# Genetic diversity and connectivity shape herbivore load within an oak population at its range limit

Tähti Pohjanmies,[1,6,†] Ayco J. M. Tack,[2,3] Pertti Pulkkinen,[4] Sakina Elshibli,[5]
Pekka Vakkari,[5] and Tomas Roslin[1]

[1]Spatial Foodweb Ecology Group, Department of Agricultural Sciences, P.O. Box 27 (Latokartanonkaari 5),
FI-00014 University of Helsinki, Helsinki, Finland
[2]Metapopulation Research Group, Department of Biological and Environmental Sciences, P.O. Box 65 (Viikinkaari 1),
FI-00014 University of Helsinki, Helsinki, Finland
[3]Department of Ecology, Environment and Plant Sciences, Stockholm University, Lilla Frescati, SE-106 91 Stockholm, Sweden
[4]Haapastensyrjä Breeding Station, Finnish Forest Research Institute, Haapastensyrjäntie 34, FI-12600 Läyliäinen, Finland
[5]Vantaa Research Centre, Finnish Forest Research Institute, PL 18, FI-01301 Vantaa, Finland

**Abstract.**   Host genetic diversity and genotypic identity have been reported to affect the abundance, species richness and species diversity of associated herbivore communities. Recent work, however, suggests that these effects are highly context-dependent and that the magnitude and direction of the effects may vary with e.g., spatial factors and the amount of genetic variation present in the host population. Here, we use observational data on a Finnish oak (*Quercus robur*) population to examine whether low genetic diversity within peripheral populations reduces the impact of host genotype on associated herbivore communities. We first compared measures of genetic variation within Finnish oak populations with those recorded in more central parts of the species' range, confirming that genetic variation within the Finnish populations is comparatively low. Despite this result, we found consistent imprints of host genetic diversity on herbivore communities: herbivore load, but not the species richness, increased with host genetic diversity in both years and both spatial scales examined. Spatial connectivity of hosts increased herbivore diversity as well as abundance. While the similarity of herbivore communities increased with the genetic similarity among hosts, the effect of geographic distance was stronger. Overall, our findings identify a major role for spatial context in structuring oak-associated herbivore communities—but we still trace detectable imprints of host genotype at multiple spatial scales even in this peripheral, genetically impoverished oak population.

**Key words:**   community genetics; extended phenotype; genetic variation; *Quercus robur*.

[6] Present address: Department of Biological and Environmental Science, P.O. Box 35 (Survontie 9 C), FI-40014 University of Jyväskylä, Jyväskylä, Finland.
† E-mail: tahti.t.pohjanmies@jyu.fi

## INTRODUCTION

The extent to which the herbivore communities of plants represent an extended phenotype of the host genotype has been the subject of recent debate (Hughes et al. 2008, Bailey et al. 2009, Tack et al. 2012). According to the framework of community genetics, genetic variation within a

population of one species may influence the dynamics and diversity of associated species—a notion for which support has been found in several empirical studies (Hersch-Green et al. 2011). In particular, genetic diversity at the level of plant individuals (i.e., heterozygosity; e.g., Tovar-Sánchez et al. 2013) or plant populations (e.g., Crutsinger et al. 2006, Johnson et al. 2006) has been proposed to affect the abundance and diversity of associated arthropod communities, and the similarity among plant individuals to affect the similarity of the associated communities (e.g., Bangert et al. 2006b). The effects of intraspecific genetic variation of host plants may occur at various levels and thus arise from various mechanisms. For example, host genetic diversity may increase the abundance of associated arthropods at the level of individual plants e.g., by herbivore preference (cf. Gripenberg et al. 2010, Kalske et al. 2014), or at the level of plant populations e.g., by increased resource availability (Crutsinger et al. 2006).

Recent work (Tack et al. 2012) stress that the realized effects of host plant genotype should be compared with other forces that may shape communities in their natural environment. In particular, it has been proposed that spatial effects—the relative position of a host plant with respect to congeneric individuals within the landscape—may dwarf genetic effects (Tack et al. 2010). In addition to spatial effects, the relative effects of host genotype may vary with the amount of genetic variation present in the host population (Bangert et al. 2006b). However, studies in community genetics have consistently focused on systems with ample genetic variation (e.g., hybrid systems). This status quo undermines the generality of current theory.

