

# Genotypic variation in a foundation tree drives ecological network structure

**Matthew K. Lau<sup>1,2,\*</sup>, Louis J. Lamit<sup>2</sup>, Rikke R. Naesbourg<sup>3</sup>, Stuart R. Borrett<sup>4</sup>, Matthew A. Bowker<sup>5</sup>, and Thomas G. Whitham<sup>1</sup>**

<sup>1</sup>Department of Biological Sciences and Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, AZ 86011, USA

<sup>2</sup>Harvard Forest, Harvard University, 324 N Main St, Petersham, MA 01366, USA

<sup>3</sup>University of California Berkeley, Berkeley, CA, USA

<sup>4</sup>Department of Biology and Marine Biology, University of North Carolina Wilmington, 601 South College Road, Wilmington, NC, 28403, USA

<sup>5</sup>School of Forestry, Northern Arizona University, Flagstaff, AZ 86011, USA

\*matthewklau@fas.harvard.edu

## ABSTRACT

Biological evolution occurs in the context of complex networks of interacting species in which natural selection defines the structure of ecological networks. Fundamental to this evolutionary process is the discovery of a genetic basis to ecological network structure. Although previous work has demonstrated that tree genotype contributes to interaction network structure at the scale of forest stands, the contribution of tree genetics to localized interaction networks at the scale of individual trees has not yet been explored. To test the degree to which tree genetics can contribute to network structure across scales from trees to stands, we conducted quantitative modeling of interaction network for a community of epiphytic lichens in a long-term experimental common garden of genotyped trees of a foundation species (*Populus angustifolia*). We found three main results: 1) Tree genotype strongly contributed to network structure explaining over a third of the variation in lichen interaction networks, 2) Multiple aspects of interaction network structure varied in response to genotype, including network size, the number of interactions, linkage density and connectance, 3) At the stand scale, we also found significant modular structure of plant-lichen networks resulting in part from the combination of trees of the same genotype tending to have similar community compositions and supporting similar lichen interaction networks dominated by positive interactions. These results support the hypothesis that variation in ecological interaction networks can result from genetically based variation in foundation species. Although these results are for a community of sessile organisms in close proximity to the tree, this study opens the possibility for a genetic basis to both direct and indirect interactions among species in complex communities.

## 1 Introduction

2 Evolution occurs in the context of complex networks of interacting species. In ecological communities, community dynamics  
3 depend on key interactions<sup>1</sup> that occur in species interaction networks, such as: trophic<sup>2</sup> and mutualistic<sup>3</sup> interaction networks.  
4 Phylogenetic patterns in ecological networks support the importance of evolutionary processes in shaping species interactions,  
5 community structure and ecosystem processes<sup>7,8,13</sup>. Community genetics studies<sup>9</sup> have shown that genetic variation in founda-  
6 tion species<sup>4</sup> plays a significant role in defining distinct communities of interacting organisms: such as, endophytes, pathogens,  
7 lichens, arthropods, and soil microbes. Multiple studies have now demonstrated that genetic variation influences numerous  
8 functional traits (e.g., phytochemical, phenological, morphological) produces a multivariate phenotype<sup>5</sup> tha contributes to  
9 variation in associated communities<sup>6</sup>.

10 Additional work has provided support for the hypothesis that not only does composition vary among genetically distinct  
11 genotypes of foundation species but it also impacts the structure of the network of species interactions in these communities<sup>2,7</sup>.  
12 Also, work by Toju 2018, Toju2015, Toju2014 observed consistent patterns of centralized interactions of species modules  
13 focused around hubs of plant-fungal interactions. In other words, a small number of plant and fungal symbionts tended to have  
14 have disproportionate numbers of interactions with other species and likely are the drivers in determining community assembly,  
15 structure and dynamics.

