Ecological and Evolutionary Interaction Network Exploration: Addressing the Complexity of Biological Interactions in Natural Systems with Community Genetics and Statistics

Matthew K. LAU[*1], Thomas G. WHITHAM[*1,2], Louis J. LAMIT[1] and Nancy C. JOHNSON[*1,2]

[*1] Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011-5640
[*2] Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, AZ 86011-5640
Corresponding Author e-mail: mkl48@nau.edu

Abstract

Ecological communities play an integral role in determining ecosystem functions. However, community-level patterns and processes are complex because they are typically comprised of many interacting components. Therefore, pair-wise reductionist investigations of interactions among species are unlikely to reveal the dynamics of the whole community. Here, we present results from a study of the interactions among members of a lichen community associated with different genotypes of a foundation tree species, *Populus angustifolia*. Three key findings emerge. First, null-model based analysis of species co-occurrence patterns suggest that interactions are likely contributing to lichen community structure. Second, the pattern of co-occurrences and pair-wise correlations of lichen species suggest that interactions among lichens are primarily facilitative. Third, the significance and magnitude of co-occurrence patterns vary among genotypes of *P. angustifolia* suggesting that the strength of facilitative interactions among lichens is tree genotype dependent. In combination, direct and indirect plant genetic effects on the interactions of lichens appear to play an important role in defining the lichen community. We believe that a community genetics approach focused on foundation species will allow researchers to better understand the selection pressures that shape communities and that many unexpected outcomes will emerge. From this perspective we discuss future research directions that employ greater analytical power to further quantify the complex network of species interactions within communities.

INTRODUCTION

Ecosystems are changing rapidly in response to anthropogenic pressures, such as climate change (Davis and Shaw 2001) and non-native species invasions (Vitousek et al. 1996). It is imperative to the future well-being of society that ecosystem functions are maintained in the face of mounting ecosystem state-changing forces. Thus, ecologists are charged with the task of understanding the factors that control the stability and resilience of ecosystem functions. In this regard, it is important that we understand interactions among organisms in communities because they contribute both directly and indirectly to ecosystem services (Naeem et al. 1994).

Mechanistic studies of the linkage between community structure and ecosystem function are difficult because of the great complexity of interactions among a myriad of factors (Schmitz and Booth, 1997). One major advance in studying the dynamics of ecosystems has been the direction of studies toward a focus on foundation species (i.e., species that have large ecosystem-wide effects). The foundation species concept introduced by Dayton (1972), encapsulates the concepts of dominant species, keystone species and ecosystem engineers. As such, these species have been shown to direct the dynamics of ecosystems (Ellison et al. 2005a). For example, the loss of foundation species, Eastern Hemlock (Tsuga canadensis),

from an invasion by an exotic aphid-like pest (Adelges tsugae) in Eastern North America has caused rapid shifts in plant and ant community composition (Ellison et al. 2005b). This suggests that understanding how a foundation species is likely to respond to environmental perturbations, such as exotic species invasions or climate change, will provide important insights about the dynamics of the ecosystem as a whole.

The foundation species perspective has enabled the growth of the field of community genetics, which is defined as the study of the genetic interactions that occur between species and their abiotic environment in complex communities (Whitham et al. 2006). From an evolutionary perspective, community ecology can be viewed as the study and quantification of the interspecific sources of natural selection. As one species changes evolutionarily other species that interact with it will likely change as well. This has been documented in pair-wise and multi-species studies (see Ehrlich and Raven 1964, Whitham et al. 2003, Johnson and Agrawal 2005). Studying the community genetics of foundation species makes it possible to begin to quantify the evolutionary forces in communities, including complex interactions among species (see Whitham et al. 2006).