Oaks (Quercus spp.) are as a genus characterized by high levels of genetic variation within and among species and within conspecific populations (Kremer and Petit 1993). Throughout their range, oaks harbor a diverse community of insect species. They may be considered foundation species in the temperate forests of the northern hemisphere, where their abundance is currently in decline (Lindbladh and Foster 2010). The pedunculate oak (Quercus robur) grows in northern Europe at the northern limit of its natural range. As a likely consequence, the diversity of chloroplast DNA (cpDNA) in the

Q. robur populations of northern Europe has been found to be lower than in central Europe (Petit et al. 2002). In addition to the marginal location, low genetic variation in north European Q. robur populations may derive from small population sizes, the absence of other, interfertile oak species, and the historic fragmentation of habitats (Vakkari et al. 2006).

Here, we use observational data from a natural system to examine the effects of genetic variation in Finnish populations of Quercus robur at their northern range edge on the associated community of galling and leaf-mining herbivores. In particular, we ask: (1) Will the genetic diversity at the individual level (i.e., heterozygosity) affect the structure of the herbivore assemblage occupying the trees? (2) Will host genetic diversity affect the herbivore assemblage at a neighborhood scale, i.e., clusters of trees within the landscape? (3) Will the genetic similarity among hosts increase the similarity of their herbivore communities? (4) Are the results observed here conditional on their setting at the range margin of the host, i.e., are the oaks of Finland genetically more uniform than are oaks at the core of their European range?

## METHODS

### Study design

Quercus robur occurs naturally in the southwestern archipelago and coastal zone of Finland (Ferris et al. 1998). To quantify the level of genetic diversity characterizing Finnish Q. robur populations, we measured the genetic variation within three tree stands in south-western Finland: one in Inkoo, one in Salo, and one on the island of Wattkast (Fig. 1A). All three stands are scattered in structure and located in a mosaic of agricultural areas, water, and bare rock. Samples of trees were genotyped using 15 nuclear microsatellite loci (for details, see Appendix A). Genetic variation within each population was measured as allelic richness (A), calculated in Arlequin v3.5.1.3 (Excoffier and Lischer 2010).

