1972, Schemske *et al.* 1978, Motten 1986, Whigham 2004).

To ensure that I was focusing on an assemblage of species that share resources, I defined the spring ephemeral community using three criteria. First, all species were herbaceous vascular angiosperms. Some early blooming trees and shrubs may share pollinators with spring ephemerals (e.g. *Cornus florida, Lindera bezoin*) but are not considered part of this community because they acquire resources and reproduce at different spatial and temporal scales than understory forbs. Second, all species are native to Eastern North America (Voss 1972) and grow in forests throughout the Carolinian Life Zone (Theberge 1989) of south-western Ontario and eastern Michigan. Carolinian forests are characterized by mesic maple-beech forests or oak savannah, with some influence of conifers such as white pine (*Pinus strobus*) and hemlock (*Tsuga canadensis*). Third, all species begin to flower sometime between the first frost free periods in late March and canopy closure in the first week of May (Schemske *et al.* 1978).

Community Measurements

I recorded the composition of spring ephemeral communities that occur in forests across south-western Ontario. Differences in species co-occurrence were noted between three different spatial scales: plots within transects, transects within sites, and whole sites. Species that co-occurred in replicates of each scale were considered members of the same community. At six forest sites I inventoried co-occurring species in transects composed of plots to measure medium and small-scale community composition (Table 2). These forest sites were spread across my study region to ensure the northern Lake Erie watershed was equally represented. They range in size from the 22 hectare southern forest Point Pelee, to Backus Woods which spanned 232 hectares (Table 2). These sites are some of the largest native hardwood forests in the region. Though all sites contain hiking trails, the understories were free from heavy recreational disturbance. The forests chosen were minimally invaded by exotic understory plants but *Alliaria petiolata*, *Chelidonium majus*, and *Taraxacum officianle* were frequent in disturbed areas along the path and site edges. Data collection was conducted between March 26th and May 13th 2010.

At each site I set up thirteen 60m transects through the understory. I placed transects to target the patchy distribution of spring ephemeral communities in the landscape. Transect locations selected had more than four focal species present, and were oriented to avoid stands of water, fallen trees, or trails. Transects varied in distance from each other across sites, but never overlapped. Each transect contained 30 2 × 2 m plots placed end to end in a line that ran through the centre of a patch of ephemerals. Because some transects were placed within a 60 m radius of each other, not all plots within the same transect are more similar to each other than they are to plots of a neighbouring transects. Therefore, transects may not serve as an appropriate block, and

in our analysis we assumed that plots within transects were independent of each other. If this assumption is incorrect, then our Type I error rate will be inflated. In each plot I recorded the presence of co-occurring spring ephemeral species as a measure of small-scale community composition, (n=2340). I measured medium-scale community composition by compiling a list of all species from plots within each transect (n=78).

To increase my replication at the site scale, I recorded the presence of my focal species at 86 additional forest sites in the Carolinian Life Zone from previously conducted inventories (Table 1). Sites varied in size, but each forest constituted an individual stand, often fragmented by human land use, and therefore independent. The sites chosen for this purpose were composed primarily of hardwood forest. All sites were located within or near the northern Lake Erie watershed. Most sites are privately owned woodlots, managed and inventoried by local conservation authorities; the rest are public conservation areas or parks. Both primary and secondary forest sites were included in the study, and diversity ranged from 6 to 48 focal species. Surveys were obtained from the Ontario Ministry of Natural Resources, the Thames Valley Conservation Authority, the Michigan Natural Features Inventory, and also from herbaria at the University of Guelph, the University of Western Ontario, and the Royal Ontario Museum.

Floral-Trait Measurements

I measured seven traits to characterize the flowers of community members. Three of these traits describe floral morphology, three describe flower colour, and one describes flowering phenology. Depending on the rarity of the species being collected, 1-12 flowers were harvested from natural populations for measurements of morphology and colour (Figure 1). The majority of flowers were sampled at sites where transect inventories were conducted, but flowers of uncommon species were harvested from conservation areas at the Royal Botanical Gardens in Burlington Ontario. Prior to measurement, samples were stored in plastic vials and placed on ice.

Flower orientation was measured for each sample before it was harvested for further trait measurements. Because the angle that an insect approaches a flower differs among species and functional groups (Ushimaru & Hyodo 2005, Sargent & Vamosi 2008), flower orientation may dictate which pollinators are most likely to visit (Ushimaru & Hyodo 2005). Orientation was measured as the angle between the centre of the flower's receptacle and a vertical line, often represented by the flower spike or plant stem (Figure 1c). I used a small level to determine the vertical plane and a protractor to estimate the orientation angle to the nearest five degrees.

After harvesting I measured the restriction of each flower as the angle between opposing sides of the perianth. Highly restrictive flowers may allow pollinators with specialized foraging

behaviours or mouthparts to access floral rewards (Wissel *et al.* 1977, Fenster *et al.* 2004). For species with modified nectar spurs such as *Aquilegia canadensis, Viola rostrata* and *Phlox divaricata,* restriction was measured as the angle of the tube opening. For simple flowers, restriction was measured from the angle between opposite sides of the corolla. Restriction for *Arisaema triphylum* was measured using the angle between the top and bottom lips of the spathe (Figure 1d). The restriction angle was measured using a protractor, rounded to the nearest five degrees, and averaged among species with more than one flower sample.

I estimated flower size by measuring the mass of each species' flower because it is a consistent way to represent flower size across unrelated taxa with varying flower morphologies and levels of generalisation (Fenster *et al.* 2004). Samples used for the traits above were trimmed to include only sepals, petals and reproductive organs and were dried at 55^{o}C for three days. For *Arisaema triphylum*, samples were trimmed to include the spathe and spadix only because the spathe-spadix complex is an individual display analogous to solitary flowers. The dry mass was averaged for each species and used to estimate flower size. Like restriction and orientation, flower size may indicate the species or functional group of insects that are prime pollinators (Ishii 2006). Large bodied pollinators, for example, will prefer flowers large enough to support their weight and act as a landing pad.

To avoid assigning colour values subjectively (Arnold *et al.* 2009), I quantified colour using light reflectance spectra, measured with an Ocean Optics spectrometer (Dunedin, Florida, USA). Measurements were taken from the inner surface of one petal from each sample for most species, and the inside top of the spathe for *Arisaema triphyllum*. Colour was quantified from spectral readings as the percent reflectance of each wavelength between 250nm (ultra-violet) and 700nm (red). Values ranged from 0, for wavelengths that had 0% reflectance, to 1, for those wavelengths that had 100% reflectance. The output was averaged every 3 nm into a series of 127 bins (Grill & Rush 2000) to reduce the amount of reflectance data used in later analyses. Reflectance values were averaged for each species. Variation in reflectance was greater between species than within species (data not shown).