Our view beyond the effects of a foundation species is still limited if we do not begin to incorporate greater details about the effects of the self-organizing process of interactions among the associated community members and their subsequent feedbacks. Evidence suggests that interactions among community members are likely to play an important role in determining community structure. The structure of relationships among species has been shown to be an important property of communities (Dunne et al. 2002, Bascopmte et al. 2006). In addition the presence of feedbacks (Bever 2002) and indirect effects (Ohgushi et al. 2007) have also been shown to play an important role. For example, Johnson et al. (2010) found that the source of arbuscular mycorrhizal communities had an effect on the reproductive output of different ecotypes of a foundation grass species. If interactions among community members associated with a foundation species are weak, then solely focusing on the dynamics of the foundation species can provide robust predictions of ecosystem dynamics. However, if these community interactions are strong or non-linear (e.g., thresholds), then inferences that do not include them will be unlikely to predict ecosystem dynamics. To illustrate this point, consider two hypothetical interaction network structures (Fig. 1): one in which the community is linked together only through the foundation species (A) and another where the foundation species is still central to the community but the associated species interact with each other to form a complicated web (B). In community A, a change in the foundation species can potentially affect all species in the community, but the effect will be direct as long as feedback effects are
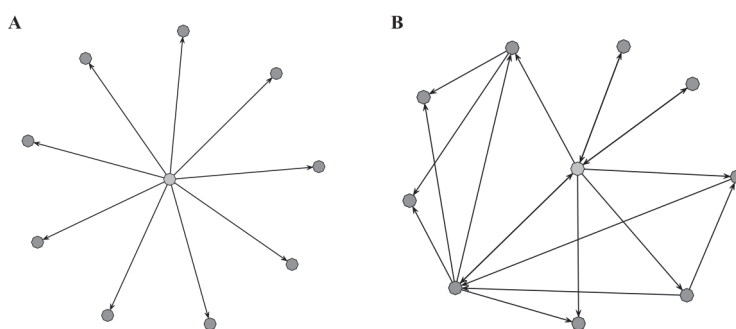

Fig. 1. Two network graphs of how foundation species influence associated organisms and how associated organisms can influence each other to influence community structure. Vertices (dots) and edges (arrows) represent species and interactions, respectively. The direction of the arrowhead indicates the direction of the interaction. In each case the foundation species is the central vertex with associated species radiating around it. Graph (A) shows a situation where there is a unilateral effect of the foundation species on the associated community (i.e., all interactions are direct via the foundation species). (B) shows a more complicated interaction network with the same richness in which some species do not interact directly with the foundation species and some species affect the foundation species to influence other species (e.g., interspecific indirect genetic effects).

small. However, in community B, the change in the foundation species will ripple though the community and could be amplified by interactions among other species creating a community-wide effect that would be much harder to predict. Unfortunately, experimental manipulation of communities to tease apart multi-species interactions are typically intractable. Field-based observational data, however, is often easier to obtain and may provides more reliable information about species relationships, which we utilize here.

We present the results of analyses of communities of epiphytic lichens associated with a foundation tree species, *Populus angustifolia*. This cottonwood species is a dominate tree of riparian habitat found throughout the interior mountains of western North America, including parts of the U. S., southern Canada and northern Mexico (Eckenwalder 1984). Previous studies have demonstrated that tree genotype plays a major role in defining the canopy arthropod community, soil microbial community, trophic interactions and even nutrient cycling (Shuster et al. 2006, Bailey et al. 2006, Schweitzer et al. 2008, Whitham et al. 2006). Although these communities are either known or suspected to strongly interact with the tree, other community members such as epiphytic lichens were not thought to be sensitive to sub-specific variation in tree traits and, thus, not be influenced by the effects of tree genotype. However, recent observations suggest that lichen communities do differ in composition among P. angustifolia genotypes (L. J. Lamit et al. unpublished). We use this lichen community dataset to explore how a community genetics approach combined with co-occurrence analyses can reveal novel interactions and unexpected community structure. Two major questions were addressed. First, is there evidence that interactions among species associated with a foundation tree species contribute to community structure? Second, do these interaction effects vary with foundation tree species genetics? In light of the results of these analyses we discuss potential research and modeling methods that could help elucidate community-level patterns of species interactions and their implications for community genetics.