We examined the community-level effects of host genotype within the Q. robur population on Wattkast, focusing on two spatial scales: individual trees and tree neighborhoods. One hundred trees were randomly selected (Fig. 1B) and surveyed for c. 20 galling and leaf-mining
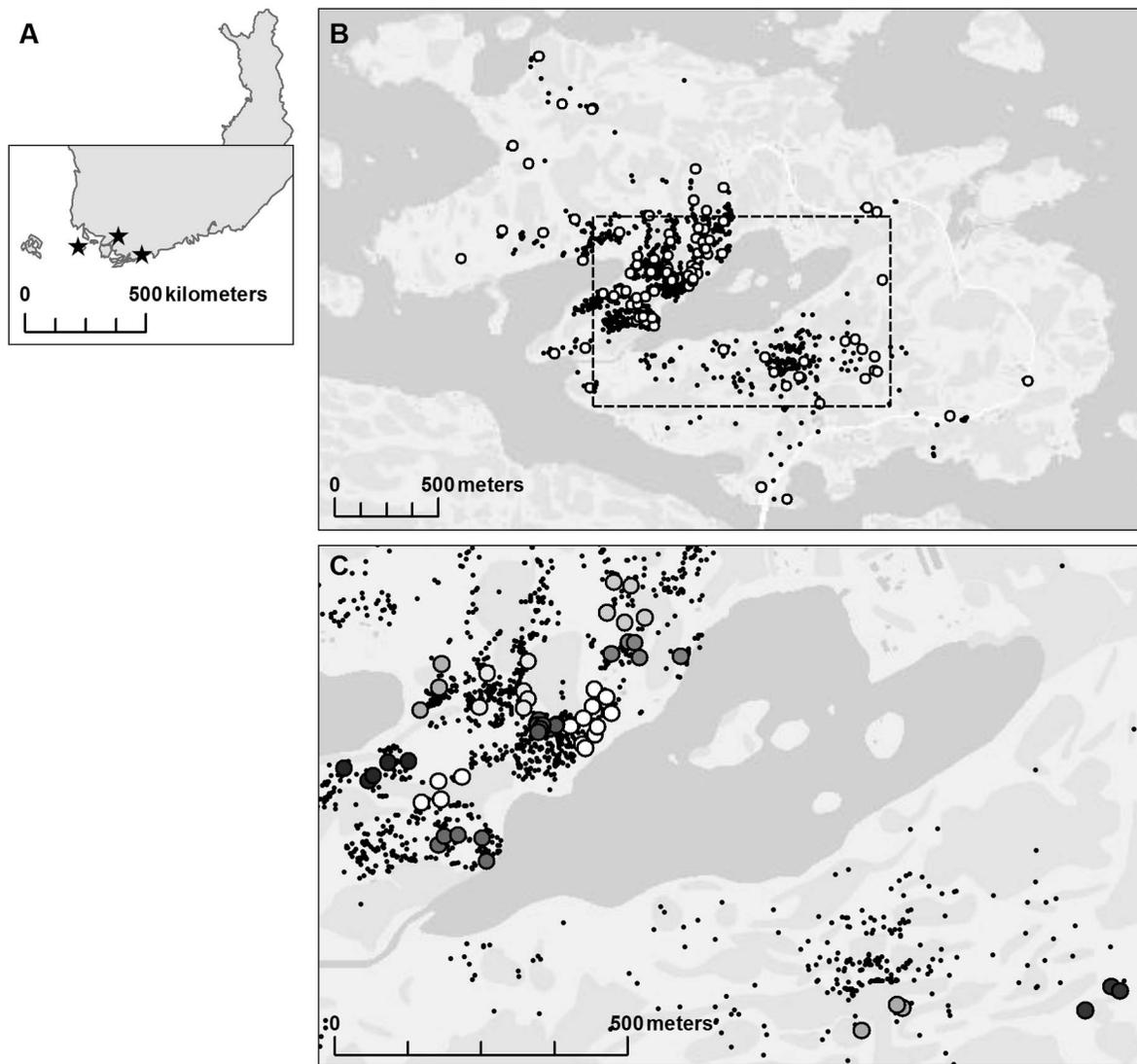
Fig. 1. Locations of the study populations, surveyed trees, and tree neighborhoods. (A) Locations of the three oak populations in south-western Finland within which levels of genetic variation were quantified. The locations are marked on the map with black stars. (B) A map of the island of Wattkast. All individual oak trees on the island are marked on the map with black dots, and the 100 trees surveyed for herbivores with white dots. The dashed square marks the area enlarged in (C). (C) A close-up of a part of Wattkast. Tree neighborhoods, as identified for the analyses, are marked on the map with different shades of grey. Background maps copyrighted by the National Land Survey of Finland.

herbivores in both 2006 and 2007. Tree neighborhoods were defined as including a minimum of three trees located within a maximum distance of 120 m of each other, corresponding to the average dispersal distance of one of the miner species, *Tischeria ekebladella* (Appendix A in Tack and Roslin 2011). Eleven such neighborhoods were identified in the data, with the number of trees in a neighborhood ranging from 3 to 12 (Fig. 1C). The neighborhoods were mutually exclusive, and together included a total of 60 out of the 100 trees surveyed. For further details on the study design and the herbivore surveys, see Appendix B.

At the level of individual trees, herbivore communities were described by total species richness, total herbivore abundance, and the Shannon-Wiener index of diversity. Adopting the approach of Tovar-Sánchez et al. (2013), we described the genetic diversity of individual trees as level of heterozygosity, which we measured as internal relatedness (IR; Aparicio et al. 2006). Values of IR can vary between −1 and 1, with negative IR values indicating higher heterozygosity and positive values higher homozygosity. For a more intuitive interpretation of the results, we used −(IR) in the analysis, so that higher values indicate higher heterozygosity.

For the neighborhoods, total species richness and total herbivore abundance were calculated by adding up the data over the trees in the neighborhoods (total number of unique species encountered and sum of herbivore abundances). These values were rarefied to correct for unequal neighborhood sizes: all unique combinations of three trees were sampled for neighborhoods of size >3, species richness and herbivore abundance were calculated across each such sample, and the resultant values were averaged. These averages were then used as estimates of neighborhood-level metrics. The genetic diversity within neighborhoods was described as allelic richness (A), corrected for the variation in the numbers of trees in the neighborhoods by the rarefaction method of Hurlbert (1971). The method was used to calculate estimates of the expected number of alleles at each locus in a random sample of 3 individuals from the neighborhoods of size >3. Thus, the measures of genetic variation, species richness, and herbivore load were all treated with effectively similar corrections for unequal neighborhood sizes.

