A geographic mosaic of genetic variation within a foundation tree species and its community-level consequences

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Abstract. Knowledge of the manner in which genetic variation within a tree species affects associated communities and ecosystem processes across its entire range is important for understanding how geographic mosaics of genetic interactions might develop and support different communities. While numerous studies have investigated the community and ecosystem consequences of genetic variation at the hybrid cross type or genotype level within a species, none has investigated the community-level effects of intraspecific genetic variation across the geographic range of a widespread species. This is the scale at which geographic mosaics of coevolution are hypothesized to exist. Studies at this level are particularly important for foundation tree species, which typically support numerous microbial, fungal, plant, and animal communities. We studied genetic variation across eight geographical races of the forest tree *Eucalyptus globulus* representing its natural distribution across southeastern Australia. The study was conducted in a 15-year-old common garden trial based on families derived from single-tree open-pollinated seed collections from the wild. Neutral molecular genetic variation within *E. globulus* was also assessed and compared with genetic divergence in the phenotypic and community traits. Three major findings emerged. First, we found significant genetically based, hierarchical variation in associated communities corresponding to geographical races of *E. globulus* and families within races. Second, divergence in foliar communities at the racial level was associated with genetically based divergence in specific leaf morphological and chemical traits that have known defensive functions. Third, significant positive correlations between canopy community dissimilarity and both neutral molecular genetic and leaf quantitative genetic dissimilarity at the race level supported a genetic similarity rule. Our results argue that genetic variation within foundation tree species has the potential to be a significant driver of the geographical mosaics of variation typical of forest communities, which could have important ecological and evolutionary implications.

Key words: Australia; common garden trial; community genetics; (co)evolution; Eucalyptus globulus; *forest tree; leaf morphology; neutral molecular markers; plant–animal interactions; plant secondary chemistry; provenance trial.*

Introduction

Foundation species, such as forest trees, structure communities by creating locally stable conditions for other species and by modulating and stabilizing ecosystem processes (Ellison et al. 2005, Whitham et al. 2006). An important question in modern ecology is how genetic variation within such species impacts on these effects (Whitham et al. 2006, Johnson and Stinchcombe 2007, Wade 2007). Studies of this question can provide great insight into the factors that drive community ecology (Dungey et al. 2000, Wimp et al. 2005), the importance of genetic variation in conservation and biodiversity man-

agement (Whitham et al. 2003), and the extent to which evolution in a community context is possible (Thompson 2005, Shuster et al. 2006). To date, most studies that have demonstrated a genetic basis to variation in community phenotypes have focused on hybrids (e.g., *Eucalyptus*, Dungey et al. 1997; *Salix*, Hochwender and Fritz 2004; *Quercus*, Tovar-Sanchez and Oyama 2006) or specific genotypes within a species (e.g., *Oenothera*, Johnson and Agrawal 2005; *Populus*, Shuster et al. 2006, Schweitzer et al. 2008; *Solidago*, Crutsinger et al. 2008). Several such studies have shown that phytochemical variation among plant genotypes is related to differences in their associated communities (e.g., Dungey et al. 2000, Bangert et al. 2006) and that genetically more similar plants are more likely to support more similar communities than genetically dissimilar plants (i.e., the genetic similarity rule of Bangert et al. [2006]).

The natural progression of community genetic studies is to determine whether genetic influences of foundation species can have evolutionary consequences for the community and whether feedback and reciprocal genetic interactions exist to affect the foundation species (all herein referred to as "(co)evolution," following Johnson and Stinchcombe [2007]). The development of such (co)evolutionary relationships is likely to be greatest where spatial partitioning of genetic variation occurs over scales that limit gene flow from compromising selection (Forde et al. 2007, White et al. 2007). Indeed, it is at this broader landscape level that Thompson (2005) positions the geographical mosaic of coevolution theory, describing the development and geographic variation in evolutionary relationships among individual community members. Despite decades of research demonstrating marked genetic structuring of forest tree gene pools at this spatial scale, most notably among races or provenances (Eldridge et al. 1993, White et al. 2007), no studies have assessed the community-level impacts of this variation, and reciprocally, the role of coexisting communities in the evolution of this genetic structure in foundation species.

To examine this dynamic interplay between evolutionary change in the foundation species and the structure and (co)evolution of associated communities, one would like to have common gardens containing genotypes from each race planted reciprocally within the home ranges of these races (Johnson and Stinchcombe 2007, Laine 2007, Hoeksema and Forde 2008). As this is a very time consuming and costly effort for a foundation tree species, a first step is to demonstrate that such genetically based racial differences do have a biotic impact and can structure associated communities within a single common garden. This is the goal of the present study in which we assessed eight geographic races of the foundation tree species Eucalyptus globulus within a single 15-year-old common garden and compared their associated canopy communities. A hierarchical structure in genetic variation was assessed, focusing not only on race but also on family within race. We then addressed three major hypotheses: (1) the intraspecific genetic variation associated with race and family within race has a significant effect on the structure of associated communities; (2) differences in the associated communities are reflected in molecular, morphological, and phytochemical differences among races; and (3) races that are genetically more similar also support more similar communities than those that are genetically dissimilar. Support for these hypotheses would constitute an important first step in examining the extent to which the genetic structure of a foundation species over a broad geographic range acts to drive a geographic mosaic of community structure.

