Phylogenetic distance can predict susceptibility to attack by natural enemies

J. H. Ness, E. J. Rollinson and K. D. Whitney

J. H. Ness (jness@skidmore.edu) and E. J. Rollinson, Dept. of Biology and the Environmental Studies Program, Skidmore College, 815 North Broadway, Saratoga Springs, NY 12866, USA. EJR also at: Dept. of Ecology and Evolution, Stony Brook Univ., Stony Brook, NY 11794-7626, USA. – K. D. Whitney, Dept. of Ecology and Evolutionary Biology, Rice Univ., 6100 Main St, Houston, TX 77005, USA.

If related species share enemies, variation in the damage experienced by species within a community may be predictable based on phylogeny. We examined the hypothesis that plant species more closely related to other community members experience greater herbivory by assessing leaf damage to native and exotic plants in two North American communities: an Eastern hardwood forest and a Rocky Mountain montane community. Pairwise phylogenetic distances between focal species and the hundreds of other native species in each community were calculated. We examined the influence of four measures of relatedness within each community: NND (phylogenetic distance to the nearest native neighbor), MPD (mean phylogenetic distance to the native species in the community), and two new metrics, MIPD (mean inverse phylogenetic distance) and INND (inverse nearest neighbor distance). These new metrics assume a nonlinear increase in interaction strength with relatedness; in the context of natural enemies, they posit that the sharing of enemies between any two species increases nonlinearly with their relatedness. Using regression models, we found that herbivore damage decreased with decreasing phylogenetic similarity of focal species to native species (as measured by MIPD) in both sites, although the pattern was significant only for native focal species in the montane community and exotic focal species in the hardwood forest. Similar decreases in herbivory with decreasing relatedness were detected using INND (montane natives) and MPD (hardwood forest exotics). There was no significant relationship between NND and herbivory for any of the four site by focal plant origin combinations. Our results are the first to support the hypothesis that native species can escape attack as a function of their phylogenetic dissimilarity to the larger community of native species, and to demonstrate that exotic species show these patterns in the wild (as opposed to in common gardens). We suggest that phylogenetic distance metrics assuming a nonlinear increase in interaction strength with relatedness show promise for broader application.

The theory of coevolution was founded on evidence that shared evolutionary history influences interactions with natural enemies (Ehrlich and Raven 1964). More recent work has focused on quantifying the likelihood that pairs of focal species interact with similar coeteries of natural enemies, and the degree to which the phylogenetic distance of those pairs can explain variation in that overlap (Ødegaard et al. 2005, Weiblen et al. 2006, Gilbert and Webb 2007, Gobner et al. 2009). One strength of these approaches is that they can include co-evolutionary dynamics but are not limited to contexts where co-evolution between pairs of species could have occurred (Ricciardi and Ward 2006, Futuyma and Agrawal 2009). If related species share natural enemies, the acquisition of natural enemies and the vulnerability of a population to attack may be influenced by the degree of relatedness of the focal species to other members of the community. The overlap between herbivore communities can decrease with increasing phylogenetic distances between pairs of host plants (Conner et al. 1980, Novotny et al. 2002, Ødegaard et al. 2005, Weiblen et al. 2006, Gobner et al. 2009), and the likelihood that pathogenic fungi can infect a pair of plant species can decrease with increasing phylogenetic distance between the pair (Gilbert and Webb 2007). Further, a meta-analysis that contrasted the herbivory experienced by focal species in single-species versus mixed forests demonstrated that the composition of the tree assemblage (i.e. the taxonomic proximity of one species to another) is a better predictor of variation in herbivory than is species richness (Jactel and Brockerhoff 2007). If these patterns are typical, the phylogenetic structure of a host community could be much more important to predator–prey and host–parasite interactions than is widely appreciated.