MATERIALS AND METHODS

We quantified the lichen community on the lower trunks of individual Populus angustifolia trees of known genotype planted in a common garden in Ogden, Utah, USA. The common garden was initiated in 1991 using cuttings taken from trees growing along the nearby Weber River. Tree genotypes were planted in a fully randomized design to minimize environmental influences. We sampled 16 genotypes with 3 to 8 replicates each for a total of 70 trees. In July 2008, we obtained the percent cover of each lichen species in 10 cm^2 quadrats centered at 15 cm, 50 cm and 85 cm from the ground on both the north and south side of the main trunk of each tree (total sampling area = 60 cm^2 per tree). A total of 5 lichen species were observed: *Xanthomendoza galericulata*, *Physciella melanchra*, *Candelariella deflexa*, *Caloplaca holocarpa* and *Rinodina turfacea*.

Grouping lichen community observations on each tree by genotype, we estimated the net effects of interactions among lichen species on each genotype using null model based co-occurrence analyses conducted in EcoSim (Gotelli and Entsminger 2005). Originally developed as a means to test hypotheses of assembly rules, co-occurrence analysis has developed into a statistical means to estimate the potential effects of interactions among species (Gotelli and Graves 1996). In essence, a co-occurrence statistic from the observed data is compared to the distribution of the same statistic calculated for a large set of communities that are not structured by interactions but simulated by permutation of the original data. By observing the co-occurrences in the common garden on randomly distributed replicates of each tree genotype, we can assume that any factors influencing the co-occurrence patterns other than interactions among species will introduce only random variation.

Although we explored several metrics and permutation algorithms here we present the results using the C-Score, which measures the average co-occurrence among all species pairs, developed by Stone and Roberts (1990) as our metric and a fixed-equiprobable permutation algorithm in which the species totals remain constant (fixed) for each simulation but the total number of occurrences in an observation can vary (equiprobable). This combination has performed well with respect to Type I and Type II errors in simulation tests (Gotelli 2000). We follow that standard method of using a Standardized Effect Size (SES) to compare our observed to simulated (i.e., random) communities. The SES is calculated as the observed C-Score minus the mean of the simulated C-Scores divided by the variance of the simulated data.

To explore the relationship among pairs of lichen species we examined the pair-wise correlations. As with the co-occurrence analyses above, observations were grouped by the genotype of *P. angustifolia*. Using Pearson's correlation coefficient (r) we calculated and then averaged all unique pair-wise correlations within each genotype. The regression lines used in the correlation plot are the product of a linear regression model for each species pair that was observed for *P. angustifolia* genotype RL6. The bivariate plots for the pair-wise correlations and network diagrams were generated using the statistical programming language R (R Development Core Team 2009, Butts 2009).

RESULTS

The lichen communities we examined showed evidence of variation in the degree of species interactions among tree genotypes. In the co-occurrence analysis the SES values for several of the *P. angustifolia* genotypes were significantly different from zero with values less than -2 (Fig. 2). In other words, the average co-occurrence patterns for these lichen communities were at least 2 standard deviations less than the simulated mean from the null model randomizations. Note that SES values less than zero are indicative of species co-occurring together more often than would be expected under the null-model (i.e., random species associations). In addition, the SES magnitude and statistical significance varied among genotypes with the largest being over 3X the smallest SES value.

Patterns of pair-wise correlations among lichen species were primarily positive. The mean correlations for the genotypes that had significant co-occurrence results were all greater than zero (subscripts indicate genotype): $r_{1008} = 0.23$, $r_{10} = 0.47$, $r_{WC5} = 0.94$ and $r_{RL6} = 0.81$. A bivariate plot of the lichen species on tree genotype RL6 shows that all species pairs exhibited positive relationships (Fig. 3).