As previous work (Tack et al. 2010) has reported spatial effects to be of major importance in our study system, we accounted for such imprints in all of our analyses. The connectivity of individual trees was described with a metric adopted from Tack et al. (2010). In principle, connectivity reflects the expected immigration of herbivores to a patch at maximum patch occupancy (Tack et al. 2010). At the neighborhood level, connectivity was described as the connectivity value averaged across the trees in the patch.

## Statistical analyses

To test for an effect of host genotype on herbivore community structure, we applied three sets of statistical analyses: First, we constructed generalized linear models of the herbivore community descriptors (abundance, species richness, and Shannon-Wiener diversity at the individual and neighborhood level) as functions of host connectivity and genetic diversity. A log-link and a Poisson distribution were assumed for each response variable, except for the Shannon-Wiener index, which was modeled by standard linear regression. Separate models were constructed for the individual ($n = 100$) and the neighborhood ($n = 11$) levels, with all models fitted in R v.2.15.3 (R Core Team 2013). To check for spatial autocorrelation in the observed IR values, we used a Mantel test implemented in R using the vegan package (Oksanen et al. 2013). No significant spatial autocorrelation was detected ($P = 0.23$).

Second, to examine whether species responded similarly to individual host genetic diversity, we constructed a generalized linear mixed model (GLMM) of species-specific abundances in individual trees (19 species × 100 trees × 2 years) as a function of species identity, tree connectivity, IR, and their interactions as fixed effects, and tree identity as a random effect. A Poisson distribution was assumed for the species abundances. The model was fitted using proc Glimmix in SAS for Windows (SAS Institute, Cary, NC, USA), version 9.2.

Survey year was included as an explanatory variable in all of these models, whereas data on three species (*Cynips longiventris*, *Neuroterus numismalis*, and *Tischeria dodonea*) not encountered in both years were excluded. The number of leaves examined per tree during the surveys was also included as a covariate in models fitted at the individual tree level, and a species × year interaction was added as a fixed effect in the GLMM.

Third, to examine whether genetically more similar hosts shared more similar herbivore communities, we used Mantel tests between community dissimilarity and genetic distance, between community dissimilarity and geographic distance, and a partial Mantel test between all three matrices. The tests were implemented using the vegan package for R. These tests were

Table 1. Generalized linear models of herbivore richness, abundance and diversity as functions of host connectivity, host genetic diversity, survey year, and number of leaves examined. Each response was separately modeled at the level of (A) individual trees and (B) neighborhoods of multiple trees.

| Response | Variable | Estimate | SE | $Z/t$† | $P$ |
|---|---|---|---|---|---|
| A) Individual level ($n = 100$) | | | | | |
| Richness | Genetic diversity | 0.16 | 0.18 | 0.86 | 0.39 |
| | Connectivity | 0.01 | 0.002 | 7.65 | <0.0001 |
| | Year | −0.18 | 0.06 | −2.97 | 0.003 |
| | No. leaves examined | 0.002 | 0.0002 | 9.33 | <0.0001 |
| Abundance | Genetic diversity | 0.45 | 0.06 | 7.03 | <0.0001 |
| | Connectivity | 0.02 | 0.001 | 26.74 | <0.0001 |
| | Year | −0.37 | 0.02 | −18.24 | <0.0001 |
| | No. leaves examined | 0.004 | 0.0001 | 62.61 | <0.0001 |
| Shannon-Wiener | Genetic diversity | 0.07 | 0.19 | 0.37 | 0.71 |
| | Connectivity | 0.010 | 0.002 | 5.50 | <0.0001 |
| | Year | −0.16 | 0.07 | −2.46 | 0.02 |
| | No. leaves examined | 0.001 | 0.0003 | 4.18 | <0.0001 |
| B) Neighborhood level ($n = 11$) | | | | | |
| Richness | Genetic diversity | 0.31 | 0.44 | 0.69 | 0.49 |
| | Connectivity | 0.02 | 0.01 | 2.80 | 0.01 |
| | Year | 0.02 | 0.13 | 0.16 | 0.88 |
| Abundance | Genetic diversity | 1.37 | 0.13 | 10.60 | <0.0001 |
| | Connectivity | 0.04 | 0.002 | 26.19 | <0.0001 |
| | Year | −0.30 | 0.03 | −9.40 | <0.0001 |