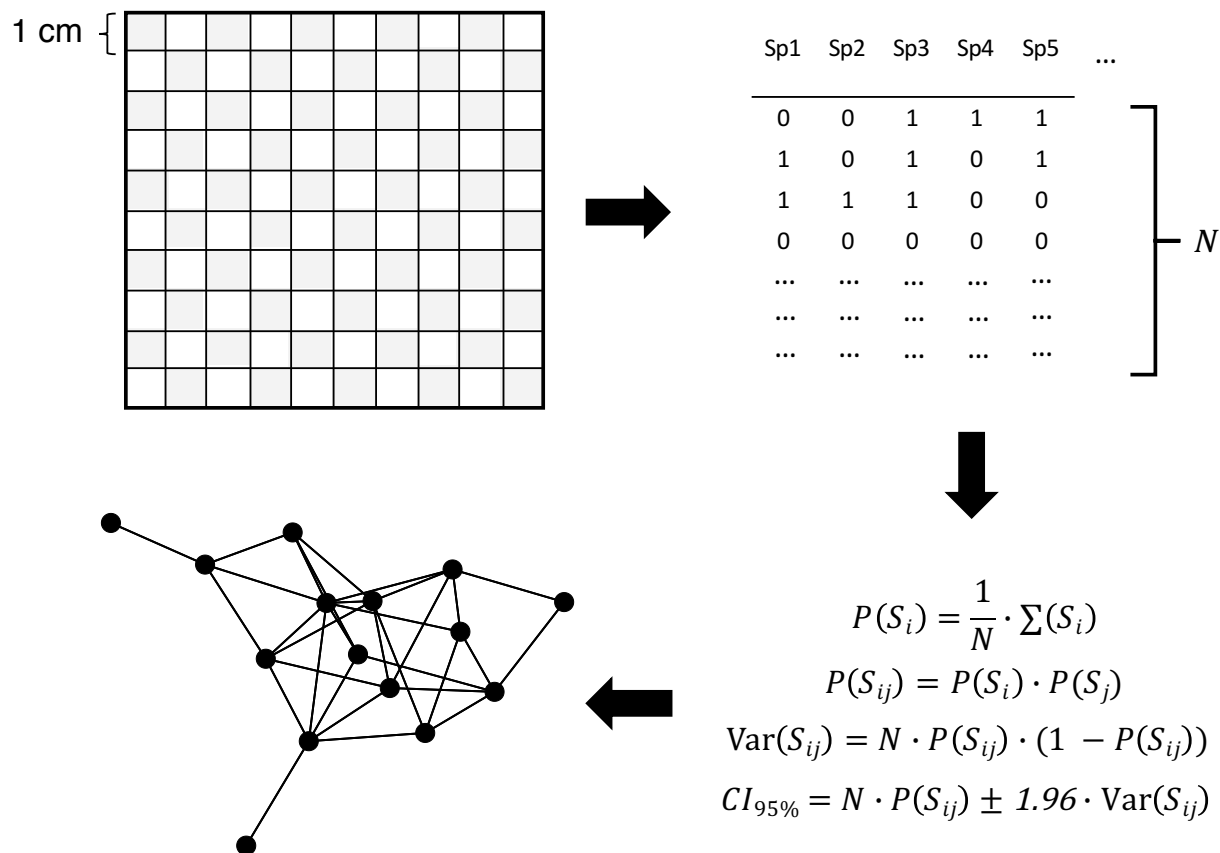
16 Here, we investigate how genetic variation in a foundation tree species determines the structure of a network of interactions  
17 among a community of lichen species. Using a long-term (20 years+), common garden experiment with replicated individuals  
18 of known genetic identity and a naturally established stand of *P. angustifolia*. We focused on a model community of 9 epiphytic  
19 lichens species, as previous research has demonstrated significant compositional responses of epiphytes to genotypic variation<sup>7,8</sup>.  
20 In addition, the life-history characteristics of lichen, having highly localized, direct contact interactions and slow population  
21 turnover rates, allowed us to assess interactions among lichen species on individual trees. We hypothesize that in natural  
22 systems evolution occurs in a community context involving interactions of complex networks of interacting species<sup>2,7,8,9</sup>.  
23 If correct, we should expect to find that network structure is genetically based in which different plant genotypes support  
24 different interaction networks and that these interactions networks can function as indicators of ecological dynamics important  
25 for conserving biodiversity. Applying a dual-scale (lichen-lichen and genotype-lichen interactions) network modeling and  
26 analyses, we then examined the genetically based impacts of *P. angustifolia* on network structure.