DISCUSSION

Genetic-based interactions affect community structure - Addressing our two main questions, there is evidence that interactions among lichen species contribute to community structure and that this effect varies among genotypes of *P. angustifolia*. Our evidence is based on the application of null-model based co-occurrence analyses that examine how the genetics of a foundation tree species influences the net effects of interactions among associated species. The co-occurrence analysis showed not only significant co-occurrence patterns, but also variation in the co-occurrence patterns among genotypes. Although the co-occurrence analysis method has been used previously to study the variation in co-occurrence patterns of insect guilds associated with the foundation tree species, *Tsuga canadensis*, (Dilling et al. 2007), it has not been used previously to examine the genetic effects of a foundation species on interactions.

Over the spatial scale of this study, non-random co-occurrence patterns can arise from the common influence of an environmental gradient or interactions among species. However, because the communities were observed in a common garden, environmental effects other than the influence of the variation in tree genetics primarily introduce random variation in species co-occurrence patterns. It is possible that other organisms, cryptic lichen species or non-lichen species (e.g., fungus mites) that were not included in these analysis, may influence the lichen community, and further observation of a broader portion of the community and natural history studies will provide more detailed information on the ultimate cause of these patterns.

A genetic component to facilitative interactions - In addition, the SES values from the co-occurrence analysis and correlations among species suggest that the interactions were primarily facilitative. All of the SES values were less than or equal to zero. Negative SES values arise when species tend to co-occur more often than is predicted by the null-model. Therefore, the negative SES values indicate that species tended to cluster together on average. This pattern is corroborated by the positive average correlation values and the pair-wise correlations within the *P. angustifolia* genotype RL6.

Thus, these results suggest that interactions within the community of lichens contribute significantly to community structure, primarily through facilitative relationships, but this depends on the genetic effects of the tree on which they were growing. Our results are in line with the findings of previous studies of the lichen community in this system which demonstrated that *X. galericulata* and the community as a whole exhibits heritable variation among *P. angustifolia* genotypes (L. J. Lamit et al. in review and unpublished).
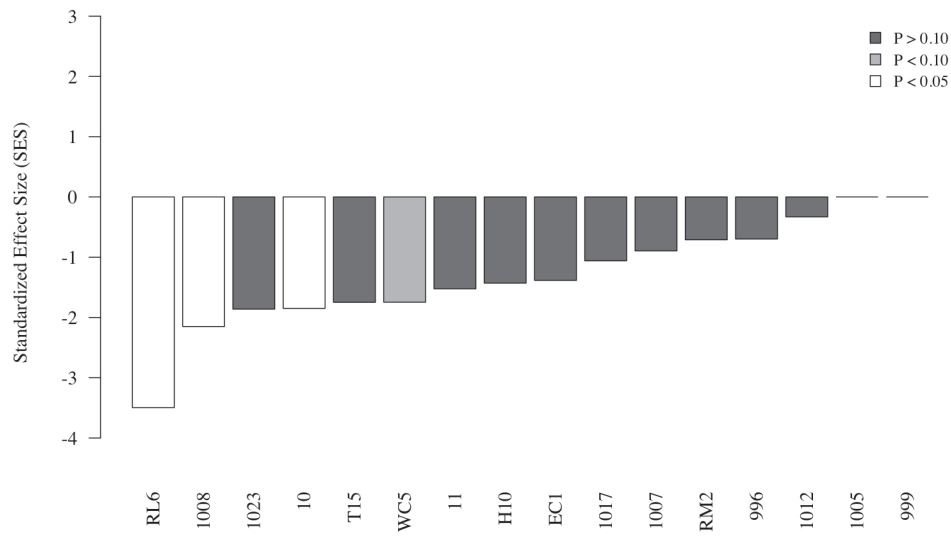
Fig. 2. Plot showing the variation of the Standardized Effect Sizes (SES) for the epiphytic lichen communities on replicated genotypes of *Populus angustifolia* growing in a common garden. Negative SES values are indicative of species being positively associated (i.e., aggregating) beyond what would be expected by chance alone. Bar colors indicate significance levels for the SES of each genotype.
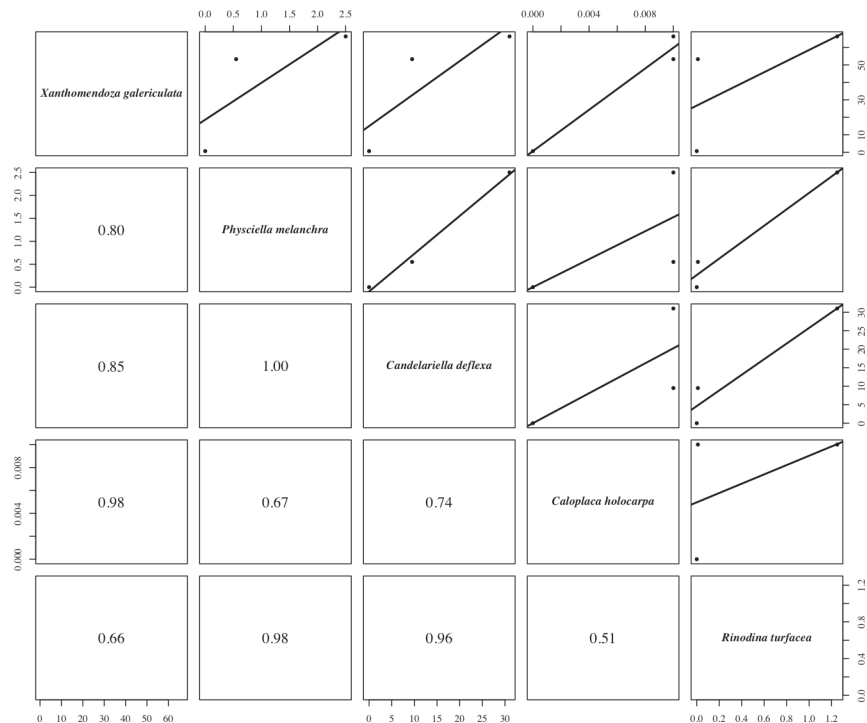