Studies of the influence of host phylogenetic structure on natural enemy attack have focused on the particular case of exotic invasive species. Differences in the propensity to avoid natural enemies is commonly held to distinguish truly invasive species from naturalized but innocuous species (Mitchell and Power 2003, Cappuccino and Carpenter 2005, Strauss et al. 2006, but see Parker and Gilbert 2007, Van Kleunen and Fischer 2009). The 'enemy release' hypothesis predicts that exotic species benefit from the loss of a subset of their natural enemies during immigration. Over time,

exotic species incrementally acquire natural enemies in their new environs (Conner et al. 1980, Van Kleunen and Fischer 2009, Grabenweger et al. 2010). The integration of exotic species into these new ecological networks can be influenced by the phylogenetic history of the participants (Vacher et al. 2010). Further, the phylogenetic similarity of the exotic to members of the recipient community can influence the rate at which exotics acquire natural enemies (Conner et al. 1980, Gobner et al. 2009) and experience damage (Hill and Kotanen 2009, Dawson et al. 2009, Pearse and Hipp 2009; but see Hill and Kotanen 2010) as well as the fitness of natural enemies that colonize these new species (Bertheau et al. 2010). These patterns are likely mediated by phylogenetic conservation of plant traits (Wiens et al. 2010, Ricciardi and Ward 2006): exotic species that are distantly related to recipient communities are more likely to have novel traits that limit their damage from herbivores adapted to the traits of the native plant community. However, little is known about the influence of phylogenetic similarity on enemy attack for native host species (but see Webb et al. 2006).

Work exploring the consequences of phylodiversity on susceptibility to natural enemy attack has also focused on particular pairwise interactions. Special emphasis has been placed on the presence or richness of congeners (Cappuccino and Carpenter 2005, Ricciardi and Ward 2006, Dawson et al. 2009), the presence or richness of confamilials (Cappuccino and Carpenter 2005, Dawson et al. 2009), the phylogenetic distance between a focal plant and the most closely related neighbor in the community (Webb et al. 2006, Hill and Kotanen 2009, 2010), the mean phylogenetic distance between a focal plant and confamilials in the community (Hill and Kotanen 2009, 2010), and the mean phylogenetic distance between a focal plant and all other species in the community (Hill and Kotanen 2009); this list is incomplete (Thuiller et al. 2010). Ideally, natural enemies and scientists will use similar criteria to distinguish functional biological units (Janzen 1979). We propose that existing approaches may either 1) overly privilege interactions between species that share a particular position in a taxonomic hierarchy, e.g. congenerics (Crozier 1997, Lambdon and Hulme 2006, Diez et al. 2008), or 2) take the opposite extreme in treating interactions between all species pairs as equally important. Further, genus and family designations have been criticized as subjective measures of relatedness that may bias results compared to quantitative estimates of phylogenetic distances (Webb et al. 2006, Proches et al. 2008, Thuiller et al. 2010).

Here, we explore the relationship between herbivory and host phylogenetic isolation for native and exotic angiosperm species in an Eastern hardwood forest and a Rocky Mountain montane community (in New York and Colorado, USA, respectively). Our work is distinguished by the pronounced role of phylogenetic distance demonstrated for native species in the wild (other studies have focused on exotic species in gardens or experimental plots) and our development of two new metrics (mean inverse phylogenetic distance, MIPD; and inverse nearest neighbor distance, INND) to quantify the phylogenetic distance of a focal species to the larger community. These new metrics assume that the degree of interaction between any two species increases nonlinearly with their degree of relatedness (Gilbert and Webb 2007), in contrast to existing metrics assuming linear relationships (Methods). We test the hypotheses that natural enemy attack decreases with a plant species' increasing phylogenetic isolation from a) the most closely related native species and b) the entire native community. We also examine whether the new metrics (INND, MIPD) better predict variation in attack than do alternative measures of phylogenetic distance.

Methods

Study sites

Eastern hardwood forest

The North Woods is a 350-acre forest owned by Skidmore College in Saratoga County, New York (43°1′N, 73°5′W; altitude 100 m a.s.l.). The deciduous forest is dominated by *Quercus*, *Acer* and *Carya*, and includes wetlands and small stands of pine and hemlock. The community was defined as all documented angiosperms occurring in the forest (321 species in 75 families, including 63 exotics representing 31 families), based on the surveys described in Van Hook (2007). Most (85%) exotic species lack a native congener in the forest, and nine families are only represented by exotic species.