I used principal component analysis (PCA) to reduce the highly correlated and multivariate data of each reflectance curve into a small set of uncorrelated variables that can account for significant portions of the total variation in the reflectance data (Grill & Rush 2000). The first PC described brightness, the variation in reflectance magnitude of all wavelengths between 400 and 700 nm, accounting for 57% of the variation in reflectance data (Figure 1g). Positive loadings for PC1 indicate high brightness. Bright colours reflect all wavelengths at a greater intensity than dull colours, regardless of the shape of the reflectance curve over the entire

spectrum (Grill & Rush 2000). Brighter flowers may be more visible in a partially shaded understory habitat (Mulligan *et al.* 1973). The second PC described the variation in reflectance of all wavelengths between 250 and 400 nm, which is the ultraviolet component of each colour (Figure 1f). This PC explained 23% of the total variation in color data. Positive loadings for PC2 indicate high ultra-violet reflectance. UV may be an important part of a plant's ability to attract pollinators as many insects can see wavelengths shorter then 400nm (Jones & Buchmann 1974). The third PC described the variation in the ratio of high to low wavelengths between 400 and 700 nm, and represents the component of hue in each color (Figure 1e; Grill & Rush 2000). In this case, hue describes the broad difference between the size of wavelengths, such as between violet and yellow. Species with high positive loadings for PC3 have red, pink or purple flowers, and species with high negative loadings have yellowish or greenish hued flowers. Hue is an important signal to pollinators in communities that are diverse in floral color traits (Gumbert *et al*. 1999).

Because species with overlapping flowering phenologies are less likely to co-exist in a community if they compete (Levin 1971, Gleeson 1981), I measured how synchronously community members flower (Figure 1a). I gathered flowering dates from voucher specimens in herbaria at the Royal Botanical Gardens (HAM), University of Western Ontario (UWO), Royal Ontario Museum (TRT) and the Canadian National Herbarium (CAN). Because plants are often collected when in flower, the recorded dates of herbarium specimens can be used to estimate flowering season of each species (Primack *et al.* 2004). In each collection, I chose specimens that were collected in my study region. *Corydalis flavula* was the one exception; I used four specimens from Ohio to serve as replicates for this rare species which was represented only twice in the herbaria I visited. Rare species were generally underrepresented in this way. My method also over-represents those species found in frequently inventoried and well-studied, often public sites. All specimens used were confirmed to be in flower on the collection date by examining the specimen and noting freshly pressed reproductive organs.

I used the range between first and last flowering date of each species to calculate how synchronously they bloom with the rest of the community. Un-ranked synchrony values, S_i , for each species i, were calculated using the following equation adapted from Augspurger (1983):

$$S_i = \left(\frac{1}{n-1}\right)\left(\frac{1}{f_i}\right)\sum_{j=1}^{n} e_{j\neq i}$$

Where e_j is the number of days both species i and j are flowering synchronously. The total number of days each species flowers, f_i , was estimated by taking the difference between the

earliest and latest recorded calendar date of flowering. Here *n* equals 52 or the total number of species in the study.

I used the average calendar date that each species flowered to rank synchrony values as either earlier or later than the total average flowering date for all species. Synchrony values for species flowering earlier than the average date were standardized as 1-S, whereas species flowering later than the average were given a final synchrony value equal to *S*. Species that flowered earliest and for the shortest amount of time such as *Sanguinaria canadensis* had small negative values (-0.6), while late and briefly blooming species like *Medeola virginica* had large positive values (+0.6). Species like *Polygonatum pubescens* and *Cardamine diphyla* with slightly positive and slightly negative synchrony values can co-flower with most other species, but only slightly after or slightly before the community average flowering date.

Community Structure Analysis

In order to assess the role of floral traits in assembly I quantified the similarity of flowers among species co-occurring in a community. The level of trait similarity among coexisting plants, can be considered a community wide trend towards a particular floral strategy, or phenotype, and this similarity is described as the phenotypic structure of that community. To do this I calculated the variance in floral traits among species in each community using the *comtrait* function in Phylocom-4.1 (Webb & Donoghue 2005, Webb *et al*. 2008). This function calculated a Standardized Effect Size (SES) in units of standard deviation to express how similar co-occurring species are in their floral traits. These values represent the likelihood that each community would assemble at random with their observed set of traits. To do this Phylocom compares the variance in trait values of each observed community to those of 1000 randomly generated null communities. Individual communities with positive SES values were considered phenotypically even or less similar in a particular floral trait than expected by chance alone. Communities with negative SES values were considered to be phenotypically clustered, or more significantly similar in a floral trait than expected by chance (Webb *et al.* 2008). Standard Effect Sizes were generated for every individual plot, transect and site.

To analyze the phenotypic structure across all replicates within a site, and at each of three scales, I tested the significance of the average SES for each trait at every site and scale combination. Average SES scores were compared to a null expectation of zero using a one-sample t-test. Significantly clustered communities suggest that facilitation for pollinators influences co-occurrence patterns, whereas communities that are significantly even in a particular trait may indicate that competition for pollinations is more important (Feldman 2004, Sargent &

Ackerly 2008). For those sites and scales with inconsistent direction or magnitude of phenotypic structure, I used a Fisher's Exact test to combine the *P* values of the independent *t*-tests and check for their overall significance.

To analyze the phenotypic structure of individual replicate plots and transects, I used the rankHi value calculated by phylocom to estimate how similar the trait variances in observed communities were to the distribution of 1000 null communities. Observed variances that fall within the top or bottom 0.25% of the 1000 null variances show significant phenotypic structuring, and correspond to the SES values used to gauge site-wide averages in trait variances. Communities with variances that ranked highest fewer than 25 times were considered significantly clustered phenotypically, while those thank ranked highest 975 times or more were considered even. Finally, the ratio of significant to non-significant replicates at each site and scale were calculated.

Because the evolutionary relationship between species may influence the level of trait similarity between them (Losos 2008, Cavender-Bares *et al.* 2009, Vamosi *et al.* 2009), I measured how related co-occurring species are on average by calculating the phylogenetic distance between. Evolutionary relatedness of two species is measured as the amount of time since they diverged from a common ancestor, and the average level of relatedness in a whole community describes the phylogenetic structure of that particular community. Species that diverged more recently are likely to share more ecological characters than distant relatives (Losos 2008). The phylogenetic tree structure and major node ages for the specie sin my community were derived from a comprehensive family level angiosperm phylogeny (Davies *et al.* 2004), and pruned to include the relevant families. Within family relationships were resolved using additional studies (Hoot & Crane 1995, Ballard *et al.* 1998, Patterson & Givnish 2002). The phylogeny used for this analysis was constructed in Mesquite2.71 (Maddison & Maddison 2004).