## 27 Methods

### 28 Field observations in common garden and natural riparian forest stands

29 The study was conducted along the Weber River, UT (USA), which is a cottonwood (*Populus* spp.) dominated riparian  
30 ecosystem. Although two native species, *Populus angustifolia* (James) and *Populus fremontii* (S. Watson), occur here and are  
31 known to hybridize, only pure or advanced generation backcrosses of *P. angustifolia* were sampled in order to avoid the effect  
32 of the hybridization between these two species.

33 A common garden was used to isolate the effect of tree genotype from the effect of the localized microenvironment associated  
 34 with each individual and spatial autocorrelation. Asexually propagated clones of genotyped *P. angustifolia* individuals were  
 35 obtained from wild collections and planted randomly in a single field (0.025 km<sup>2</sup>) at the Ogden Nature Center, Ogden, UT in  
 36 1992. A total of thirteen genotypes replicated between 3 and 8 times each, were chosen for sampling. Genotype names were  
 37 previously published<sup>2</sup>. Observations were made in the common garden in October 2010 and May 2011.



**Figure 1.** Lichen interaction networks were constructed by conducting field observations in 1 cm<sup>2</sup> cells within a 10 cm<sup>2</sup> grid on each tree using a checkerboard pattern (grey cells). Thus, a set of  $N$  total cell observations were recorded for each tree with the presence or absence of each species recorded for each cell. Applying a null-model based procedure<sup>10</sup>, we calculated and removed non-significant ( $\alpha = 0.05$ ) co-occurrences to produce the network associated with an individual tree.

38 **Make a figure of the field site and lichen on trees**

## 39 Results

40 Primary Findings:

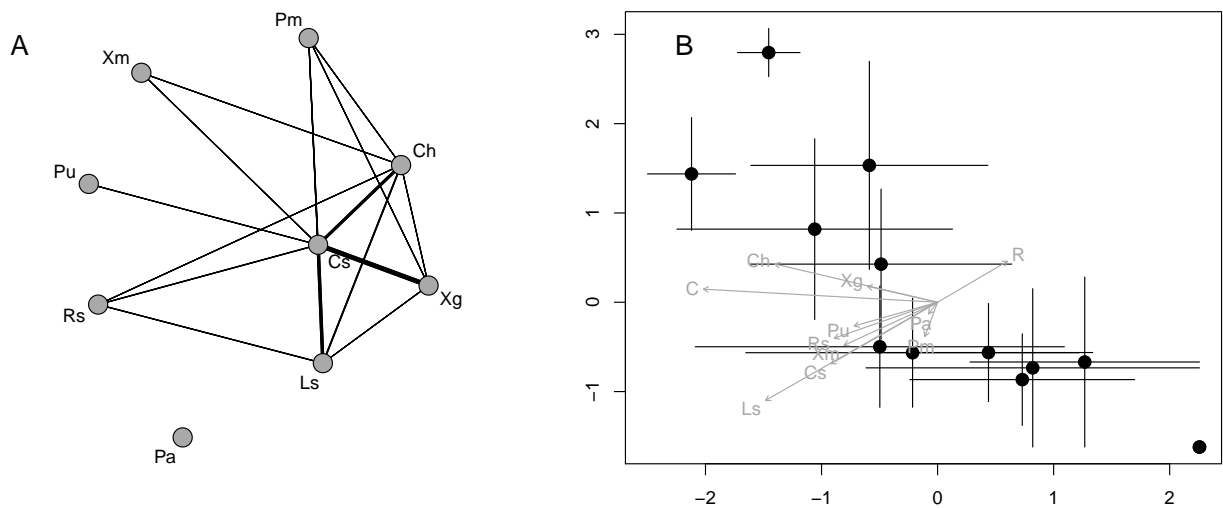
41 **Interactions between lichens and trees depended on tree genotype**