Rocky Mountain montane community

The Gothic townsite is the home of the Rocky Mountain Biological Lab (RMBL; 38°57′29″N, 106°59′06″W; altitude, 2900 m a.s.l.) in the West Elk mountains of Colorado. Habitats at the townsite are dominated by montane meadows and forests (the fescue grassland, aspen and spruce–fir community types of Langenheim (1962)). The community was defined as all angiosperms occurring in the roughly 25 km² area surrounding the Gothic townsite and was based on the survey of Frase and Buck (2007); it is comprised of 652 angiosperm species (603 natives, 49 exotics) in 63 families.

Folivory scoring

In both sites, folivory was assessed visually as the proportion leaf tissue missing or damaged by folivores, and ≥8 leaves were scored for each individual plant. Data are presented in Supplementary material Appendix 1. Because our hypotheses focus on the damage inflicted by the entire folivore community, we made no attempt to identify herbivores or parse the damage attributable to individual herbivore species.

In the Eastern hardwood forest, 44 focal species in 34 families were scored. These included 25 native and 19 exotic species. We treated *Robinia pseudoacacia* as an exotic to New York, although that species is native to more southern portions of the United States. For each species, an average of 12.3 ± 6.8 (±SD) individuals were sampled in August–October in 2006, 2007 and 2009, with different species (including exotics and natives) sampled each year. We used ANOVA to clarify whether folivory differed among the three years.

In the Rocky Mountain montane community, 41 focal species in 33 families were scored. These included 34 native and seven exotic species, reflecting the relative rarity of exotic species at the site. For each species, eight individuals were

scored during 17–26 August 2009. Because *Populus tremuloides* grows in large vegetative clones, individuals were sampled at widely-spaced intervals (50m to 1 km) to ensure each of the eight samples were independent for this species.

Phylogeny construction and phylogenetic distances

We employed Phylomatic (Webb and Donoghue 2005) using the APG III megatree (Angiosperm Phylogeny Group 2009) to construct base family-level phylogenies for each flora. Given a lack of within-family resolution, species and genera were represented as polytomies within genera and families, respectively. Branch lengths (My) were added to the phylogenies using the BLADJ algorithm in Phylocom (Webb et al. 2008) and node ages from Wikstrom et al. (2001). Phylogenies were visualized in Mesquite ver. 2.71 (Maddison and Maddison 2009).

Phylogenetic distances (in My) between all pairs of species were then calculated using the PHYDIST procedure of Phylocom (Webb et al. 2008). For each focal species, we then calculated NND (phylogenetic distance to the nearest native neighbor) and MPD (mean phylogenetic distance to all other native species). We also calculated metrics of relatedness that are based on the inverse pairwise distance between species. INND (inverse nearest neighbor distance) is calculated as (phylogenetic distance to the nearest native)$^{-1}$. MIPD (mean of inverse pairwise distances) is calculated as $\sum$(phylogenetic distance to each native) $^{-1}$/n for a community of n native species. To our knowledge, these metrics have not been employed in previous studies(see Vamosi et al. (2009) for a summary of current phylogenetic distance metrics). Both INND and MIPD increase with increasing relatedness of the focal species to others in the community, but nonlinearly. In effect, closely related species are weighted more heavily than distantly related species. They thus contrast with NND and MPD, which both assume linear relationships between interaction strength and phylogenetic distance.

Analysis: folivory and phylogenetic distance

We used simple linear regressions to test the hypothesis that folivory decreases as the phylogenetic isolation of the focal species increases. We used NND, MPD, INND and MIPD as independent variables in four models, and performed separate analyses for native and exotic species at each site (16 models total). Folivory values were averaged across individuals within species and arcsine-square root transformed prior to analysis. If folivory increases as plant species are more closely related to their neighbors, folivory would be negatively correlated with NND and MPD and positively correlated with INND and MIPD. We used species as replicates in all cases.