To estimate evolutionary relatedness between community members, I used the *comstruct* function on Phylocom-4.1 that calculated a Nearest Taxon Index for every plot, transect and site. The NTI is the average phylogenetic distance between all species in a community and their closest relative that co-occurs in that community. The patterns of average relatedness in a community describe its phylogenetic structure. Communities that are significantly phylogenetically even, or less related than expected by chance, have NTI values less than -1.96. Communities that are phylogenetically clustered have NTI values greater than +1.96 (Webb *et al.* 2002). I compared the average NTI of all replicates at each site and scale to the null expectation of zero using a series of one-sample *t*-tests. The average NTI among both plots and transects at each site was tested for significant phylogenetic strucutre at small and medium scales. The

average site NTI was used to gauge the phylogenetic structure for large scale-community compositions. For those sites and scales with inconsistent direction or magnitude of phylogenetic structure I used a Fisher's Exact test to combine the *P*-values of the independent *t*-tests, in order to detect a general trend towards phylogenetic structure.

To analyze the significant phylogenetic structure of individual replicates of plots, transects and sites, I used the rankHi values calculated by phylocom. Similar to the trait analysis above, the observed mean distances between nearest taxa that fall within the top or bottom 0.25% of the 1000 null mean distances show significant phenotypic structuring. Communities that ranked highest fewer than 25 times were considered significantly even, while those thank ranked highest 975 times or more were considered significantly clustered. The ratio of significant to non-significant replicates at each site and scale were also calculated.

NTI values were also used to test the influence of niche conservatism on the level of similarity among community members. For example, floral trait patterns in phylogenetically structured communities may be driven by physiological-trait interactions if both floral and physiological traits are conserved (Cavender-Bares *et al*. 2006, Kraft *et al*. 2007). To test for this possibility, I performed a Pearson correlation between the SES and NTI values of each site and scale to test if trait similarity and phylogenetic relatedness were correlated. A positive correlation between these values would suggest that related taxa have widely diverged floral traits (Losos 2008). I also calculated the level of conservation directly for each floral trait using the *aotf* function on Phylocom-4.1. If the evolutionary history is important for trait patterns within the community, both tests should indicate the same level of trait conservatism. To judge if any of the floral traits investigated co-vary with each other in this community, I performed a Pearson correlation between the trait values as well.

I reported the results generated from two different null models of community assembly: Model 1 and Model 2. To calculate both the SES and NTI values, Phylocom employs a set of null models to construct randomly assembled communities for comparison with observed communities (Kembel & Hubbell 2006, Webb *et al.* 2008). For each replicate community, both models construct a series of 1000 null communities, comprised of the same number of species in the observed community, and drawn from the species pool at random, without replacement. Model 1 generates null communities from a restricted local pool (forest site), and so serves as a more conservative version of neutral assembly, as it recognizes the spatial limitations of species' dispersal in the landscape (Hardy 2008). Model 2 draws species at random from the entire regional pool, which makes up all the species in the constructed phylogeny, and also the combination of all large scale site inventories. In this way it can be considered a more liberal

model of null community assembly (Hardy 2008), assuming that all species in the entire regional pool can disperse to a given community.

RESULTS

Though all species share the same habitat and bloom in early spring, they vary considerably in their floral traits, the most variable of which may explain coexistence patterns (Figure 1). Flowering synchrony was highly variable (CV=7.8). Some species flowered synchronously with the rest of the community, but not all species overlapped. Asynchronous blooming periods are found throughout the flowering season, both early and late (Figure 1a). Flower size was also considerably variable (Figure 1b; CV=1.85). Flowers ranged in orientation, but faced upward on average at 99^{o} (CV=0.60). About one third of the community is each oriented either downward ($\sim 0^{o}$), upward ($\sim 180^{o}$), or sideways ($\sim 90^{o}$). Most spring ephemerals are unrestrictive, with flowers held open on average at 113^{o} (CV=0.63), but several species have tightly restrictive tubular or bilabate flowers. Species have flowers of different colours, but most were white, yellow, or pink, and sometimes purple, maroon, brown and red. However, few species reflect ultra violet wavelengths, and most that do, like *Viola pubescens* and *Ranunculus hispidus*, have bright yellow flowers.

Few traits within species were correlated with one another. Flower restriction however was correlated with hue (r=-0.3486, P<0.01) and orientation (r=-0.6784, P<0.01), showing that restrictive flowers are usually red, orange or pink in colour, and that the most restrictive plants tend to orient downwards on average. Flower orientation was further correlated with flower brightness (r=-0.3384, P<0.02) and mass (r=-0.3106, P<0.05).

Trait Patterns

Communities were composed of species that had a significantly wider range of flower sizes than would be expected by chance (Figure 2a). Except for small-scale communities at one site (PP) the majority of plots were composed of species with dissimilar flower sizes. At the plot-scale, communities from three sites (BW, RR, HH) had species with significantly less similar flower sizes that either null model predicted. Two sites (SH, AP) were even in flower size within plots under the more liberal Model 2 only. At the transect level, three sites (SH, RR, HH) were significantly even under both models. Transects in the remaining three sites (BW, PP, AP) were dissimilar in flower mass only compared to Model 2. At the largest scale, species that co-occur within the same site also had a larger range of flower sizes than would be expected by either null model.

At all three spatial scales, community members flowered more synchronously, and had more similar flower hues than expected by chance (Figure 2b-c). Species that co-occurred within plots flowered significantly more synchronously regardless of site or model. All but one site (PP) had plot-level communities composed of species with more similarly hued flowers than expected by either model. Species coexisting within transects also flowered more synchronously than either model would expect at four sites (BW, PP, HH, AP). Three sites had assemblages of species with similar flower hues in transects under both models (BW, RR, AP) and two more had significantly clustered flower hues under model 2 only (SH, HH). Furthermore, at the largest scale, both models found that species co-occurring in the same forest bloom at a more similar time and duration than would be expected by chance. Species co-occurring in the same site were also more similar in their flower hues than expected by chance.

Community members were more similar than expected in their degree of flower brightness. Model 2 considers plot-sized communities to be significantly clustered for brightness at five sites (BW, SH, PP, HH, AP). Model 1 detects clustering at three of these same sites (SH, PP, AP), but considers the sixth (RR) to be even. Transect-scale communities showed significant patterns of floral traits under both models (Fisher's Combined, Model 1: X^2 =33.19, P=0.0009; Model 2: X^2 =23.84, P=0.0215), although the direction shifts from clustering to evenness at different sites. At the largest scale, species co-occurring in the same site have similar levels of flower brightness as well (Figure 2e).