42 • abundance

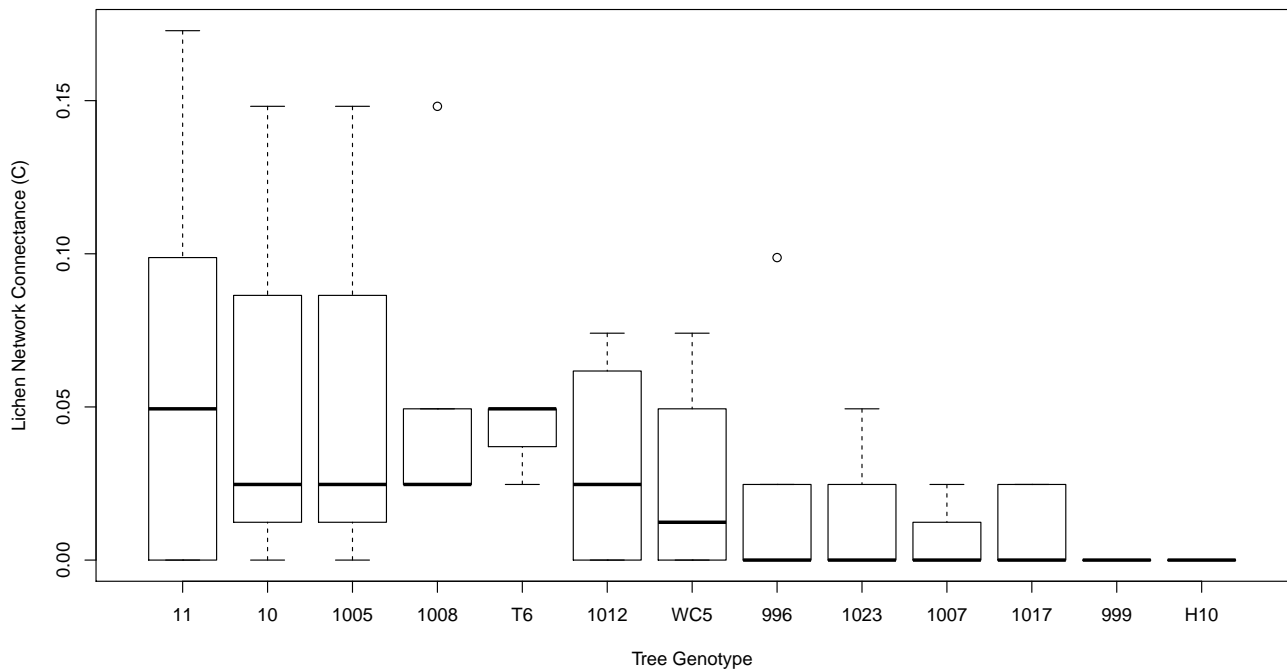
- 43 • roughness predicted by genotype
- 44 • richness not predicted by genotype
- 45 • composition
- 46 **Genotype-Lichen Interactions contributed to stand-level bipartite interaction network structure**
- 47 • bipartite network structure
- 48 **Lichen interaction network structure was genotype dependent**
- 49 • unipartite network structure predicted by genotype
- 50 **Interaction network structure was related to composition but not roughness**
- 51 • unipartite correlation with community composition
- 52 • unipartite not predicted by roughness
- 53 **Structural characteristics of networks were not predicted by genotype**
- 54 • network statistics global level
- 55 • network statistics node level
- 56 Trees acted as environmental filters contributing to interaction
- 57 Interaction network structure depending on tree genotype