We used MANOVA followed by protected ANOVAs (Scheiner 2001) to compare NND, MPD, INND, MIPD and folivore damage between the sampled exotics and native species in both communities.

Results

Phylogenetic distance and folivory: Eastern hardwood forest

The sampled exotic and native species had similar mean values of the four phylogenetic distance metrics (NND, MPD, INND, and MIPD) and of folivory (mean $\pm$ SE = 8.47% $\pm$ 1.44 and 10.45% $\pm$ 1.27 for exotics and natives, respectively) (MANOVA, Pillai's trace = 0.20, F = 1.95, DF = 5,38, p = 0.108). There were no significant among-year differences in folivory (F = 2.21, DF = 2,21, p = 0.115). Thus, we pooled data across sampling years in subsequent regression analyses relating folivory to phylogenetic distance.

Among native species, variation in folivory was not significantly related to variation in NND (simple linear regression, F = 1.40, DF = 1,23, p = 0.25, r^2 = 0.06; Fig. 1a), MPD (F = 1.80, DF = 1,23, p = 0.193, r^2 = 0.07; Fig. 1c), INND (F = 0.68, DF = 1,23, p = 0.412, r^2 = 0.03; Fig. 1b) or MIPD (F = 0.64, DF = 1,23, p = 0.431, r^2 = 0.03; Fig. 1d).

Among exotic species, variation in folivory was not significantly related to variation in NND (F = 0.06, DF = 1,17, p = 0.81, r^2 < 0.01; Fig. 1a) or INND (F = 1.86, DF = 1,17, p = 0.19; Fig. 1b). However, folivory was significantly and negatively correlated with MPD (F = 8.97, DF = 1,17, p = 0.008, r^2 = 0.35; Fig. 1c), and was significantly and positively correlated with MIPD (F = 8.81, DF = 1,17, p = 0.009, r^2 = 0.34; Fig. 1d; note reversed x-axis), indicating that exotic species phylogenetically isolated from the larger community received less damage.

Phylogenetic distance and folivory: Rocky Mountain montane community

The sampled exotic and native species differed in mean values of the four phylogenetic distance metrics (NND, MPD, INND, and MIPD) and of folivory (MANOVA, Pillai's trace = 0.30, F = 2.89, DF = 5, 34, p = 0.028). Subsequent protected ANOVAs indicated that exotics and natives had similar NND (F = 2.08, DF = 1,38, p = 0.16) and MPD (F = 0.71, DF = 1,38, p = 0.41), while the exotics had higher INND (F = 6.05, DF = 1,38, p = 0.019) and MIPD (F = 9.35, DF = 1,38, p = 0.004; Fig. 2). Mean folivory for the exotics was approximately half that experienced by the native species (mean $\pm$ SE = 3.6% $\pm$ 0.88 and 8.0% $\pm$ 1.45, respectively), although this difference was not statistically significant (F = 2.04, DF = 1,38, p = 0.16).