I found a significant, though site dependant, pattern of similarity in flower orientation and restriction among spring ephemerals that co-occur. Plot-scale communities at only two sites are clustered in flower orientation, while four are significantly even (Figure 2f). I detected significant pattern of similarity in restriction among species that coexist within plots across all sites (Fisher's Combined, Model 1: X^2 =51.78, P<0.0001; Model 2: X^2 =41.51, P<0.0001), though the direction and magnitude is site specific. Transect scale communities were significantly more or less similar than expected in flower orientation (Fisher's Combined, Model 1: X^2 =28.73, P=0.0043; Model 2: X^2 =31.66, P=0.0016), the direction of significance changing from clustering to evenness at different forest sites. Transect-scale communities across all sites showed significant patterns of restriction under Model 2 only (Fisher's Combined, Model 1: X^2 =16.88, P=0.1542; Model 2: X^2 =50.17, P<0.0001). At the largest scale, communities are significantly more clustered in flower orientation and restriction than predicted by either model (Figure 2g).

Ultraviolet reflectance demonstrated the least consistent pattern of similarity among community members across sites, scales and models. (Figure 2d). At the smallest scale, communities at all sites are either significantly clustered or even according to both models at four

sites(RR, PP, HH, AP) and one model at two (BW, SH). However, the direction of similarity changes between models at one site (HH). Transect-scale communities also showed a general pattern of similarity in this floral trait, though the direction is less consistent among sites than plot sized communities (Fisher's Combined, Model 1: X^2 =38.41, p<0.0001; Model 2: X^2 =31.85, p=0.0015). UV was the only floral trait that we did not detect any pattern for at the largest spatial scale.

When individual communities are considered on their own, only a small fraction of all replicates are significant. However, many of these significant trait patterns are in the same direction and are consistent with the results of average trait patterns across replicates at each study site. Surprisingly, some traits that do not have clear or consistent patterns on average across all replicates, have the most significant patterns within individual plot sized communities (Table 3a).

At the plot scale, most sites have more than twice as many communities that are significantly clustered in flowering synchrony than significantly even, which is consistent with the results above indicating the average plot is significantly clustered in synchrony (Table 3a. On the other hand, mass is more often significantly clustered among individual plot sized communities than, whereas on average plots tend to be even for mass. Individual communities were usually clustered rather than even for UV and brightness, but were usually even for orientation. Despite the average trend of clustering in hue, there were more individually clustered communities than even at three of six sites, and at one site there were more than twice as many even plot sized communities than clustered for hue. There were more small scale communities even for restriction than clustered at only one site for both models.

At the transect scale, even fewer individual communities had significant floral trait patterns (Table 3b). Communities were both clustered and even in their flower masses. Communities were even in their floral restriction at one transect in two sites. Five transects across two sites were even in their brightness. The remaining traits were either clustered or even, but only at one transect in the whole study.

Some individual sites had significant phenotypic structure as well (Table 4c). Twenty-one sites were significantly even in flower mass under Model 1 and 9 of these same sites were considered even for mass under Model 2. This is consistent with the average site structure. Synchrony, restriction, orientation and brightness were significantly clustered at a few sites, but were never significantly even at any site under any model. Hue was even at three sites under Model 1 only.

Phylogenetic Patterns

Most of the 52 species in this community arise from three major angiosperm lineages: Liliales, Ranunculales, and Rosids. 13 species are monocots, and all but *A. triphylum* are in the Liliales.16 species are 'basal dicots', all but *A. canadense* belonging to the Ranunculales. The remaining 23 species are higher eudicots from various orders within the Rosid clade, seven of which are species of *Viola.*

I observed that communities across all three spatial scales were often assemblages of phylogenetically even members of the regional species pool. At the largest scale, we found that communities were composed of more distantly related species than expected by either model (Figure 3). Overall, smaller scale communities were phylogenetically structured, though there were differences among sites. Plot-scale communities had significant phylogenetic patterns (Fisher's Combined, Model 1: X^2 =45.57, P<0.0001; Model 2: X^2 =82.94, P<0.0001), and at half of our study locations (SH, RR, PP) they were composed of species that are more phylogenetically even than expected by at least one model. At one site (AP), communities within plots were composed of more closely related species than predicted by both models. However, two sites (BW, HH) did not have a significant phylogenetic patterns. Transect-sized communities also showed significant phylogenetic patterns (Fisher's Combined, Model 1: X^2 =82.94, P<0.0001; Model 2: X^2 =81.56, P<0.0001), half of the sites being phylogenetically even. One site (PP) was both significantly clustered and even, depending on model choice. One site (HH) did not have a significant phylogenetic structure, and one site (AP) was significantly clustered under both models.

Individual communities often had significant phylogenetic structure as well (Table 3a). Except at Algonac Park, all other sites had more than twice as many phylogenetically even plots than clustered. The number of these plots ranged from 35-99 depending on site and model. Individual transects rarely showed phylogenetic structure. One transect at each of three sites was found to be even under both models, except again for Algonac Park which had 11 of 13 transects even under Model 2 (Table 3b). At the largest scale, both models found that only 2 sites were individually significant, but they suggest clustering rather than phylogenetic evenness (Table 3c).

Only two of seven floral traits were phylogenetically conserved among relatives. Both restriction and orientation were significantly more similar among close relatives than distant relatives (aotf, Phylocom-4.1, P=0 for both). However, the majority of variation in these two traits can be accounted for by divergence at recent nodes in the phylogeny, and so do not represent lineage-wide trait conservation. Hue is marginally conserved (P=0.046) and synchrony is not quite significantly more similar among close relatives (P=0.068). The remaining traits are

not conserved (brightness P=0.13, UV P=0.48, size P=0.20), and none were significantly diverged.

DISCUSSION

I found evidence that both facilitation of and competition for pollination resources can structure plant communities at multiple spatial scales. Communities of spring ephemerals that bloomed together were composed of species with more similarly coloured and more dissimilarly sized flowers than would be expected by chance (Figure 2a-c). Species that co-occurred also flowered more synchronously than those that flowered apart (Figure 2b). Unlike other studies of community assembly (Cavender-Bares *et al.* 2006) which found scale-dependant patterns of functional-trait similarity, I observed the same patterns consistently across spatial scales, which suggests that species with similar floral traits interact over broad distances for shared pollinators (Johnson *et al.* 2010).