Materials and Methods

The system

Eucalyptus globulus is a dominant or codominant foundation tree species of native forests distributed across large areas of southeast Australia (Fig. 1). It is a typical representative of a genus that dominates forest and woodland communities of non-arid Australia (Wardell-Johnson et al. 1997). The natural patterns of genetic variation within E. globulus have been studied intensively, and it has become a model species for forest genetic research (Potts et al. 2004). Common garden trials totalling tens of thousands of trees, grown from open-pollinated seed of nearly 600 mother trees have shown significant differences among these open-pollinated families from throughout the natural geographical range of E. globulus. In E. globulus, maternal effects (i.e., seed size and germination time) on growth decay rapidly after field planting (Lopez et al. 2003), and crossing studies have shown a high correlation between average male (factorial matings) and open-pollinated female genetic effects for most traits studied (Potts et al. 2004), supporting an additive genetic interpretation of these parental differences (Eldridge et al. 1993, White et al. 2007). This quantitative genetic variation has been summarized by partitioning the native gene pool of this species into 13 geographic races (Dutkowski and Potts 1999, Potts et al. 2004), among which considerable variation in neutral microsatellite markers has been found (Steane et al. 2006). There is also a strong hierarchical pattern to this quantitative genetic variation, with considerable variation being identified at the race, locality within race, and family (open-pollinated seed lot from a single tree) within locality levels for many traits (Dutkowski and Potts 1999, Potts et al. 2004).

Field trial and sampling

Canopy community variation was assessed at the West Ridgley common garden trial in northern Tasmania (41°17′ S, 146°51′ E). The trial was established in a randomized incomplete block design with 4485 plants grown from open-pollinated seed from 421 trees from throughout the natural distribution of E. globulus (Fig. 1; Jordan et al. 1994, Potts and Jordan 1994). Eight races (Fig. 1) were selected to represent the majority of the known geographic range and the quantitative and molecular genetic variation of the species available in the trial (Dutkowski and Potts 1999, Steane et al. 2006). Ten families from each race and two trees per family were selected randomly from across replicates, resulting in a total of 160 trees. The trees were felled when they were 15 years old and ~25 m in height, with most foliage-bearing branches being above 15 m. Sampling in May (autumn) represented the end of the growing season and the end of the majority of canopy community activity for that season. All analyses were based on samples taken from the top 2–3 m of the canopy.

Molecular and quantitative genetic assessments

Samples for chemical analyses were cool-stored for transportation, then stored frozen. Both primary chemistry (nitrogen, carbon, and hydrogen) and secondary
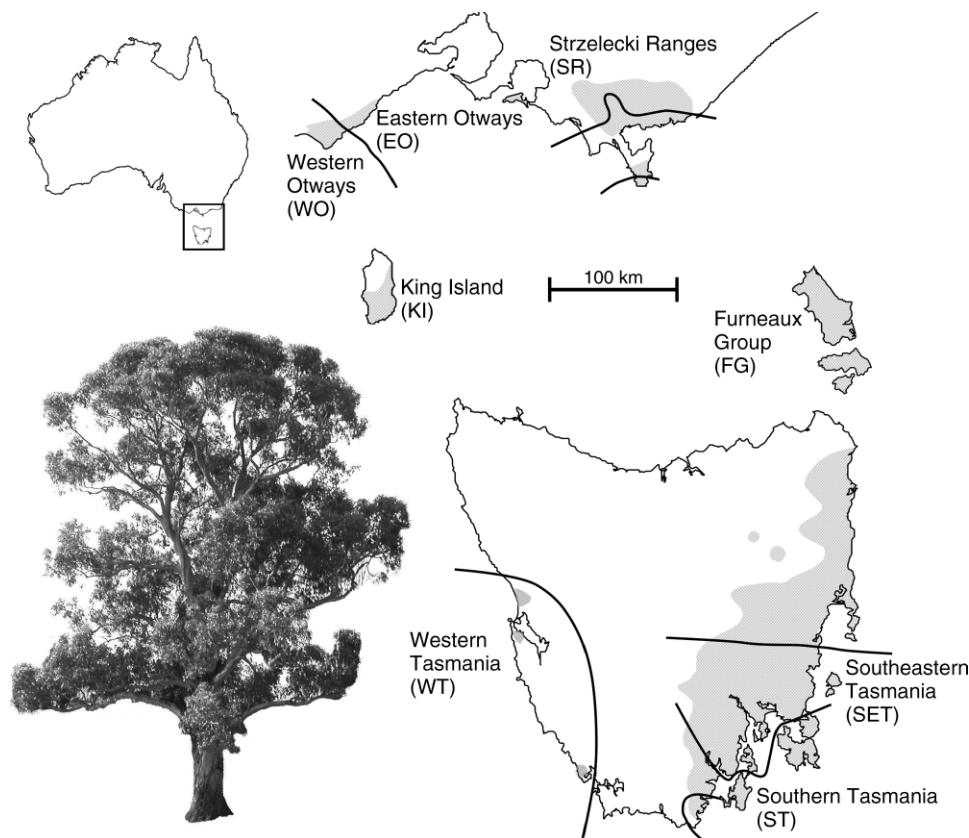
FIG. 1. Natural distribution of *Eucalyptus globulus* (photo) across southeast Australia (gray shading; source: G. M. Jordan) and the delineated racial classifications of the species (based on Dutkowski and Potts [1999]). Only races assessed in the current work have been labeled.