Among native species, variation in folivory was not significantly related to NND (F = 1.19, DF = 1,31, p = 0.283, r^2 = 0.04; Fig. 2a) or MPD (F = 2.61, DF = 1,31, p = 0.116, r^2 = 0.08; Fig. 2c). There were significant positive relationships between folivory and both INND (F = 4.66, DF = 1,31, p = 0.38; r^2 = 0.13; Fig. 2b) and MIPD (F = 7.69, DF = 1,31, p = 0.009, r^2 = 0.20; Fig. 2d; note reversed x-axis in Fig. 2b and 2d), indicating that native species phylogenetically isolated from their closest relatives and the larger community received less damage.
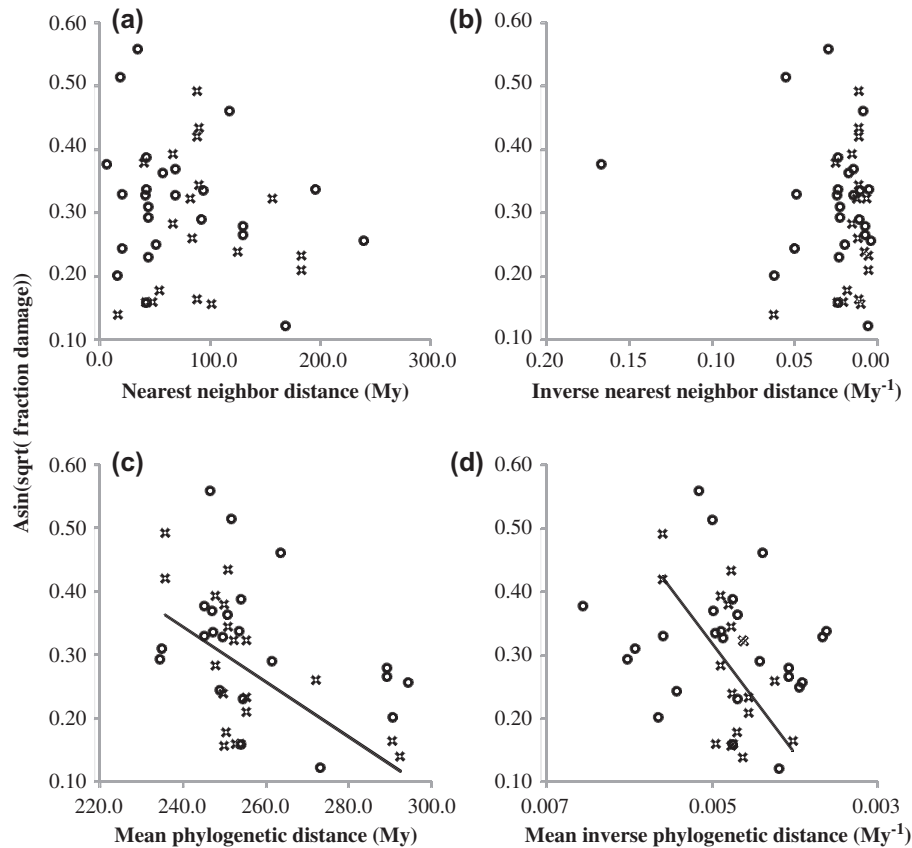
Figure 1. Eastern hardwood forest site: relationships between measures of phylogenetic distance and folivory damage for exotic (×) and native (○) plant species. Phylogenetic similarity of focal species to natives decreases from left to right; note that the x-axes in (b) and (d) have been reversed to preserve this interpretation. Lines indicate significant relationships for exotic plant species.

Among exotic species, variation in folivory was not significantly related to variation in NND (F = 0.59, DF = 1,5, p = 0.477, r^2 = 0.11; Fig. 2), MPD (F = 0.17, DF = 1,5, p = 0.699, r^2 = 0.03; Fig. 2), INND (F = 0.91, DF = 1,5, p = 0.39; r^2 = 0.18) or MIPD (F = 0.0004, DF = 1,5, p = 0.995, $r^2 < 0.01$; Fig. 2).

Discussion

Our study demonstrates that the damage experienced by both exotic and native plant species can be influenced by their phylogenetic proximity to members of the native community. This is the first demonstration of such a pattern for exotic species in wild populations, and for native species in any setting. It supports earlier work focusing on exotic species in constructed garden communities (Dawson et al. 2009, Hill and Kotanen 2009, Pearse and Hipp 2009) and demonstrates an influence of community-wide phylogenetic distance that is not well described by among-species variation in distance to the most closely related neighbor (NND, Webb et al. 2006) or average distance to native species (MPD, Hill and Kotanen 2009, 2010). This influence is revealed via a new metric of phylogenetic distance, MIPD, which has the novel property of weighting closer relatives more than distant relatives.