This study is the first to attribute pollinator mediated facilitation to the structuring of diverse plant communities. I found that communities were composed of species with a similar flowering synchrony, hue, and usually the same brightness. In this case, co-flowering species benefit from the shared attractiveness of a cohesive visual display (Thomson 1981), because pollinators often forage consistently from flowers of a single colour (Chittka *et al.* 1999, Leonard *et al*. 2011). Small flowered, uncommon species have a limited display often benefit from co-flowering with large, common species with a similarly coloured flowers (Moeller 2004, Feldman 2004, McEwan & Vamosi 2010). This is consistent with the observation that flowers are both even in size but clustered in synchrony, hue and brightness. Communities were also composed of plants with significantly similar degrees of floral restriction, possibly driven by facilitation between species that share more specialized guilds of pollinators (Moeller 2004), such as bumble bees, butterflies, or hummingbirds.

I found evidence that both competition and facilitation mediated by colour traits can drive community assembly. Clustering of flower hue in spring ephemeral communities suggests facilitation, and is contrast to the evenness of colour traits found by McEwan & Vamosi (2010) in sub-alpine meadow communities. Flower colour may not be an ecologically equivalent trait in all communities (Lazaro 2006). Differences in seasonal light intensity and efficiency of bird pollinators at higher altitudes (Kay *et al.* 2006) may influence the observed contrasting pattern of hues between understory and subalpine meadow communities. Similarity in flower hue and synchrony may be influenced by the light environment (Endler 1993). Species that flower together in the same patch may share an optimal flower hue for attracting pollinators in particular

wavelengths of ambient light. For example, blue flowering species will reflect more under ambient blue light, than will red flowers. Though light gaps could cause clustering of plants with similarly coloured flowers without pollinator facilitation, the community would still be structured by floral traits. The two other components of colour we studied flower brightness and UV reflectance, showed significant though site-specific pattern for clustering and evenness, which suggests these colour traits can be associated with both facilitation or competitive exclusion, depending on the specific community. Ambient light can influence the perception of colour by animals (Endler 1993), and so the brightness and UV reflectance of one species' flower may not be equivalent in all environments. Differences in light environment among sites caused by differences in dominant canopy species may impact the relative importance of these two colour components on pollinator attraction.

Although previous studies have shown that plants, including some spring ephemeral species, compete for pollination (Schemske *et al.* 1978), these results are the first to show that this could result in competitive exclusion between species with similar flowers. Competition can displace the flowering times of large flowered species that co-occur (Mosquin 1971), and if the phenologies of similar sized species are displaced, then the phenologies of dissimilar species should overlap. This is consistent with our results of synchronously blooming species that also have dissimilarly sized flowers. Flower size was the only trait I measured that was consistently even among community members across the majority of sites, and all scales. While trait evenness demonstrates that completion for pollination occurs, it also reveals that competition may not be the most influential type of interaction that plants can have through their flowers. Since communities were clustered for most floral traits, facilitation between plant species with similar floral traits may be a source of selection for the observed convergence in floral phenotypes between co-flowering species.

Spring ephemeral communities were assembled into groups of highly unrelated species. This is similar to other studies which have found evidence for phylogenetic evenness in plant and animal communities (Cavender-Bares *et al.* 2009) because of niche conservatism and exclusion of ecologically similar species (Losos 2008). However few floral traits we studied, particularly those that explained the structure of the community most, were phylogenetically conserved. This is consistent with the results of McEwan & Vamosi (2010) who found evidence for flower colour lability among species that co-occur. My results however most closely mirror those of Cavender-Bares *et al*. (2006) who attributed phylogenetic evenness to environmental filtering of unrelated species that have converged on similar traits to allow them to thrive in the same environment. While the floral traits we investigated are not significantly divergent among taxa, they are

phylogenetically labile and have converged nonetheless. Here, pollinator mediated facilitation may have helped to drawn together unrelated taxa with similar traits.

I found evidence that functional traits are important determinants of species co-existence patterns. Spring ephemeral communities were phenotypically structured in their floral traits, and despite the lack of floral trait conservation, the communities we studied were phylogenetically structured as well. Phylogenetic evenness may result from competition for light between close relatives with conserved traits associated with photosynthesis (Prinzing *et al.* 2001), but not with pollinator attraction. Plant traits involved in capturing sunlight (Moore & Vankat 1986), or other abiotic resources (Whigham 2004, Gilbert & Lechowicz 2004) may be influencing assembly patterns in this community as well. Both phenotypic and phylogenetic patterns show that the traits are important for creating and maintaining compositional structure of communities (Kraft *et al.* 2008), and that neutral models cannot effectively explain coexistence within this particular assemblage of plants (Honnay *et al.* 2001, Hubbell 2001, Bell *et al*. 2005).

My study faced four design limitations. First, community inventories were based on presence/absence data only, which over-represent rare species and under-represent common species. Consequently, trait similarity and phylogenetic relatedness are more conservatively estimated here using presence absence data, than would be if abundance data were used (Hardy 2008). Second, this study used observational methods in order to best represent patterns of natural systems. Because this study was not manipulative it is impossible to infer pollinator mediated assembly as an absolute cause of the floral patterns that I observed. However, the strength and consistency in evenness and clustering of flower hue, synchrony and size demonstrate that these patterns could not have occurred simply by chance. I found no clear relationship between evolutionary relatedness and floral similarity among community members, likely because few floral traits were significantly conserved, but communities were nonetheless structured phylogenetically. By comparing the pollination success of a target species growing alone to their success when co-flowering with similarly flowered species (Moeller 2004, Ghazoul 2006), further manipulative research can isolate which pairs, or groups of spring ephemeral species are competing with or facilitating each other, and so driving the trait patterns I observed. The third design limitation that this study faced was the independent treatment of all plots within a site. The plots were inventoried in groups that formed transects, and therefore plots within the same transect are likely more similar than plots in other transects. However, transects could not be treated as blocks because some transects were placed within a 60 m of radius of each other, and plots from different transects were often closer to each other than plots within the same transect. Only twenty five percent of transects were within 60 m of each other. Fourth and finally, in

performing such a large number of t-tests I have to expect that at least five percent of my results are significant by chance alone and it is not possible to decipher which.

By quantifying the functional relationship between coexistence and trait similarity, my results provide a framework for predicting patterns of biological diversity in the landscape (McGill *et al.* 2008). This has both theoretical and practical consequences. The predictability of community composition on various local scales suggests that communities are in fact individual ecological units composed of functionally integrated species (Ricklefs 2008). Predictability also allows us to recreate natural patterns, aiding in ecological policy making and ecosystem restoration (Calder 2000). For example, facilitative relationships could increase the pollination success of reintroduced rare plant species (Handel 1997, Forup *et al.* 2008) that might otherwise succumb to competition (Vamosi *et al.* 2006). The flowers of ideal facilitative hosts may have different sized flowers than the target rare species, but share the same flower colour, be equally restrictive and bloom synchronously. I propose that these floral traits describe an important component of a species' ecological niche by which it can be predictably sorted into or excluded out of its local community.