metabolites (total oils, 1,8-cineole [the dominant oil in *Eucalyptus*], total phenolics, and condensed tannins) were assayed (see O'Reilly-Wapstra et al. [2007] for methods). The two dominant isomers of formylated phloroglucinol compounds (FPCs) in *E. globulus* (sideroxylonal A and macrocarpal G) were assayed using high-performance liquid chromatography (HPLC). Analyses of total oils and 1,8-cineole were conducted on frozen, fresh samples, while the remaining chemicals were assayed from freeze-dried, ground samples. The oil analyses followed O'Reilly-Wapstra et al. (2007) with the exception that each sample was extracted in three aliquots. Secondary chemicals were selected on the basis of their documented involvement in plant–animal interactions and, in particular, their plant defensive roles (Dungey et al. 2000, Lawler et al. 2000, O'Reilly-Wapstra et al. 2004). The results for these chemical analyses have been published previously in O'Reilly-Wapstra et al. (2007), except for total oils and 1,8-cineole, which were new data based on a modified method. The latter samples were also scanned with a near-infrared reflectance (NIR) spectrometer (Bruker MPA FT-NIR, Ettlingen, Germany) to provide an overall assessment of phytochemical variation without providing information on actual chemical content (Foley et al. 1998, Richardson et al. 2003). Spectra were collected between 7692 and 4348 cm^{-1} (1300 and 2300 nm) at a resolution of 4 cm^{-1}. Prior to analysis, spectra were converted to the first derivative (11 smoothing points) and subjected to a standard normal variate transformation with Unscrambler (version 9.6; CAMO ASA, Oslo, Norway). Samples from each tree within a family were pooled for both chemical and NIR spectra analyses.

Three typical fully expanded leaves were removed from the top of the canopy of the felled trees for analysis of leaf morphological variation. Six morphological traits were chosen to document leaf size and shape (Table 1), and two characters known to influence susceptibility of *Eucalyptus* leaves to arthropod herbivory (ratio of leaf lamina to margin thickness, Nahrung et al. 2001; specific dry mass, Steinbauer 2001) were measured and family averages were calculated. Molecular variation based on eight microsatellite loci has been published previously by Steane et al. (2006). These data were not from the trees assessed in the current work but represented neutral marker variation within and between wild trees of the same races as those studied. The molecular data were used to reflect differentiation between races, independent of selection.

TABLE 1.   Herbivore and fungal species assessed to determine the community-level impacts of intraspecific genetic variation within *Eucalyptus globulus*.

Species	Type	Symptom of species	χ^2	P
Cicadoidea sp. 1	arthropod	"cicada" stem damage	7.0	0.43
Galling arthropod sp. 1	arthropod	galls developed on petiole	15.0	**0.037**
Gonipterus scutellatus (Gyllenhal)	arthropod	oblong holes in leaf lamina	19.3	**0.007**
Hypertropha tortriciformis (Guenee)	arthropod	large necrotic patch on leaf lamina due to epidermal cells being rasped off	11.4	0.12
Myllorhinus dentiferus (Bohemann)	arthropod	swelling of the branch stem	8.6	0.28
Paropsisterna agricola (Chapuis)	arthropod	scalloping of margins of lamina	15.0	**0.037**
Phylacteophaga froggatti (Riek)	arthropod	raised necrotic lesions with central hole on lamina	5.8	0.57
Psylloidea/Hymenoptera sp. 1	arthropod	galls on lamina	9.2	0.24
Aulographina eucalypti (Cooke & Mass.)	fungus	irregular raised surface necrosis on lamina	14.1	0.05
Lesion fungus sp. 1	fungus	elongated raised lesion on leaf midrib	6.6	0.47
Lesion fungus sp. 2	fungus	black "pin-prick" lesions across lamina	9.8	0.20
Lesion fungus sp. 3	fungus	raised "pimple-like" lesions ~5 mm in diameter on lamina	11.8	0.11
Lesion fungus sp. 4	fungus	round, raised lesions ~1 mm in diameter on lamina	13.1	0.07
Lesion fungus sp. 5	fungus	lesions on the branch stem	23.7	**0.001**
Lesion fungus sp. 6	fungus	small round lesions >1 mm on lamina	3.3	0.86
Mycosphaerella sp. 1	fungus	irregularly shaped lesions >10 mm on lamina	14.2	**0.048**