Several mechanisms could explain the observed negative relationship between phylogenetic distance and herbivore damage. First and most obviously, phylogenetic conservation of enemies could play a role. In this scenario, close relatives share herbivore species, and herbivores of locally speciose plant clades could therefore reach high densities and inflict greater per capita damage. If species-rich systems tend to be phylogenetically overdispersed and/or contain fewer closely related species per unit area, this mechanism could also explain why herbivory levels are often lower in more diverse communities (Jactel and Brockerhoff 2007, Tonhasca and Byrne 1994, Hillebrand and Cardinale 2004, Balvanera et al. 2006). Second, phylogenetic conservation of habitat and species–area relationships may play a role. In this scenario, plant species of common habitats would tend to have many close relatives in the community because relatives would share habitat tolerances and the large spatial area of the habitats would translate to high plant species richness. Plant species of rare habitats would have fewer relatives present (because of restricted spatial area) and thus have relatively high measures of phylogenetic distance. Simultaneously, habitat size would drive herbivore abundances: for example, in larger habitats herbivores might be better able to avoid Allee effects or stochastic local extinction events. Thus plant species of common habitats would have low measures of phylogenetic distance and
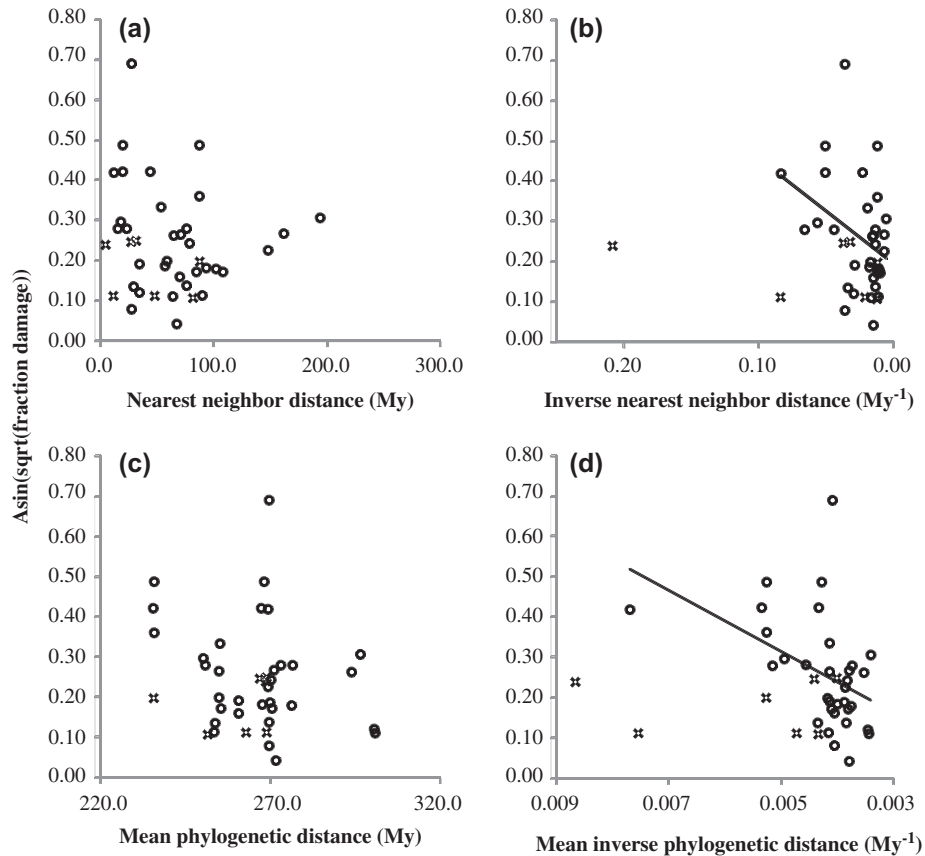
Figure 2. Rocky Mountain montane site: relationships between measures of phylogenetic distance and folivory damage for exotic (×) and native (○) plant species. Phylogenetic similarity of focal species to natives decreases from left to right; note that the x-axes in (b) and (d) have been reversed to preserve this interpretation. Lines indicate significant relationships for native plant species.

experience high levels of damage, with the converse being true in rare habitats.