Response	Predictor	p-value	H2
Percent Lichen Cover	Tree Genotype	0.0396	0.17
Lichen Species Richness	Tree Genotype	0.1351	0.1
Percent Rough Bark	Tree Genotype	2e-04	0.38
Lichen Network	Genotype	0.0411	0.17
Number of Network Links	Genotype	0.0812	0.15
Network Centrality	Genotype	0.1299	0.12

**Table 1.** Genotypic effects of cottonwood trees on the associated lichen community.



**Figure 2.** Significant lichen interaction network structure resulting from tree genotypic variation was observed in the common garden. A) A network diagram showing significant interactions averaged over all trees shown as edges connecting lichen species shown as vertices. B) Genotype centroids (points) of NMDS ordinated lichen networks ( $\pm 1$  S.E.). Arrows show the magnitude and direction of correlation of the ordinated networks with tree bark roughness (R), network connectance and lichen species abundances (Xg = *Xanthomendoza galericulata*, Xm = *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Candelariella subdeflexa*, Rs = *Rinodina* (unknown species), Ls = *Lecanora* (unknown species), Pm = *Phyciella melanchra*, Pa = *Phycia adscendens*, Pu = *Phycia undulata*).



**Figure 3.** Connectance significantly varied among genotypes.



## Discussion

Trait variation + assembly + ecosystem function

These findings support the hypothesis that genotypic variation in a foundation species contributes to the structure of a network of interacting species that might be least expected to exhibit such structure.

**TGW: MIGHT BE GOOD TO CITE PAPERS ON COMEPTITION IN LICHENS OR OTHER ORGANIZING FACTORS TO BACK UP THE LEAST EXPECTED STATEMENT. AS EPIPHYTES WE MIGHT NOT EXPECT THEM TO CARE.**

**MKL: This is a job for Lamit and Rikke.**

Several lines of evidence support this conclusion. First, the wild stand showed significant interaction network structure (Fig. 1a and b); and both tree genotype and the genetically based tree trait, bark roughness, was a strong predictor of co-occurrence patterns (Fig. 2a).

**TGW: I THINK WE NEED TO EMPHASIZE THE LONG-TERM NATURE OF OUR COMMON GARDEN STUDY AS VERY FEW COMMON GARDEN STUDIES OF LICHENS LIKELY EXIST. ANY REFS ON THIS? IF TRUE MIGHT WANT TO MENTION THIS UP FRONT IN INTRO.**

**MKL: Same here. This is a job for Lamit and Rikke.**

Second, in a long-term common garden study, network (Fig. 1b) structure showed a high degree of similarity to the wild stand network structure (Fig. 1c and d). Third, tree genotype was a significant predictor of SES values (Fig. 2a), displaying significant correlation with a genetically linked trait, bark roughness, both in the common garden (Fig. 2a) and in a naturally established stand of trees (Fig. 2b). Last, both of the bipartite genotype-species networks in the common garden and natural stand displayed significant modularity, suggesting that genotypic variation is leading to the formation of evolutionarily dynamic compartments within the community. Thus, just as numerous studies have shown that plant genotype can affect species richness, abundance, diversity, and composition and previous work has demonstrated that evolutionary processes shape ecological networks<sup>11,12</sup>, our study includes genetics in an empirical investigation that combines both experimental common garden findings along with studies in the wild that are in close agreement.

Our results point to the importance of understanding the community level effects of genetic variation and corroborate previous findings of the importance of plant genetics in shaping community structure and ecosystem processes<sup>13</sup>. This study highlights the potential for indirect effects of genetic variation to propagate through networks of interacting species and trophic levels. Altering the structure of interaction networks presents a means for genetic effects to be magnified within the system of interacting species. For example, Keith et al. (2017) showed that the genetics based interactions of aphid resistant and aphid susceptible trees resulted in different interaction networks of their associated arthropod communities composed of 139 species. At the scale of ecosystems, trophic networks or food webs direct and control the rates of energy and nutrient flux<sup>14</sup>. Furthermore, in a predator-prey-plant study, Smith<sup>15</sup>, showed that the interactions among species across trophic levels depended on plant genotype.