Fig. 3. Bi-variate plots for pair-wise species combinations of epiphytic lichen species present on *Populus angustifolia* genotype RL6 in the common garden. Each species is listed on the diagonal. The upper panels show the bi-variate plots with least squares regression lines. The lower panels have the Pearson's correlation value for each correlation.

Understanding ecological systems in the face of the complexity of numerous interacting species is a long standing problem in ecology (Darwin 1859). Traditionally, studies of biodiversity have primarily focused on the number and proportion of species in ecosystems (Bascompte, 2009); however understanding the web of interactions among species is important for predicting community dynamics. For example, in a study of the interaction between the tree, *Juniperus monosperma*, and the mistletoe, *Phoradendron juniperinum*, the introduction of a third species, a seed dispersing bird, *Myadestes townsendi*, altered the net effect of the interaction between the juniper and the mistletoe from parasitism to mutualism (van Ommeren and Whitham 2002). Although empirical studies have demonstrated that foundation species have strong direct effects on community structure (e.g., insects, fungi and birds - Dickson and Whitham 1996, mycorrhizal fungi - Sthultz et al. 2009), our findings indicate that the genetics of foundation species can have indirect effects on the structure of associated communities by influencing the interactions among species, which as the above example demonstrates, may have unexpected outcomes. Because the interactions among associated species are in part determined by the genetics of the foundations species, understanding these genetic effects on interactions will be important in scaling from local (i.e., genetics of individuals) to community and ecosystem-level patterns, which is important for understanding ecological systems in general (Levin 1992, Brooker et al. 2009).

Focusing on foundation species presents a starting place for studying ecological and evolutionary interaction networks. We can apply the results of the present study to make more refined predictions about the dynamics of the bark lichen communities associated with cottonwoods. For example, evidence from empirical and theoretical studies suggest that facilitation is important community dynamics, diversity and evolution (Rudgers and Maron 2003, Velland 2008, Bronstein 2009). Specifically, mathematical modeling indicates that facilitation can lead to greater community stability depending on local levels of environmental severity (Butterfield 2009). Thus, those genotypes that promote facilitation among associated lichen species will tend to have more stable communities of lichen and lichen associated species, such as mites (Acarina), springtails (Collembola), slugs and snails (Gastropoda) and endolichenic fungi (see Brodo, Sharnoff and Sharnoff 2001, Arnold et al. 2009).