† $Z$-values for richness and abundance modeled with Poisson regression; $t$-value for Shannon diversity modeled with standard linear regression.

performed for data from year 2006 and 2007, respectively. For individual trees, genetic distance was measured with Rousset's $\hat{a}$, computed with SPAGeDi v.1.4 (Hardy and Vekemans 2002). At the neighborhood level, genetic distance was measured by pairwise $F_{ST}$, calculated in Arlequin with default settings. Geographic distance between two neighborhoods was defined as the distance between their centroids. For constructing the community dissimilarity matrices, data on species abundances were transformed into relative abundances by dividing each species-specific abundance with the total herbivore abundance observed on the tree/in the neighborhood. The community dissimilarity matrices were computed using the vegan package for R with the Bray-Curtis index as the community dissimilarity measure. Sites in which no species had been observed were excluded from the data, leaving at the individual level $n = 92$ trees in 2006 and $n = 93$ trees in 2007. There were no empty sites at the neighborhood level.

## RESULTS

As expected, genetic diversity among Finnish oak populations proved comparatively low. The average allelic richness varied between 9.37 in Wattkast and 13.44 in Inkoo. The numbers of alleles per locus in Finnish populations were, on average, lower than those recorded in more central populations in Europe (Appendix C: Table C1).

Despite low overall variation, genetic diversity left a statistically significant imprint on herbivore abundance, and these patterns were similar at both individual and neighborhood scales: higher individual heterozygosity and higher neighborhood-level allelic richness were associated with higher herbivore abundance (Table 1). A consistent imprint of genetic diversity was detected at the level of individual herbivore species: higher heterozygosity was found to increase the species-specific abundances of herbivores. In the GLMM, the species × heterozygosity interaction and the three-way species × connectivity × heterozygosity interaction were non-significant ($F_{18,3607} = 0.61$, $P = 0.90$, and $F_{19,3607} = 0.44$, $P = 0.98$, respectively), suggesting that most species respond to heterozygosity in the same way. When these non-significant interactions were dropped, the main effect of heterozygosity proved statistically significant ($F_{1,97} = 5.17$, $P = 0.03$). In contrast to the impact of genetic diversity on herbivore abundance, there was no detectable impact of genetic diversity on either species richness or Shannon-Wiener diversity (Table 1).

Unlike genetic diversity, spatial context had a

Table 2. Correlations between herbivore community dissimilarity, geographic distance, and genetic distance among (A) individual trees and (B) tree neighborhoods measured using Mantel and partial Mantel tests.

| | 2006 | | 2007 | |
| --- | --- | --- | --- | --- |
| Community dissimilarity vs | r | P | r | P |
| A) Individual level | | | | |
| Genetic distance | 0.10 | 0.02 | 0.14 | 0.002 |
| Geographic distance | 0.36 | 0.0001 | 0.39 | 0.0001 |
| Genetic distance\|Geographic distance | 0.03 | 0.28 | 0.05 | 0.15 |
| B) Neighborhood level | | | | |
| Genetic distance | 0.68 | 0.003 | 0.45 | 0.01 |
| Geographic distance | 0.68 | 0.01 | 0.60 | 0.002 |
| Genetic distance\|Geographic distance | 0.34 | 0.03 | 0.001 | 0.50 |

*Note:* Shown are the Mantel statistics computed (*r*) and their significance (*P*) based on 10,000 permutations of the community dissimilarity matrix.

clear effect on all of the descriptors of herbivore community structure at both the individual and the neighborhood level, with higher connectivity increasing the richness, diversity, and abundance of herbivores (Table 1). For individual herbivore species, tree connectivity and the species × connectivity interaction also had significant effects ($F_{1,97} = 7.67$, $P = 0.01$, and $F_{18,3644} = 4.46$, $P < 0.0001$, respectively), suggesting that host connectivity increases herbivore abundance in general, but that different species respond to it in different ways.