Site differences in patterns for native versus exotic species

We found that herbivore damage decreased with decreasing phylogenetic similarity for native (but not exotic) focal species in the Rocky Mountain montane community and exotic (but not native) focal species in the Eastern hardwood forest community. We have no clear explanations for this site difference in which class of species showed strong patterns, but three hypotheses are worth mentioning. First, there are relatively few exotics in the montane community dataset (n = 7), reflecting the general rarity of exotics there (Frase and Buck 2007); thus the lack of a relationship for exotics at that site could be an issue of statistical power. Second, damage was quite low for exotics in the montane community (mean of 3.6%), perhaps making it difficult to distinguish phylogenetically structured variation in attack from noise. Third, the spatial scale at which we circumscribed the communities differed: relative to the Eastern forest community, the montane community included a much larger spatial area and a higher species count. To the extent that herbivore presence and attack are related to phylogenetic similarity of neighbors only in a focal species' immediate vicinity, it could be that the montane community as we circumscribed

it included many species not present in the sampling site, thus reducing the ability to see patterns and perhaps explaining the lack of a relationship for exotics there. However, this last hypothesis is not consistent with our failure to detect a relationship between phylogenetic similarity and attack for native species in the Eastern forest community, which was circumscribed at a much smaller scale.

New metrics of phylogenetic distance

Earlier work highlighted how vulnerability to attack by natural enemies can be mediated by the presence of co-occurring species at particular taxonomic levels, including congeners (Cappuccino and Carpenter 2005, Ricciardi and Ward 2006, Dawson et al. 2009) and confamilials (Cappuccino and Carpenter 2005, Strauss et al. 2006, Dawson et al. 2009, Hill and Kotanen 2009, 2010). However, taxonomic status has been characterized as a subjective and artificial measure of relatedness, one that may bias results compared to using quantitative phylogenetic distances (Webb et al. 2006, Proches et al. 2008, Thuiller et al. 2010). As a result, existing phylogenetic distance metrics (NND and MPD) may have some advantages over taxonomic status. However, NND and MPD make assumptions about the types of relatives influencing a given interaction that may be unrealistic, and thus they may not provide the most insight into some community patterns. MIPD and INND make different

assumptions. For example, MIPD assumes that all species in the community might matter, but not equally so; its value is derived from its ability to 1) utilize quantitative estimates of phylogenetic distances (as do NND and MPD) and 2) incorporate the influences of multiple species weighted by their relatedness to the focal species, instead of focusing on one relative (NND), one taxonomic position (congeneric/confamilial analyses), or all relatives indiscriminately (MPD). Although the phylogenetic proximity of the nearest native neighbor has a greater influence on MIPD than does the proximity of any other single species, that influence accounts for a small percentage of the MIPD value. For example, in the Eastern hardwood community, the percentage of the MIPD numerator (Σ(phylogenetic distance to each native species)$^{-1}$) contributed by the nearest neighbor is 1.4% $\pm$ 1.2 (mean $\pm$ SD) for native focal species and 2.3% $\pm$ 2.2 for exotic focal species.

Although no one metric will best explain the variation in interspecies interactions in all settings (Thuiller et al. 2010), MIPD and INND are useful descriptions of the relatedness of a species to the larger community. MIPD explained 34 and 20% of the among-species variation in damage for exotic species in an Eastern hardwood forest and native species in a Rocky Mountain montane community, respectively, and INND explained 13% of the among-species variation in damage for native species in the Rocky Mountain montane community. MIPD and INND had equally strong or stronger relationships with the response variable than did the standard forms of the metrics (NND and MPD). As the former pair of metrics assume a nonlinear (and the latter pair a linear) increase in interaction strength with relatedness among species, our results suggest that the nonlinear assumption may be more accurate. Note, however, than none of the metrics used in this study are designed to explain the proportion of damage that is phylogenetically structured, i.e. is a consequence of the position in an evolutionary tree rather than the consequence of that position relative to other branches (Hill and Kotanen 2010).