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TABLES & FIGURES

Table 1:
Presence/Absence: Shaded boxes represent a species presence at each of the forest sites visited.

		Presence/ Absence					
Species	**Authroity**	**BW**	**RR**	**SH**	**PP**	**AP**	**HH**
Aquilegia canadensis	L.	■	■	■	■	■	■
Geranium maculatum	L.	■	■	■	■	■	■
Maianthemum canadense	Desf.	■	■	■	■	■	■
Maianthemum racemosum	L. (Link)	■	■	■	■	■	■
Podophyllum peltatum	L.	■	■	■	■	■	■
Polygonatum pubescens	(Willd.) Pursh	■	■	■	■	■	■
Viola cucullata	Aiton	■	■	■	■	■	■
Viola pubescens	Aiton	■	■	■	■	■	■
Arisaema triphyllum	L (Schott.)	■	■	■	■	■	
Claytonia virginica	L.	■	■	■		■	■
Ranunculus abortivus	L.	■	■	■	■	■	
Sanguinaria canadensis	L.	■	■	■	■		■
Trillium grandiflorum	(Michx.) Salisb	■	■	■	■		■
Viola conspersa	Rchb.	■	■	■		■	■
Cardamine diphylla	(Michx.) Alph. Wood	■	■	■			■
Cardamine douglassi	Britton	■		■	■		■
Caulophyllum thalictroides	L. (Michx.)	■	■			■	■
Uvularia grandiflora	Sm.	■	■	■	■		
Viola rostrata	Pursh	■	■	■			■
Anemone quinquefolia	L.		■	■		■	
Asarum canadense	L.	■	■	■			
Cardamine concatenata	(Michx.) O. Shwartz	■	■		■		
Erythronium americanum	Ker Gawl	■	■	■			
Galium aparine	L.	■		■	■		
Hepatica nobilis var nobilis	Mill.	■		■			■
Maianthemum stellatum	L. (Link)	■			■	■	
Mitella diphylla	L.	■		■			■
Osmorhiza longistylis	(Torr.) DC	■			■	■	
Phlox divaricata	L.	■	■		■		
Polygonatum biflorum	(walter) Elliot	■			■		■
Trillium erectum	L.	■	■	■			
Viola blanda	Willd.	■		■		■	
Claytonia caroliniana	Michx.	■				■	
Dicentra cucullaria	(L.) Bernh.		■		■		
Hepatica nobilis var acuta	(Pursh)Steyerm	■	■				
Medeola virginica	Christm.	■		■			
Osmorhiza claytonii	(Michx.) C.B. Clarke	■			■		
Panax trifoliusvar var. roseus	N. Coleman	■					■
Prosartes lanuginosa	(Michx)D. Don	■		■			
Tiarella cordifolia	L.	■		■			
Trientalis borealis	Raf.	■		■			
Actaea pachypoda	Elliot	■					
Actaea rubra	(Aiton) Willd.	■					
Thalictrum thalictroides	(L.) A.J. Eames & B. Boivin			■			
Corydalis flavula	(Raf.) DC.				■		
Dicentra canadensis	(Goldie) Walp.		■				
Erigenia bulbosa	(Michx.)Nutt.		■				
Erythronium albidum	Nutt.		■				
Polygala paucifolia	Willd.		■				
Ranunculus hispidus	Michx.					■	
Viola canadensis	L.		■				
Viola sagittata	Aiton	■					

Table 2:
Site abbreviations and locations

Sites	Abbreviation	Latitude	Longitude	Size (h)
Backus Woods	BW	42°40'23.70"N	80°29'56.15"W	232
Spooky Hollow	SH	42°42'50.48"N	80°20'23.80"W	51
Rare Reserve	RR	43°22'44.49"N	80°20'37.33"W	62
Point Pelee	PP	41°55'50.66"N	82°30'51.56"W	23
Haven Hill	HH	42°38'31.60"N	83°33'38.92"W	102
Algonac Park	AP	42°39'16.29"N	82°31'45.52"W	123