On average, genetically more similar trees and tree neighborhoods shared more similar herbivore communities (Table 2). However, a similar effect was observed for geographic distance: on average, the closer to each other two trees/ neighborhoods were located, the more similar were their herbivore communities. This correlation was stronger than that between genetic and community similarity in all but one case, the neighborhood level in 2006 (Table 2). Reflecting this, the association of genetic and community similarity weakened to non-significant when all three distance matrices were compared, i.e., when the geographic distances were accounted for (Table 2).

## DISCUSSION

We detected a clear imprint of host genotype on the associated herbivore communities both at the scale of individual trees and of tree neighborhoods: herbivore abundance was strongly affected by both host genetic diversity and spatial connectivity. Importantly, the effects of host genotype emerged despite our finding that Finnish oak populations sustain less genetic variation than do oak populations at the core of their range, and despite the suggestion that the relative importance of genetic versus environmental effects may be smaller within genetically impoverished populations (Bangert et al. 2006*b*). However, in contrast to the majority of previous studies (Crutsinger et al. 2006, Johnson et al. 2006, Hersch-Green et al. 2011), we detected no impact of host genetic diversity on the diversity of the herbivore community.

While comparisons of allelic richness between samples of different size are admittedly problematic (Leberg 2002), our data offer convincing evidence that the genetic diversity of Finnish populations is lower than that characterizing more central stands. In itself, the loss of genetic diversity from populations at the range margin is consistent with theory (Eckert et al. 2008) and matches with patterns observed in terms of cpDNA variation within *Q. robur* populations (Petit et al. 2002). While maternally inherited cpDNA may show somewhat different levels of variation than nuclear microsatellites (Petit et al. 2005), the levels of nuclear microsatellite diversity detected in the present study suggest that the historical colonization processes have affected both (Ferris et al. 1998). In terms of average allelic richness, genetic variation within the *Q. robur* population on Wattkast was also the lowest measured among the three Finnish populations. Despite all these considerations, the genetic variation present within the population is apparently sufficient to cause detectable effects on herbivore load.

In terms of the imprints of host genetic diversity detected, our results were strikingly

consistent over species and spatial scales: the heterozygosity of individual hosts as well as the allelic richness within tree neighborhoods had a statistically significant, positive effect on both the overall abundance and the species-specific abundances of herbivores. These results agree with previous findings that host genotypic diversity at the patch or population level increases arthropod abundance (Crutsinger et al. 2006, Johnson et al. 2006), and that the heterozygosity and genotype of individual hosts may affect herbivore abundance to significant degrees (Evans et al. 2012, Kalske et al. 2014). Effects of heterozygosity have previously been reported e.g., by Tovar-Sánchez et al. (2013), who found total arthropod biomass to decrease with increasing heterozygosity of the host and interpreted this as a potential sign of weaker defense in more homozygous hosts. Our results, conversely, suggest that higher heterozygosity may lead to higher susceptibility. We hypothesize that the galler and leaf-miner species in our study may respond positively to heterozygosity, which, assuming that heterozygosity is associated with vigor, matches with numerous observations testing the plant vigor hypothesis (Price 1991, Cornelissen et al. 2008).

While the imprints of host genetic diversity on herbivore abundance were clear, herbivore species richness and diversity were not detectably affected by host genetic diversity at either spatial scale. This finding contrasts with several previous reports of herbivore diversity increasing with population-level genotypic diversity. Such patterns have been explained by additive and non-additive effects (Crutsinger et al. 2006, Johnson et al. 2006, Tack and Roslin 2011), i.e., by sampling among host genotypes with specific communities (additive effects) and synergistic effects realized in mixtures of multiple host genotypes (non-additive effects). It seems likely that genetic diversity within an individual host does not produce the structures, functions, or interactions that create either additive or non-additive effects. Nonetheless, we also failed to find any effects of host genetic diversity on species richness at the neighborhood level—but then again, we measured neighborhood-level genetic diversity by average allelic richness, which is not strictly analogous to genotypic diversity (Hughes et al. 2008). Thus, the current results do not suffice as evidence for a lack of host genetic diversity

reflecting into a lack of effect on herbivore diversity. Instead, they suffice to demonstrate that what limited genetic diversity there is, reflects into detectable variation in herbivore abundance.