Statistical exploration of interaction networks - As shown in our lichen community study, statistical analyses of community abundance datasets can compliment experimental approaches for exploring interactions among species and directing further observations and experiments to develop and test theory. Null-model based co-occurrence analysis is not only a useful method to measure and test for the net effects of species interactions but also has a large literature base with a long history (Weiher and Keddy 1999). However, one limitation of the application of co-occurrence analysis to investigate interaction networks is that its focus is on the net effects of species interactions. Thus, other methods are needed to elucidate the structure of the interaction network.

Analysis of correlations among species is a simple means to probe datasets for species interaction information, especially when we already have hypotheses about the interactions (e.g., trophic relationships). Although correlation analysis is limited by the causal interpretability of pair-wise correlations, especially when species relationships are likely to be non-linear, its results still provide useful information in the face of difficulties in experimental manipulation of the many numerous pairs of species not to mention their higher dimensional interactions (Shipley 2000). A promising analysis using temporal, rather than spatial (as is the case with our lichen data), species covariances has recently been developed using reverse engineering mathematics originally developed for detecting the structure of gene interaction networks (Jarrah et al. 2007). This method has been used in other fields, such as gene expression networks, but has only recently been applied to ecological interaction networks (Vera-Licona and Laubenbacher 2008).

In an uncertain future of human induced environmental shifts (Breshears et al. 2005) it is important that environmental scientists have a firm understanding of the structure and dynamics of ecological networks (see Cohen 1978, Pascual and Dunne 2006), especially if network theory is broadly applicable across many fields (Barabási 2009). As ecosystems change, changes in the interactions among species will affect the stability and functioning of ecosystems. By resolving the structure of interspecific interaction networks, we can make better predictions of ecosystem dynamics, such as predicting species

extinction risks (Allesina and Pascual 2009) and assessing the viability of whole communities (Ebenman and Jonsson 2005). This will require the greater use of analytical methods, especially when experimental research is limited.

References

Allesina, S. and M. Pascual (2009) Googling food webs: can an eigenvector measure species' importance for coextinctions?. PLoS Computational Biology, 5: e1000494-e1000494.

Arnold, A. E., J. Miadlikowska, K. L. Higgins, S. D. Sarvate, P. Gugger, A. Way, V. Hofstetter, F. Kauff and F. Lutzoni (2009) Hyperdiverse fungal endophytes and endolichenic fungi elucidate the evolution of major ecological modes in the Ascomycota. Systematic Biology, 58: 283-297.

Bailey, J. K., S. C. Wooley, R. L. Lindroth and T. G. Whitham (2006) Importance of species interactions to community heritability: A genetic basis to trophic-level interactions. Ecology Letters, 9: 78-85.

Barabási, A. -L. (2009) Scale-free networks: a decade and beyond. Science, 325: 412-413.

Bascompte, J. (2009) Disentangling the web of life. Science, 325: 416-419.

Bascompte, J., P. Jordano and J. M. Olesen (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. Science, 312: 431-433.

Bever, J. D. (2002) Negative feedback within a mutualism: Host-specific growth of mycorrhizal fungi reduces plant benefit. Proceedings of the Royal Society of London, 269: 2595-2601.

Breshears, D. D., N. S. Cobb, P. M. Rich, K. M. Price, C. G. Allen, R. G. Balice, W. H. Romme, J. H. Kastens, M. L. Floyd, J. Belnap, J. J. Anderson, O. B. Myers and C. W. Meyer (2005) Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences, 102: 15144-15148.

Brodo, I. M., S. D. Sharnoff and S. Sharnoff (2001) Lichens of North America, Yale University Press, New Haven, CT, pp.59-60.

Bronstein, J. L. (2009) The evolution of facilitation and mutualism. Journal of Ecology, 97: 1160-1170.