Notes: A description of damage symptoms is provided along with the results from nonparametric Kruskal-Wallis tests for response to racial variation within *E. globulus* (n within race = 20). Canopy community variation was assessed at the West Ridgley common garden trial in northern Tasmania, Australia. Reference collections of all symptoms are held at the School of Plant Science, University of Tasmania. Significant values ($P < 0.05$) are in boldface.

Canopy community assessment

The canopy communities were characterized using a symptom-based approach. Leaves and small branches that had any form of damage or distortion were plucked from the upper canopy of the felled trees for three minutes and dried. Sixteen symptoms that were discrete, easily distinguishable, and assignable unambiguously to one or more causal organisms were assessed on each leaf (Table 2). The main organism causing each symptom was identified where possible according to Elliott and deLittle (1984) and Keane et al. (2000) and by consultation with specialists and reference collections. Reference collections for this study are held at the School of Plant Science, University of Tasmania. Each sample was assessed by scoring the proportion of items (leaves and small branches) affected by each symptom on a five-level categorical scale (no items affected, 1–25%, 26–50%, 51–75%, and 75–100% of leaves affected), and class midpoints were used for analyses.

Statistical analyses of genetic variation

The existence of community-level impacts of genetic variation among races of *E. globulus* and families within races was assessed using multivariate and univariate approaches. The multivariate analysis was conducted by first calculating a Bray-Curtis dissimilarity matrix summarizing the raw community data set. A distance-based multivariate ANOVA using the software PERMANOVA6 (Anderson 2001, McArdle and Anderson 2001) was conducted on this matrix, testing the effects of race and family within race. The community variation between races was summarized using a two-dimensional, nonmetric multidimensional scaling ordination undertaken with Primer (version 6.1.9; Roborough, Plymouth, UK) and using the same dissimilarity matrix. Nonparametric Kruskal-Wallis tests were used to test the effects of race on specific symptoms (Proc NPAR1WAY of SAS, version 9.1; SAS Institute, Cary, North Carolina, USA).

To confirm the existence of genetic differences in molecular and quantitative traits between races within this trial, neutral molecular markers and quantitative morphological and chemical (assayed and NIR spectra) traits were analyzed as follows. (1) Neutral microsatellites: The eight microsatellite loci presented in Steane et al. (2006) were reassessed by conducting an analysis of molecular variation (AMOVA in GenAlEx; Peakall and Smouse 2006, see Steane et al. 2006 for methods) testing for molecular divergence among the specific subset of races used in the present study. (2) Morphology and assayed chemistry: Each morphological trait and assayed chemical was analyzed using a univariate model that tested the fixed effect of race (Proc GLM of SAS). Family was not included as a nested factor in these analyses due to the chemical assays being conducted on samples that were pooled within families. This was followed by canonical discriminant analyses and multivariate ANOVAs (Proc CANDISC of SAS), which were conducted separately for the morphological and chemical data sets, using race as a grouping factor. (3) The NIR spectra: The dimensionality of the NIR spectra data was reduced to 20 principal components using Unscrambler (version 9.6; CAMO ASA). These principal components explained 99.3% of the spectral variation and were used to assess divergence amongst races in NIR spectra with the above CANDISC procedure.

TABLE 2. Morphological and chemical traits assessed in the analysis of quantitative genetic variation in adult leaf samples of *Eucalyptus globulus*.