## 0.1 Units of evolutionary potential: Moving beyond species pairs

Although our study was conducted with a community of lichens, these results should be generalized to other groups of diverse organisms around the world that also exhibit significant genetic signals at the community level<sup>16,17</sup>, although spatial scale of interactions should be considered<sup>18</sup> Bangert et al. 2006. As heritable variation is the raw material for natural selection to act upon, a genetic basis for interaction network structure indicates evolutionary dynamics should be considered at the community level and that conserving genetic variation is important to consider in efforts to restore or preserve complex species interactions and their associated ecosystem functions<sup>19</sup>. With such findings, it appears that we are closer to understanding the evolutionary drivers of Darwin's entangled bank and the interconnectedness of species in complex communities.

## References

1. Fontaine, C. *et al.* The ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.* **14**, 1170–81 (2011). URL <http://www.ncbi.nlm.nih.gov/pubmed/21951949>. DOI 10.1111/j.1461-0248.2011.01688.x.
2. Bascompte, J., Jordano, P. & Olesen, J. M. Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance. *Science* (80-. ). **312**, 431–433 (2006). URL <http://www.sciencemag.org/cgi/content/abstract/312/5772/431>. DOI 10.1126/science.1123412.
3. Rafferty, N. E. & Ives, A. R. Phylogenetic trait-based analyses of ecological networks. *Ecology* **94**, 2321–33 (2013).
4. Ellison, A. M. *et al.* Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* **3**, 479–486 (2005). URL [http://www.esajournals.org/doi/abs/10.1890/1540-9295\(2005\)003\[0479:LOFSCF\]2.0.CO;2?journalCode=fron](http://www.esajournals.org/doi/abs/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2?journalCode=fron). DOI 10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2.
5. Holeski, L. M., Hillstrom, M. L., Whitham, T. G. & Lindroth, R. L. Relative importance of genetic, ontogenetic, induction, and seasonal variation in producing a multivariate defense phenotype in a foundation tree species. *Oecologia* **170**, 695–707 (2012). DOI 10.1007/s00442-012-2344-6.
6. Bailey, J. K. *et al.* From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **364**, 1607–16 (2009). URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2690499&tool=pmcentrez&rendertype=abstract>. DOI 10.1098/rstb.2008.0336.
7. Winfree, R., Gross, B. J. & Kremen, C. Valuing pollination services to agriculture. *Ecol. Econ.* **71**, 80–88 (2011). URL <http://www.sciencedirect.com/science/article/pii/S092180091100334X>. DOI 10.1016/j.ecolecon.2011.08.001.