The general association of host genetic relatedness and community similarity, coined the 'genetic similarity rule', has been observed, for instance, in cottonwood-based systems (Bangert et al. 2006a, b) and in tropical epiphytic bromeliads (Zytynska et al. 2012). In the present study, we found genetic similarity among hosts to increase the similarity of their herbivore communities, but also geographic proximity among hosts increased community similarity. With the effects of geographic distances accounted for, the association of community similarity and genetic relatedness generally dwindled into statistical non-significance. This result suggests that in our study system, imprints of spatial context may override those of host genotype. Such an interpretation is further supported by previous findings from oak-based food webs in Finland, where effects of host genotype have been proposed to be secondary to those of landscape configuration (Tack et al. 2010). Notably, the absence of a genetic similarity pattern cannot be directly ascribed to the lower genetic diversity of *Quercus robur* at the range margin: Gossner et al. (2015) recently found that within the core area of the oak distribution (Bavaria, southern Germany) the degree of genetic similarity among mature oaks was not reflected in the associated insect communities.

Importantly, however, the effects of the spatial context failed to smudge all imprints of host genotype. While host connectivity proved a significant factor influencing herbivore abundance, richness, and diversity, the effects of host genotype on herbivore abundance remained statistically significant even when connectivity was included in the models. Moreover, while our results suggest that different herbivore species respond to host connectivity in different ways (as likely due to differences in dispersal ability), responses to host heterozygosity proved consistent across all species. Thus, both landscape context and host genotype seem to come with independent effects, and both may be important in determining herbivore community structure. These results agree closely with previous observations that individual variation in host plant quality is strong enough to cause local adaptation

by herbivore populations to their hosts, but that the strength of such adaptation will vary with the landscape context (Tack and Roslin 2010).

While our paper primarily focuses on the impact of genetic diversity and spatial connectivity on herbivore community patterns, we note that the results can also be interpreted from the perspective of tree fitness. As low-level herbivory may strongly affect the fitness of oak trees (Crawley 1985), and as our results reveal a strong link between genetic diversity, habitat configuration, and herbivore load, they suggest that tree fitness will vary predictably across the landscape. Exploring the impact of genetic diversity and the position of a tree within the landscape on tree fitness and the evolution of tree resistance will thus offer an interesting avenue for future research.

In conclusion, our study reveals how imprints of host genotype and spatial context may be found even in genetically impoverished host populations at the margins of their range. By doing so, it points to intriguing interactions between host diversity and herbivore communities across landscapes in any part of the host's range.

## Acknowledgments

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SUPPLEMENTAL MATERIAL

## APPENDIX A

### Details on the genotyping procedures

The Inkoo oak population consists of approximately 100 trees, the Salo population of approximately 300 trees, and the Wattkast population of approximately 1900 trees. In Inkoo, all trees with diameter at breast height >5 cm (n = 96), and in Salo, 35 randomly selected trees were sampled for genotyping in the autumn of 2004. In Wattkast, 194 randomly selected trees were sampled in September 2011.

Sampled individuals were genotyped using 15 nuclear microsatellite loci (Dow et al. 1995, Steinkellner et al. 1997, Kampfer et al. 1998). DNA was extracted from leaf samples using the E.Z.N.A. extraction protocol (E.Z.N.A. SP Plant Mini Kit D5511-02; Omega Bio-Tek, Norcross, GA, USA). Twelve pairs of primers were used to amplify the microsatellite loci in the extracted DNA. The PCR amplification reactions were performed in a volume of 13 µL. Four different multiplex reaction mixtures were made using QIAGEN Multiplex PCR Kit. Forward primers were fluorescently labeled with Beckman's WeI1RED (Beckman Coulter, Brea, CA, USA). Genotyping was carried out using a CEQ 8000 genetic analyzer (Beckman Coulter); 1 µL of amplified DNA and 24 µL of DNA Size Standard were loaded into 96-well plates. Allele visualization and scoring were performed using the fragment analysis module CEQ 8000 software (Beckman Coulter).