| | Univariate analysis | | | Mantel correlations | | | |
| | | | | Microsatellite | | Community | |
Description	Transfor-mation	F	P	r	P	r	P
Morphology							
Leaf curvature†	none	3.0	**0.008**	−0.09	0.66	0.25	0.10
Length of lamina (mm)	log_{10}	7.2	**<0.001**	−0.08	0.66	0.40	**0.018**
Lamina width at widest point (mm)	none	2.8	**0.012**	0.12	0.28	0.05	0.41
Specific dry mass per unit area (gm)‡	none	10.7	**<0.001**	0.33	**0.048**	0.45	**0.007**
Length along mid-rib to widest point (mm) of lamina	none	3.6	**0.002**	−0.14	0.76	0.25	0.10
Leaf lamina to margin thickness ratio (see Steinbauer 2001)	none	3.8	**<0.001**	−0.22	0.87	−0.15	0.79
Length of petiole (mm)	none	2.1	0.05	0.2	0.15	−0.13	0.76
The acute angle of the leaf tip (°)	none	0.5	0.85	−0.01	0.51	−0.25	0.90
Primary chemistry							
Carbon (%DM)	none	6.7	**<0.001**	0.34	**0.040**	−0.13	0.75
Hydrogen (%DM)	none	2.2	**0.045**	−0.07	0.62	−0.26	0.91
Nitrogen (%DM)	none	2.4	**0.029**	−0.04	0.57	0.14	0.23
Secondary metabolites							
Total phenolics (mg/g DM, equivalence of gallic acid)	none	2.6	**0.021**	0.07	0.35	0.15	0.23
Condensed tannins (mg/g DM, equivalence of sorghum tannin)	none	11.8	**<0.001**	0.51	**0.003**	0.61	**<0.001**
Macrocarpal G (mg/g DM, equivalence of macrocarpal A)	none	15.4	**<0.001**	0.24	0.11	0.33	**0.046**
Sideroxylonal A (mg/g DM)	log_{10}	6.9	**<0.001**	0.20	0.16	0.20	0.15
Total oil (mg/g DM, equivalence of cineole)	none	2.7	**0.015**	0.41	**0.015**	0.08	0.34
1,8-cineole (mg/g DM)	none	4.1	**<0.001**	0.26	0.09	0.00	0.50

Notes: The results from univariate tests of racial variation, the transformations conducted on each trait, and the results from pairwise Mantel correlations between the traits and both microsatellite and canopy community variation are provided. For all F, df = 7, 70. Significant values are in boldface.

† Distance of the midrib from a linear line drawn between the lamina tip and base (mm).

‡ Mean of two disks taken from widest point of lamina (disk width = 5.5 mm). See Nahrung et al. (2001).

Mantel correlations (XLSTAT version 2006.5; Addinsoft SARL, Paris, France) were conducted to test the hypothesis that trees that are more genetically similar support more similar communities of organisms. These genetic correlations were conducted between distance matrices summarizing divergence at the race level in the canopy community (Bray-Curtis dissimilarity), microsatellite markers (Nei's genetic distance), all leaf morphological traits (Mahalanobis distance), and total leaf chemistry (as assessed by the NIR spectra variation, Mahalanobis distance). Additional Mantel tests were conducted comparing the neutral genetic marker and canopy community matrices with the individual morphological and assayed chemical traits. Finally, partial Mantel tests were conducted to assess the correlation between neutral markers and community variation while controlling for influences of quantitative traits.

RESULTS

Community responses to genetic variation within *E. globulus*

Our results confirmed the first hypothesis that both geographical races and families within races would support different communities of organisms in a common garden. The multivariate testing of the community data set showed significant variation among races ($F_{7,72} = 2.1$, $P = 0.002$) and families within races ($F_{72,80} = 2.0$, $P = 0.046$). The randomized design meant that these results represented genetically based differences in community composition. The majority of the racial variation appeared to be driven by differences between the Australian mainland races and those from the Bass Strait islands, with the Tasmanian races tending to be intermediate (Fig. 2). Five of the 16 symptoms assessed differed significantly in their frequency among the races of *E. globulus* (Table 1), with a divergent response to the mainland and Bass Strait island populations notable for *Paropsisterna agricola* and *Gonipterus scutellatus* (Fig. 2).