- 121 **8.** Zytynska, S. E., Fay, M. F., Penney, D. & Preziosi, R. F. Genetic variation in a tropical tree species influences the associated  
122 epiphytic plant and invertebrate communities in a complex forest ecosystem. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **366**,  
123 1329–1336 (2011). DOI 10.1098/rstb.2010.0183.
- 124 **9.** Thompson, J. N. *Relentless Evolution* (University of Chicago Press, 2013).
- 125 **10.** Araújo, M. B., Rozenfeld, A., Rahbek, C. & Marquet, P. A. Using species co-occurrence networks to assess the  
126 impacts of climate change. *Ecography (Cop.)*. **34**, 897–908 (2011). URL [http://dx.doi.org/10.1111/j.](http://dx.doi.org/10.1111/j.1600-0587.2011.06919.x)  
127 [1600-0587.2011.06919.x](http://dx.doi.org/10.1111/j.1600-0587.2011.06919.x)5Cn<http://doi.wiley.com/10.1111/j.1600-0587.2011.06919.x>.  
128 DOI 10.1111/j.1600-0587.2011.06919.x.
- 129 **11.** Guimarães, P. R., Jordano, P. & Thompson, J. N. Evolution and coevolution in mutualistic networks. *Ecol. Lett.* **14**, 877–85  
130 (2011). URL <http://www.ncbi.nlm.nih.gov/pubmed/21749596>. DOI 10.1111/j.1461-0248.2011.01649.x.  
131 [arXiv:1012.5461v2](https://arxiv.org/abs/1012.5461v2).
- 132 **12.** Moya-Laraño, J. Genetic variation, predator-prey interactions and food web structure. *Philos. Trans. R. Soc. Lond. B. Biol.*  
133 *Sci.* **366**, 1425–37 (2011). DOI 10.1098/rstb.2010.0241.
- 134 **13.** Whitham, T. G. *et al.* A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.* **7**,  
135 510–523 (2006). DOI 10.1038/nrg1877.
- 136 **14.** Borgatti, S. P. & Everett, M. G. A Graph-theoretic perspective on centrality. *Soc. Networks* **28**, 466–484 (2006). DOI  
137 10.1016/j.socnet.2005.11.005.
- 138 **15.** Smith, D. S., Bailey, J. K., Shuster, S. M. & Whitham, T. G. A geographic mosaic of trophic interactions and selection: trees,  
139 aphids and birds. *J. Evol. Biol.* **24**, 422–9 (2011). URL <http://www.ncbi.nlm.nih.gov/pubmed/21091573>.  
140 DOI 10.1111/j.1420-9101.2010.02178.x.
- 141 **16.** Rowntree, J. K., Shuker, D. M. & Preziosi, R. F. Forward from the crossroads of ecology and evolution. *Philos. Trans. R.*  
142 *Soc. Lond. B. Biol. Sci.* **366**, 1322–8 (2011). URL [http://rstb.royalsocietypublishing.org/content/](http://rstb.royalsocietypublishing.org/content/366/1569/1322.full)  
143 [366/1569/1322.full](http://rstb.royalsocietypublishing.org/content/366/1569/1322.full). DOI 10.1098/rstb.2010.0357.
- 144 **17.** Whitham, T. G. *et al.* Community specificity: Life and afterlife effects of genes (2012).
- 145 **18.** Zook, A. E., Eklof, A., Jacob, U. & Allesina, S. Food webs: Ordering species according to body size yields high degree of  
146 intervality. *J. Theor. Biol.* **271**, 106–113 (2010). URL [http://www.sciencedirect.com/science/article/](http://www.sciencedirect.com/science/article/pii/S0022519310006405)  
147 [pii/S0022519310006405](http://www.sciencedirect.com/science/article/pii/S0022519310006405). DOI 10.1016/j.jtbi.2010.11.045.
- 148 **19.** Evans, D. M., Pocock, M. J. O. & Memmott, J. The robustness of a network of ecological networks to habitat loss. *Ecol.*  
149 *Lett.* **16**, 844–52 (2013). URL <http://www.ncbi.nlm.nih.gov/pubmed/23692559>. DOI 10.1111/ele.12117.

## 150 **Acknowledgments**

151 This work was supported by the National Science Foundation grant (DEB-0425908) and Integrative Graduate Research  
152 Traineeship (IGERT) fellowships for M.L. and L.L. The Ogden Nature Center staff helped to maintain the common gardens.  
153 Lichen sampling was supported by Todd Wojtowicz, Luke Evans and David Solance Smith.

## 154 **Author contributions statement**

155 M.L. and L.L. conceived the study, M.L. and L.L. conducted the field work, R.N. assisted in lichen identifications, M.L. wrote  
156 the first draft of the manuscript, S.B. and T.W. contributed substantively to the conceptual development, T.W. established the  
157 common garden. All authors contributed to revisions of the manuscript.

## 158 **Additional information**