While MIPD seems particularly well suited to characterizing host phylogenetic similarity in the context of enemy attack, we emphasize that it may be broadly useful. Other types of ecological interactions such as competition and facilitation are likely to be structured such that the presence of multiple related species matters, and such that the effect of each relative increases nonlinearly with its phylogenetic similarity. Likely examples include phylogenetically structured transitions from facilitation to competition (Valiente-Banuet and Verdu 2008, Verdu et al. 2009), the phenomenon of associational resistance between neighboring plant species (Tahvanainen and Root 1972, Hillebrand and Cardinale 2004, Jactel and Brockerhoff 2007), and the links between species richness and community/ecosystem functioning (Balvanera et al. 2006).

Predicting herbivory in communities: future directions

Adding abundance data to models including phylogenetic structure could substantially improve predictive power. Metrics such as those employed in our analyses treat all relatives at a given phylogenetic distance from the focal as equally influential. However, the relative abundances of particular species can influence how they donate and/or share herbivores with other species (Gobner et al. 2009). In our Eastern hardwood forest site, *Quercus rubra* and *Acer saccharum* accounted for 37 and 30% (respectively) of the fallen leaf mass collected in autumn litter fall traps deployed in 2007 and 2009 (unpubl.). An overwhelming proportion of the plants in this forest are near at least one individual of each tree species. That ubiquity could augment the phylogenetic signals of these species as perceived by other species (e.g. the potential for those common species to act as a source of natural enemies to other species). Common species may also be more readily colonized by herbivores or retain those herbivores differently; it may be no coincidence that the dominant tree in the hardwood community (*Q. rubra*) experienced more than twice the folivory of other species with comparable NND, MPD, INND and MIPD (data not shown).

More work is needed on the effects of missing data (e.g. incomplete species lists) on predicting herbivory in a phylogenetic context. We hypothesize that an omitted species is likely to be rare and that, all else being equal, rare species are less likely than common species to act as ecological or evolutionary sources of natural enemies for other species in the community. Whether this same generalization would also apply to cryptic species (e.g. two sister taxa not yet distinguished by taxonomists describing the flora) is unclear.

Future studies are needed to explicitly examine effects of spatial scale on the relationships between phylogenetic distance metrics and enemy attack, as phylogenetic patterns are frequently scale-dependent (Cavender-Bares et al. 2006, Kraft and Ackerly 2010). In some contexts, increases in richness may coincide with decreases in the density of any one species. Species may also have idiosyncratic spatial scales that best reveal the influences of the phylogenetic distance of other species in the community, and species may perceive the boundaries of communities differently. If natural enemies readily move between the focal community and the surrounding matrix, a description of the focal community alone may be an inaccurate description of the community perceived by the natural enemy. In our study, the montane flora describes a large spatial area, and the hardwood forest study site is embedded in a landscape that is largely more of the same. As a result, our descriptions may remain robust in the face of interactions that link the study sites with the larger community. The converse is also intriguing; the interactions between two adjacent communities could be quantified based on the degree to which a phylogenetically informed model derived from one community is altered with the inclusion of information regarding the species present in the neighboring community.

Conclusions

Plant traits such as apparency, leaf longevity, architecture and secondary chemistry clearly contribute to the interspecific variation in attack by natural enemies. Our results indicate that the phylogenetic similarity of a given plant species to the larger community integrates across these varied traits and predicts interactions with natural enemies. Our results

thus support the emerging combination of empirical and theoretical work demonstrating that phylogenetic structure influences multiple aspects of communities, from the realized host breadth of natural enemies, to spatial structuring of heterospecific individuals within a community, to the pace and direction of community assembly and succession (Webb et al. 2006, Clay et al. 2008, Emerson and Gillespie 2008, Valiente-Banuet and Verdu 2008, Cavender-Bares et al. 2009, Vamosi et al. 2009, Whitney et al. 2009, Vacher et al. 2010). Our approach uses novel phylogenetic distance metrics that posit a nonlinear increase in interaction strength with relatedness among species. Such metrics offer a framework for exploring mechanisms underlying other patterns, including the increased susceptibility of insular island communities to invasion and the tremendous among-community variation in performance of individual species (including exotics) that seem, at first blush, to be unpredictable.

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