Molecular and quantitative genetic variation within *E. globulus*

The quantitative genetic analysis of the plant traits also supported the second hypothesis that racial variation in molecular, morphological, and phytochemical traits exists among races of *E. globulus* in the trial. Multivariate variation in neutral genetic markers was significant (AMOVA, $P < 0.01$). Significant univariate variation was found for most quantitative traits assessed (Table 2), and at the multivariate level, highly significant variation was evident in assayed chemistry (Wilks'
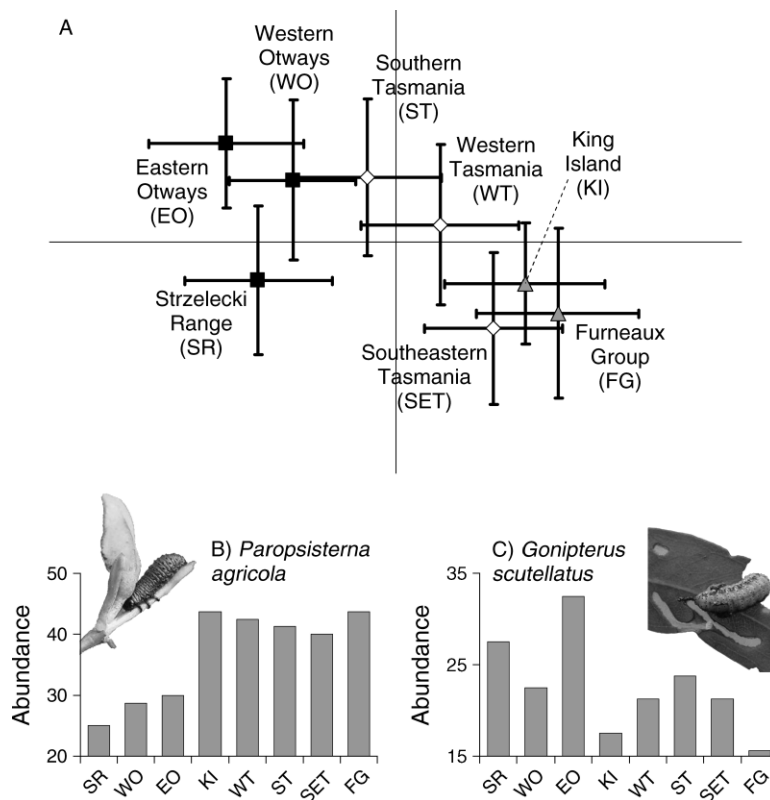
FIG. 2. The responses of a canopy community of fungi and arthropod herbivores to racial genetic variation within *Eucalyptus globulus*. (A) A two-dimensional nonmetric multidimensional scaling (nMDS) ordination summarizing the multivariate community response. The symbol for each race mean (±SE) indicates the geographical region to which the race belongs (squares, mainland Australia; diamonds, Tasmania; triangles, Bass Strait islands). (B, C) The abundances (percentages of leaves affected) of two herbivores that were found to vary significantly in response to race.

lambda MANOVA, $F_{63, 367} = 5.04$, $P < 0.0001$), morphology (Wilks' lambda MANOVA, $F_{56, 786} = 3.69$, $P < 0.001$), and NIR spectral phenotype (Wilks' lambda MANOVA, $F_{140, 363} = 4.42$, $P < 0.001$).

Testing the genetic similarity rule in E. globulus

The results supported our third hypothesis, that genetically similar races support more similar communities, whereas genetically less similar races support dissimilar communities. Significant Mantel correlations (r) occurred between racial divergences in canopy community and neutral microsatellite genetic data ($r = 0.35$, $P = 0.033$), as well as between canopy community and total leaf morphological ($r = 0.51$, $P = 0.002$) and NIR spectral variation ($r = 0.64$, $P < 0.001$; Fig. 3). Spectral divergence was also correlated with divergence in neutral markers ($r = 0.50$, $P = 0.003$), while divergence in total leaf morphology was not correlated with divergence in either the markers ($r = 0.17$, $P > 0.05$) or NIR spectra ($r = 0.20$, $P > 0.05$) (Fig. 4). Partial Mantel correlations showed that the significant relationship between neutral molecular marker and community divergence was not evident after accounting for either overall leaf chemistry (NIR spectra) ($r = 0.04$, $P = 0.43$) or total morphology ($r = 0.30$, $P = 0.06$; Fig. 4). These

findings suggest that the marker–community link is mediated through quantitative attributes of the foliage.

Integrating racial divergence in specific quantitative leaf chemical and morphological traits showed that the correlation between overall neutral marker and community divergence was attributable, at least in part, to correlated divergence in just a selection of the quantitative traits assessed (Table 1, Fig. 3). The neutral markers were correlated significantly with only one of the eight morphological traits (specific dry mass, $r = 0.33$, $P = 0.048$) and only three of the nine assayed chemicals (carbon [$r = 0.34$, $P = 0.040$], condensed tannins [$r = 0.51$, $P = 0.003$], and total oils [$r = 0.41$, $P = 0.015$]). Four morphological and secondary chemical traits were correlated with the racial divergence in the canopy community, the two most notable being specific dry mass per unit area ($r = 0.45$, $P = 0.007$) and condensed tannins ($r = 0.61$, $P < 0.001$). Both of these traits were also correlated with the neutral markers and, once partial Mantel tests were conducted to control for their influence, the significant correlation between microsatellites and community variation became nonsignificant ($r = 0.24$ and 0.05, respectively; $P > 0.05$). Two traits were correlated with community divergence but not microsatellite divergence. These were the
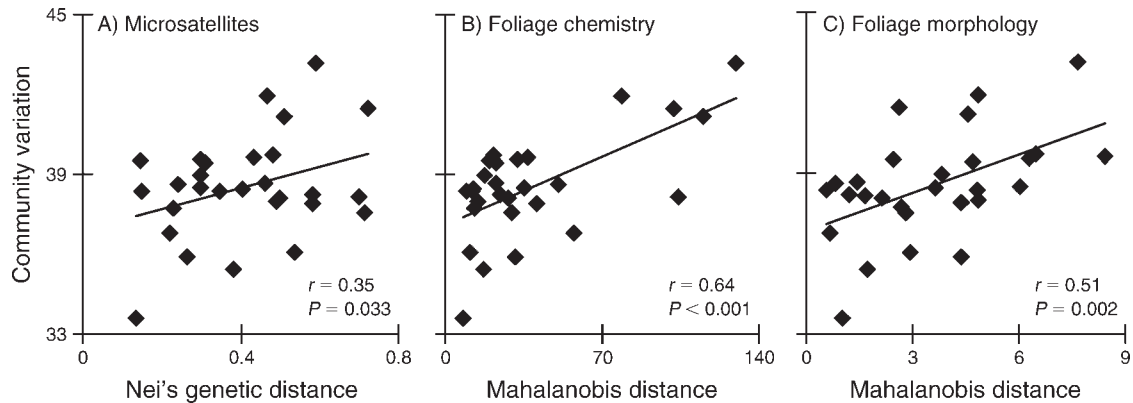
Fig. 3. Testing the genetic similarity rule of Bangert et al. (2006) in *Eucalyptus globulus* at the geographic race level. Plots describe pairwise Mantel correlations comparing distance matrices summarizing canopy community variation (Bray-Curtis dissimilarity) with those for (A) neutral molecular genetic (Nei's genetic distance) and quantitative genetic divergence in (B) foliage chemistry (as assessed using near-infrared reflectance, NIR; Mahalanobis distance) and (C) morphology (Mahalanobis distance) within a common garden.