Brooker, R. W., R. M. Callaway, L. A. Cavieres, Z. Kikvidze, C. J. Lortie, R. Michalet, F. I. Pugnaire, A. Valiente-Banuet and T. G. Whitham (2009) Don't diss integration: a comment on ricklefs's disintegrating communities. American Naturalist, 174: 919-927.

Butterfield, B. J. (2009) Effects of facilitation on community stability and dynamics: Synthesis and future directions. Journal of Ecology, 97: 1192-1201.

Butts, C. T. (2009) sna: Tools for Social Network Analysis, R package version 2.0-1.

Cohen, J. E. (1978) Food Webs and Niche Space, Princeton University Press, Princeton, NJ.

Darwin, C. (1859) On the Origin of Species by Means of Natural Selection, John Murray, London.

Davis, M. B. and R. G. Shaw (2001) Range shifts and adaptive responses to quaternary climate change. Science, 292: 673-679.

Dayton, P. K. (1972) Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica, B.C. Parker (Ed.), Proceedings of the colloquium on conservation problems in Antarctica, Lawrence, KS, Allen Press.

Dickson, L. L. and T. G. Whitham (1996) Genetically-based plant resistance traits affect arthropods, fungi, and birds. Oecologia, 106: 400-406.

Dilling, C., P. Lambdin, J. Grant and L. Buck (2007) Insect Guild Structure Associated with Eastern Hemlock in the Southern Appalachians. Environmental Entomology, 36: 1408-1414.

Dunne, J., R. Williams and N. Martinez (2002) Food-web structure and network theory: the role of connectance and size. Proceedings of National Academy of Sciences, 99: 12917- 12922.

Ebenman, B. and T. Jonsson (2005) Using community vaiability analysis to identify fragile systems

and keystone species. Trends in Ecology and Evolution, 20: 568-575.

Eckenwalder, J. E. (1984) Natural intersectional hybridization between North American species of Populus (Salicaceae) in sections Aigeiros and Tacamahaca. II. Taxonomy, Canadian Journal of Botany, 62: 325-335.

Ehrlich, P. R. and P. H. Raven (1964) Butterflies and plants: a study in coevolution. Evolution, 18: 586-608.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. von Holle and J. R. Webster (2005a) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment, 9: 479-486.

Ellison, A. M., J. Chen, D. Diaz, K. -B. Chelsea and M. Lau (2005b) Changes in ant community structure and composition associated with hemlock decline in New England, B. Onken and R. Reardon (Eds.), Proceedings of the 3rd symposium on hemlock woolly adelgid in the eastern United States, Morgantown, WV, USDA Forest Service.

Gotelli, N. J. and G. R. Graves (1996) Null Models in Ecology, Smithsonian Institution Press, Washington, DC.

Gotelli, N. J. (2000) Null model analysis of species co-occurrence patterns, Ecology, 81: 2606-2621.

Gotelli, N. J. and G. L. Entsminger (2005) EcoSim: Null models software for ecology, Version 7.72, Acquired Intelligence Inc. & Kesey-Bear.

Jarrah, A., R. Laubenbacher, B. Stigler and M. Stillman (2007) Reverse engineering of polynomial dynamical systems. Advances in Applied Mathematics, 39: 477-489.

Johnson, N. C., G. W. T. Wilson, M. A. Bowker, J. Wilson and R. M. Miller (2010) Resource limitation is a driver of local adaptation in mycorrhizal symbioses. Proceedings of the National Academy of Sciences; IN PRESS.

Johnson, M. T. J. and A. A. Agrawal (2005) Plant genotype and the environment interact to shape a diverse arthropod community on Evening Primrose. Ecology, 86: 874-885.

Lamit, L. J., M. A. Bowker, L. M. Holeski, R. R. Naesborg, S. C. Wooley, M. Zinkgraf, R. L. Lin-

droth, T. G. Whitham, C. A. Gehring (in review) The genetics of a foundation tree species influence a dominant bark lichen, Oecologia.

Levin, S. A. (1992) The problem of pattern and scale in ecology. Ecology 73(6): 1943-67.