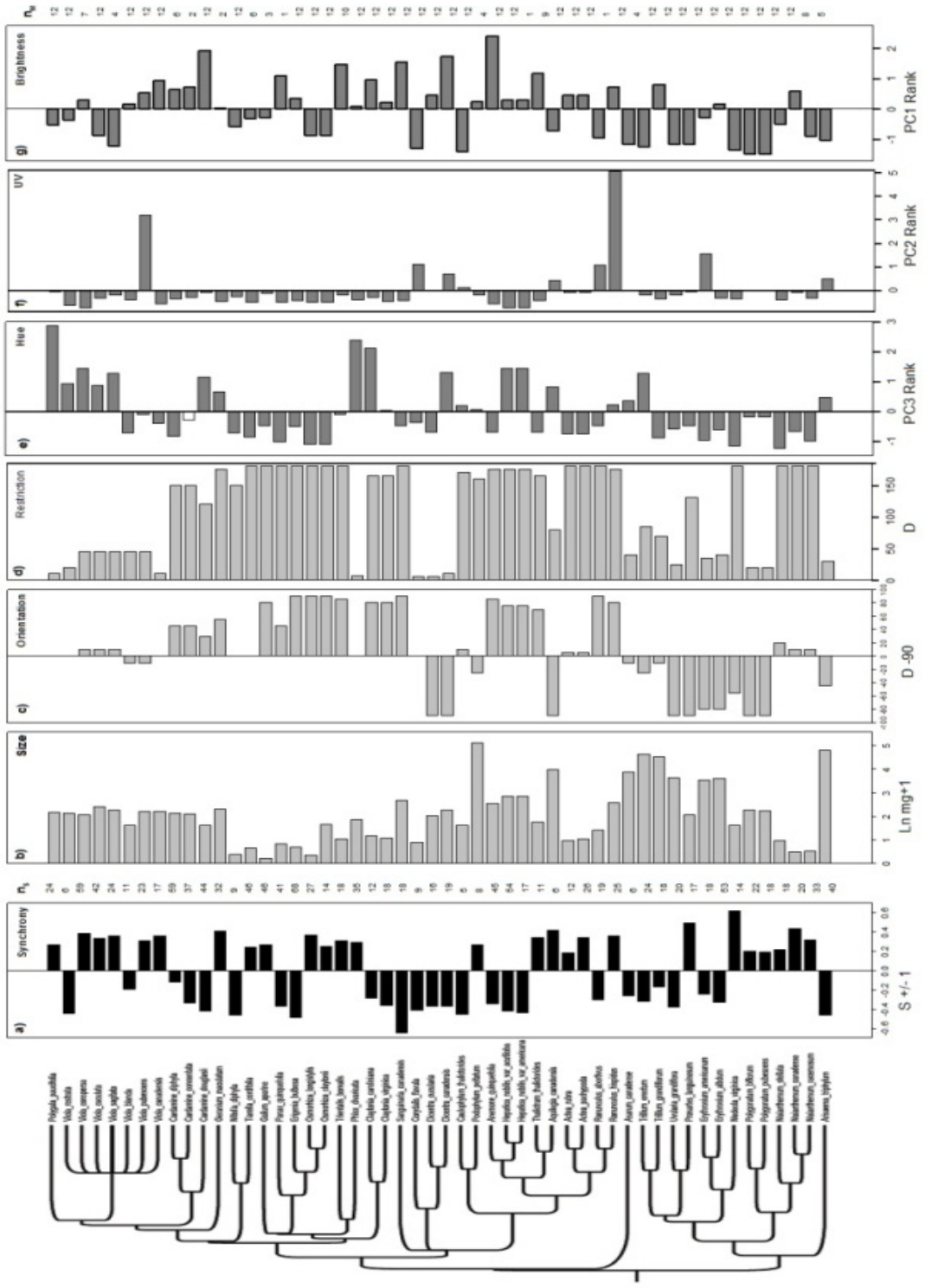

Figure 1. Trait values and phylogenetic relationship of all species used. Panel b) shows the natural log of species masses for a clearer graphical representation. The axis of the graph in panel c) is shifted to 90^{o} to highlight the differences in downward and upward facing flowers.

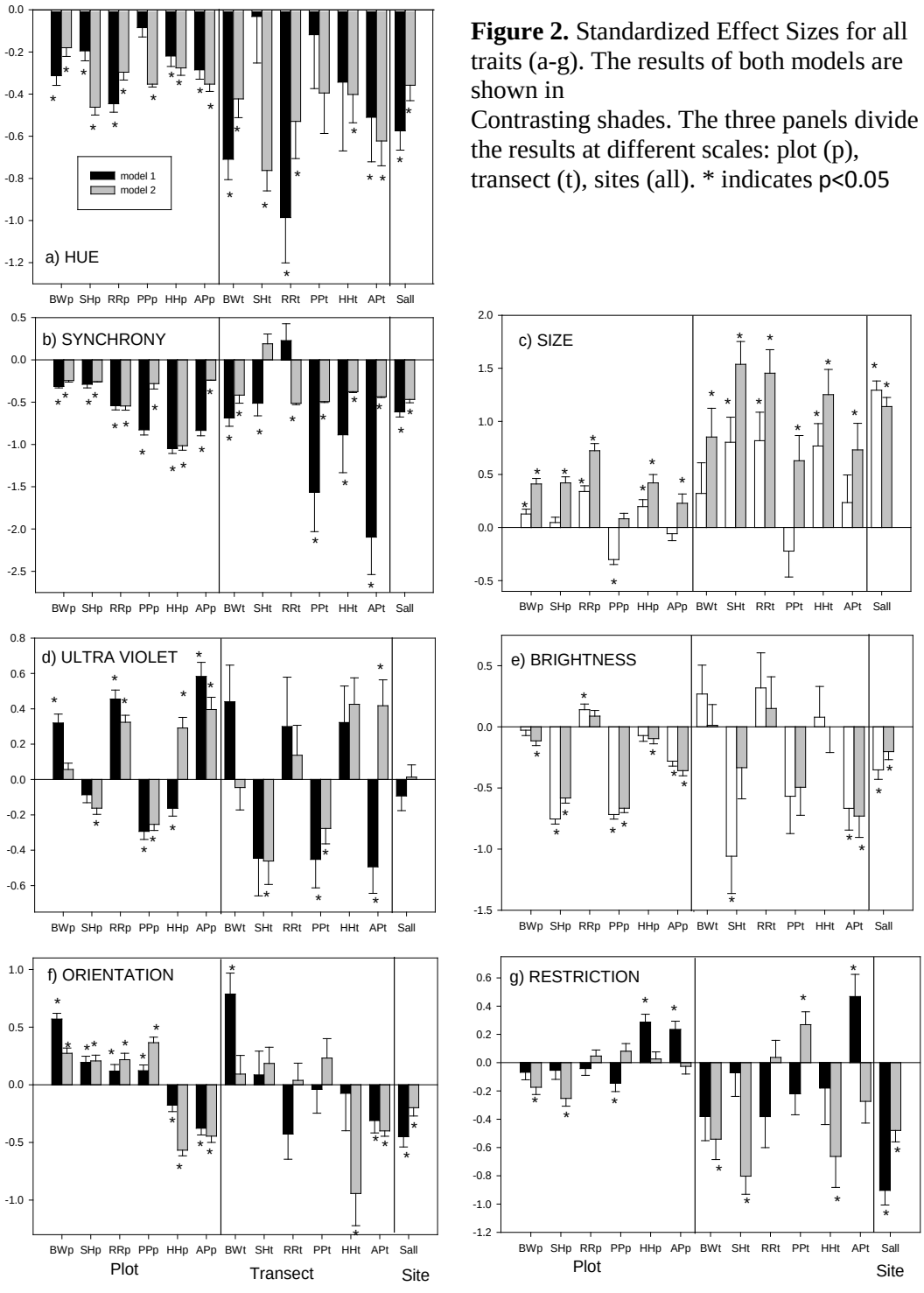

Figure 2. Standardized Effect Sizes for all traits (a-g). The results of both models are shown in
Contrasting shades. The three panels divide the results at different scales: plot (p), transect (t), sites (all). * indicates p<0.05