chemical macrocarpal G ($r = 0.33$, $P = 0.046$) and the morphological trait lamina length ($r = 0.40$, $P = 0.018$).

DISCUSSION

Community responses to geographic races of E. globulus

The demonstration of significant community variation associated with genetic variation among races and families within races of *E. globulus* supports our hypothesis that intraspecific genetic variation within a foundation species can affect dependent communities at multiple genetic scales. Our findings also support the genetic similarity rule of Bangert et al. (2006) at two levels. First, this rule is supported by our demonstration of similar canopy communities on trees of the same geographic races or families within races in a common
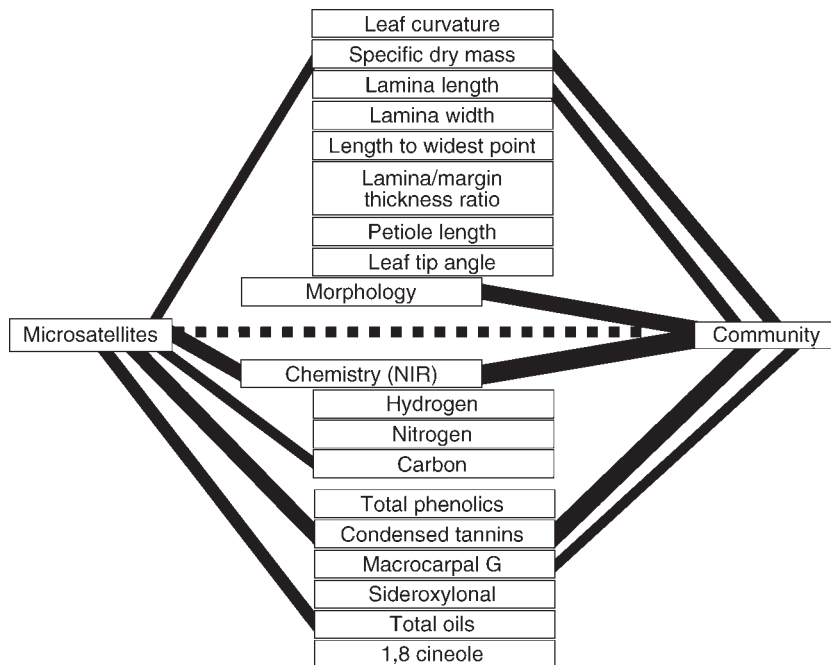

Fig. 4. Correlations between molecular genetic, leaf quantitative genetic, and canopy community variation in *Eucalyptus globulus*. Relationships were assessed at the racial level using Mantel tests. The quantitative genetic traits involved both morphological and chemical assessments, with chemical variation being assessed using foliar near-infrared reflectance (NIR) spectra and individual chemical assays. Connectors are provided only where significant correlations were found, and width of connectors indicates the level of correlation (see *Results* and Table 1 for data). The significant correlations between microsatellites and community variation became nonsignificant when partial Mantel tests were conducted controlling for the effects of condensed tannins and specific dry mass (hence the broken line).

garden experiment designed to identify genetic variation. Second, the rule is supported at the race level by the significant correlations found between distance matrices summarizing genetic dissimilarity in neutral molecular markers, leaf quantitative genetic traits (morphological and NIR spectra), and the canopy community, demonstrating that races of *E. globulus* that are more genetically similar are likely to support more similar communities. The similarity rule was first demonstrated in *Populus*, which has a very different evolutionary history from *Eucalyptus* (Ladiges et al. 2003, Hamzeh and Dayanandan 2004). Consequently, the generality of this finding appears to be enhanced.