## APPENDIX B

### Additional details of the study design

The presence and abundance of more than twenty insect herbivore species were surveyed on the oaks of Wattkast in 2006 and 2007. Data was collected on a comprehensive sample of trees selected by stratified random sampling, as aimed at covering trees across the island and representing different spatial settings (see, e.g., Gripenberg and Roslin 2005, Gripenberg and Roslin 2008, Tack et al. 2010).

For each tree, galling and leaf-mining herbivores were surveyed by randomly selecting twenty primary shoots from each tree, then recording the number of leaves in the shoot and the presence and abundance of each herbivore species. 20 of the species surveyed were observed within the sample of 100 trees used in the present study (Table B1). Given large variation in abundance between generations of gallers, the sexual and asexual generations of *Andricus pseudoinflator* and *Neuroterus quercusbaccarum* were recorded and treated as separate taxa.

Table B1. List of insect herbivore species encountered in a sample of 100 oak trees on Wattkast in 2006 and 2007, and their feeding mode (from Tack et al. 2010).

| Order | Family | Genus and species | Feeding mode |
|---|---|---|---|
| Diptera | Cecidomyiidae | *Macrodiplosis dryobia* | Galler |
| Homoptera | Triozidae | *Trioza remota* | Galler |
| Hymenoptera | Cynipidae | *Andricus callidoma* | Galler |
| Hymenoptera | Cynipidae | *Andricus curvator* | Galler |
| Hymenoptera | Cynipidae | *Andricus pseudoinflator* | Galler |
| Hymenoptera | Cynipidae | *Cynips longiventris* | Galler |
| Hymenoptera | Cynipidae | *Neuroterus numismalis* | Galler |
| Hymenoptera | Cynipidae | *Neuroterus quercusbaccarum* | Galler |
| Hymenoptera | Tenthredinidae | *Profenusa pygmaea* | Miner |
| Lepidoptera | Coleophoridae | *Coleophora* spp. | Miner |
| Lepidoptera | Eriocraniidae | *Dyseriocrania subpurpurella* | Miner |
| Lepidoptera | Gracillariidae | *Caloptilia alchimiella* | Miner |
| Lepidoptera | Gracillariidae | *Phyllonorycter* spp. | Miner |
| Lepidoptera | Nepticulidae | *Ectoedemia albifasciella* | Miner |
| Lepidoptera | Nepticulidae | *Stigmella* spp. | Miner |
| Lepidoptera | Tischeriidae | *Tischeria dodonea* | Miner |
| Lepidoptera | Tischeriidae | *Tischeria ekebladella* | Miner |
| Lepidoptera | Bucculatricidae | *Bucculatrix ulmella* | Other |
| Lepidoptera | Heliozelidae | *Heliozela sericiella* | Other |
| Lepidoptera | Tortricidae | *Ancylis mitterbacheriana* | Other |

## Appendix C

Table C1. Level of genetic variation encountered in Finnish oak populations compared with European populations. Numbers of alleles detected in the three oak populations studied here (top part of table) as compared with results for the same loci detected in *Quercus robur* populations elsewhere in Europe (lower part of table). Note that sample sizes (*n*) vary.

| Location | *n* | Locus | | | | |
|---|---|---|---|---|---|---|
| | | A36 | A9 | A1-5 | Z104 | Q13 |
| Finland, Wattkast | 194 | 15 | 13 | 13 | 22 | 11 |
| Finland, Salo | 35 | 11 | 12 | 12 | 24 | 12 |
| Finland, Inkoo | 96 | 9 | 11 | 11 | 14 | 5 |
| Mean | | 11.67 | 12 | 12 | 20 | 9.33 |
| France (Streiff et al. 1998) | 183 | 19 | 14 | 17 | 29 | 12 |
| Germany (Degen et al. 1999) | 228 | 17 | 14 | 15 | 33 | ... |
| | 85 | 13 | 11 | 12 | 28 | ... |
| UK (Cottrell et al. 2003) | 388 | 20 | 12 | 20 | 31 | 12 |
| | 58 | 28 | 16 | 20 | 25 | 15 |
| Romania (Curtu et al. 2007) | 65 | 16 | 13 | 14 | 30 | 8 |
| Turkey (Yücedağ and Gailing 2013) | 50 | 15 | ... | 12 | 17 | ... |
| | 50 | 15 | ... | 12 | 17 | ... |
| Mean | | 17.88 | 13.33 | 15.25 | 26.25 | 11.75 |