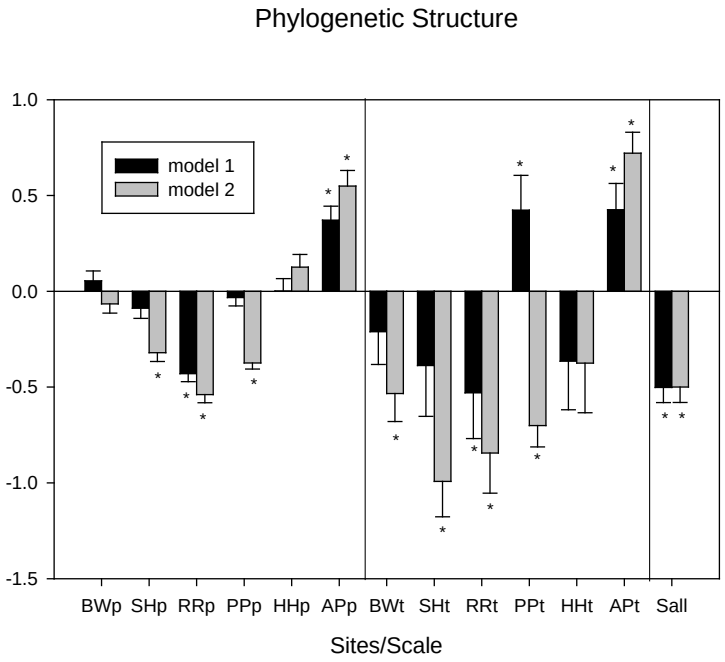

Figure 3:. Average Net Relatedness Indices of communities at different sites, scales. The NTIs of the two models are shown in contrasting shades. The three panels divide the results at different scales: plot (p), transect (t), sites (all). Site names are given as two letter abbreviations.
* indicates $p<0.05$

Plot Scale		SH							
		Synch.	Mass	Rest.	Orient.	Hue	Bright.	UV	MNT
Model1	Even	0	9	31	7	3	38	2	60
	Clustered	1	13	12	2	4	1	8	17
		**		*	*		**	**	**
Model2	Even	0	14	0	1	2	14	0	72
	Clustered	3	4	5	1	3	2	7	16
		**	*	*			**	**	**
		BW							
		Synch.	Mass	Rest.	Orient.	Hue	Bright.	UV	MNT
Model1	Even	1	8	3	20	3	4	7	35
	Clustered	8	2	14	1	2	3	2	11
		*	**	**	**			*	**
Model2	Even	1	10	1	3	1	0	3	36*
	Clustered	1	1	9	1	0	1	4	7
			**	**	**	*	*		**
		RR							
		Synch.	Mass	Rest.	Orient.	Hue	Bright.	UV	MNT
Model1	Even	5	6	5	1	0	2	2	78
	Clustered	4	1	3	3	6	3	2	0
			**		*	*			**
Model2	Even	0	10	2	2	0	2	0	99
	Clustered	4	0	1	1	0	2	1	0
		*	**					*	**
		PP							
		Synch.	Mass	Rest.	Orient.	Hue	Bright.	UV	MNT
Model1	Even	2	20	36	25	11	2	6	41
	Clustered	44	22	20	6	4	9	14	7
		**			**	*	*	**	**
Model2	Even	0	29	42	27	0	2	0	39
	Clustered	31	6	8	2	3	3	7	4
		**	*	*	**	*		**	**
		HH							
		Synch.	Mass	Rest.	Orient.	Hue	Bright.	UV	MNT
Model1	Even	6	19	29	4	3	1	5	45
	Clustered	32	6	5	1	8	8	8	16
		**	**	*	*	**	**		**
Model2	Even	0	36	0	0	0	1	0	43
	Clustered	15	5	0	1	3	4	3	20
		**	**		*	**	**	*	**
		AP							
		Synch.	Mass	Rest.	Orient.	Hue	Bright.	UV	MNT
Model1	Even	0	17	22	8	0	1	1	47
	Clustered	16	8	7	10	7	3	11	27
		**	**	*		**	**	*	
Model2	Even	0	42	0	9	0	1	1	55
	Clustered	13	5	5	8	1	3	1	37
		**	**	*		**	**		

Table 3a: The number of individual plots that are significantly clustered or even for each trait, site and model. * Indicates that there are more than twice as many plots significantly clustered than even, or more than twice as many even than clustered. ** Indicates that both models detect the majority of significant plots are in the same direction and that there are more than twice as many plots in this direction than the other.

Transect Scale SH

		Synch.	Mass	Rest.	Orient.	Hue	Bright.	UV	MNT
Model1	Even	0	0	0	0	0	2	0	0
	Clustered	0	1	0	0	0	0		0
			**				*		
Model2	Even	0	0	0	0	0	0	0	0
	Clustered	0	4	0	0	0	0	0	0
			**						

BW

		Synch.	Mass	Rest.	Orient.	Hue	Bright.	UV	MNT
Model1	Even	0	0	0	0	0	0	0	1
	Clustered	0	0	0	0	0	0	0	0
									*
Model2	Even	0	0	0	0	0	0	0	0
	Clustered	0	2	0	0	0	0	0	0
			*						

RR

		Synch.	Mass	Rest.	Orient.	Hue	Bright.	UV	MNT
Model1	Even	0	0	1	0	1	0	0	0
	Clustered	0	0	0	0	0	0	0	1
				*		*			**
Model2	Even	0	5	0	0	0	0	0	0
	Clustered	0	0	0	0	0	0	0	1
			*						**

PP

		Synch.	Mass	Rest.	Orient.	Hue	Bright.	UV	MNT
Model1	Even	5	0	0	0	0	3	0	0
	Clustered	0	0	0	0	0	0	0	0
		*					*		
Model2	Even	0	0	0	0	0	0	0	0
	Clustered	0	0	0	0	0	0	0	0

HH

		Synch.	Mass	Rest.	Orient.	Hue	Bright.	UV	MNT
Model1	Even	3	0	1	2	2	0	0	1
	Clustered	0	1	0	0	0	0	0	0
			**	**	*	*			**
Model2	Even	0	0	1	0	0	0	0	1
	Clustered	0	2	0	0	0	0	0	0
			**	**					**

AP

		Synch.	Mass	Rest.	Orient.	Hue	Bright.	UV	MNT
Model1	Even	7	1	0	0	0	0	0	1
	Clustered	0	0	0	0	0	0	0	0
		*	*						**
Model2	Even	0	0	0	0	0	0	0	11
	Clustered	0	1	0	0	0	0	1	1
			*						**

Table 3b: The number of individual transects that are significantly clustered or even for each site and model. * Indicates that there are more than twice as many transects significantly clustered than even, or more than twice as many even than clustered. ** Indicates that both models detect the majority of significant transects are in the same direction and that there are more than twice as many transects in this direction than the other.

All Sites									
		Synch.	Mass	Rest.	Orient.	Hue	Bright.	UV	MNT
Model1	Even	0	21	1	0	3	0	0	0
	Clustered	6	0	9	2	1	2	0	4
		**	**	**	**	*	**		**
Model2	Even	0	9	0	0	0	0	0	0
	Clustered	2	0	1	2	0	1	0	4
		**	**	**	**		**		**

Table 3c: The number of individual sites that are significantly clustered or even for each trait and model. * Indicates that there are more than twice as many sites significantly clustered than even, or more than twice as many even than clustered. ** Indicates that both models detect the majority of significant sites are in the same direction and that there are more than twice as many sites in this direction than the other.