Naeem S., L. J. Thompson, S. P. Lawler, J. H. Lawton and R. M. Woodfin (1994) Declining biodiversity can affect the functioning of ecosystems. Nature, 368: 734-737.

Ohgushi T., T. P. Craig and P. W. Price (2007) Indirect interaction webs: an introduction, T. Ohgushi, T. P. Craig and P. W. Price (Eds.), Ecological Communities: Plant Mediation in Indirect Interaction Webs, Cambridge University Press, New York, pp. 3-15.

Pascual, M. and J. A. Dunne (2006) Ecological networks: linking structure to dynamics in food web, M. Pascual and J. A. Dunne (Eds.), Ecological networks: Linking structure to dynamics in food webs, Oxford University Press, New York, p. 3-24.

R Development Core Team (2009). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Rudgers, J. A. and J. L. Maron (2003) Facilitation between coastal dune shrubs: A non-nitrogen fixing shrub facilitates establishment of a nitrogen fixer. Oikos 102: 75-84.

Schmitz, O. J. and G. Booth (1997) Modelling food web complexity: The consequences of individual-based, spatially explicit behavioural ecology on trophic interactions. Evolutionary Ecology, 11: 379-398.

Schweitzer, J. A., J. K. Bailey, D. G. Fischer, C. J. LeRoy, E. V. Lonsdorf, T. G. Whitham and S. C. Hart (2008) Plant-soil-microorganism interactions: heritable relationship between plant genotype and associated soil microorganisms, Ecology, 89: 773-781.

Shipley, B. (2000) Cause and Correlation in Biology: A User's Guide to Path Analysis, Structural Equations and Causal Inference. Cambridge University Press.

Shuster, S. M., E. V. Lonsdorf, G. M. Wimp, J. K. Bailey and T .G. Whitham (2006) Community heritability measures the evolutionary consequences of indirect genetic effects on community structure. Evolution, 60: 991-1003.

Stone, L. and A. Roberts (1990) The checkerboard

score and species distributions. Oecologia, 85: 74-79.

Sthultz, C. M., T. G. Whitham, K. Kennedy, R. Deckert and C. A. Gehring (2009) Genetically based susceptibility to herbivory influences the ectomycorrhizal fungal communities of a foundation tree species. New Phytologist 184: 657-667.

van Ommeren, R. J. and T. G. Whitham (2002) Changes in interactions between juniper and mistletoe mediated by shared avian frugivores: parasitism to potential mutualism. Oecologia, 130: 281-288.

Velland, M. (2008) Effects of diversity on diversity: Consequences of competition and facilitation, 117: 1075-1085.

Vera-Licona, P. and R. Laubenbacher (2008) Inference of ecological interaction networks. Annales Botanici Fennici, 45: 459-464.

Vitousek, P. M., C. M. Dantonio, L. L. Loope and R. Westbrooks (1996) Biological invasions as global environmental change. American Scientist, 84: 468-78.

Weiher, E. and P. Keddy (1999) Ecological Assembly Rules: Perspectives, Advances, Retreats, E. Weiher and P. Keddy (Eds.), Cambridge University Press, p. 1-20.

Whitham, T. G., W. P. Young, G. D. Martinsen, C. A. Gehring, J. A. Schweitzer, S. M. Shuster, G. M. Wimp, D. G. Fischer, J. K. Bailey, R. L. Lindroth, S. Woolbright and C. R. Kuske (2003) Community and ecosystem genetics: A consequence of the extended phenotype. Ecology, 84: 559-573.

Whitham T. G., J. K. Bailey, J. A. Schweitzer, S. M. Shuster, R. K. Bangert, C. J. LeRoy, E. V. Lonsdorf, G. J. Allan, S. P. DiFazio, B. M. Potts, D. G. Fischer, C. A. Gehring, R. L. Lindroth, J. C. Marks, S. C. Hart, G. M. Wimp and S. C. Wooley (2006) A framework for community and ecosystem genetics: From genes to ecosystems. Nature Reviews Genetics, 7: 510-523.