The genetic correlations at the race level also demonstrate that intraspecific neutral marker variation can be used to predict community variation. Molecular markers such as microsatellites are generally presumed to be selectively neutral and, therefore, reflect change due to drift and mutation. The magnitude of divergence of neutral molecular markers between populations is expected to increase with time since isolation, a trend that may not relate to that observed in markers or traits that are under selection (Steane et al. 2006, Whitlock 2008). While we argue that the genetically based community divergence is driven by genetically based phenotypic variation in quantitative traits, the link between the neutral markers and genetically based dissimilarity in community phenotypes may arise where both molecular and quantitative trait divergence are influenced by drift or isolation time (Steane et al. 2006, Whitlock 2008). Alternatively, this association could arise when migration and expansion routes of populations parallel environmental gradients. The latter is probably the case in *E. globulus* (Jordan et al. 2000, Freeman et al. 2001) and indeed many other forest tree species with broad geographic ranges (e.g., Hewitt 1999).

In our experimental system, the association between phenotypic (overall chemical [NIR] and morphological variation) and community divergence at the racial level appears to be associated, at least in part, with genetic variation in just a selection of the specific morphological and chemical traits assessed, in particular specific dry mass, lamina length, condensed tannins, and macrocarpal G. Community-level responses to genetic variation in condensed tannins has also been demonstrated within a *Populus* hybrid system (Bangert et al. 2006, Whitham et al. 2006). Such genetically based variation in morphological and chemical traits in *Eucalyptus* may act to drive community variation by influencing colonization and population growth (i.e., fungal populations, Carnegie and Ades 2005, Milgate et al. 2005a), reproductive behavior (i.e., oviposition preference, Rapley et al. 2004b), and herbivory (Jones et al. 2002, Jordan et al. 2002, O'Reilly-Wapstra et al. 2002, Rapley et al. 2004c). These traits may also influence multiple community members directly (Andrew et al. 2007) or indirectly. In the latter case, the biotic environment of particular races or families, for example, may be unsuitable for particular

species due to competitive or predatory interactions (McGuire and Johnson 2006, Johnson and Agrawal 2007). Evidence for this exists in *E. globulus*, where the density of *Mycosphaerella* fungal lesions is influenced by the genetics of *E. globulus* (Milgate et al. 2005a, Freeman et al. 2008), and in turn, higher densities of *Mycosphaerella* can reduce the amount of herbivory by autumn gum moth larvae (*Mnesampela privata*, Jones et al. 2002).

Foundation species as drivers of geographic mosaics of community (co)evolution

Our findings from a common garden have demonstrated the potential for a mosaic of community structure to exist across the natural distribution of *E. globulus*, which is driven by genetic variation within this foundation species. The extent to which the community of dependent organisms responds to this surface of genetic variation at an evolutionary level, however, has not been assessed. While the studies that have founded the geographical mosaic of coevolution theory (reviewed in Thompson 2005) have been conducted at equivalent spatial scales to the current work, evolutionary interactions between foundation trees and their interacting organisms have typically been conducted as pairwise or tri-species studies. In the case of *E. globulus* there is increasing evidence of multispecies genetic interactions. Given that sedentary organisms, such as fungi and galling and larval insects, cannot relocate following their establishment on leaves, the observed variation in their abundance across different races in the current study is likely to reflect differences in their fitness (Shuster et al. 2006). Such variation in larval insect and gall abundance in particular represents direct measures of the fitness consequences of oviposition preferences by parental adults (see Dungey and Potts 2003, Rapley et al. 2004a). In addition, as mobile species choose resources that optimize their survival and reproductive output, the variation observed will, to some extent, also reflect tree genetic influences on their fitness (Rausher 1983, Awmack and Leather 2002). As there are likely to be shared fitness consequences for community members associated with races of *E. globulus*, selection is expected to be occurring at a community level (Shuster et al. 2006, Johnson and Stinchcombe 2007). With feedback, such genetically based community-level interactions offer the potential for evolution of genetic covariances between the foundation species and community members across this broad geographic scale (Moran and Whitham 1988, Evans et al. in 2008).

Evidence for genetic covariation involving *E. globulus* is emerging from studies of its interaction with the leaf pathogen *Mycosphaerella cryptica*. Genomic regions within *E. globulus* associated with foliar susceptibility to *M. cryptica* have been identified (Freeman et al. 2008), and the specialization of different biotypes of *Mycosphaerella* on resistant and susceptible genotypes of *E. globulus* has also been reported (Milgate et al. 2005b). In addition, other studies have demonstrated the feedback effects that community members can have on

fitness correlates of *E. globulus*. These include negative effects of herbivores on tree growth, survival (Floyd et al. 2002, Jordan et al. 2002), and flower abundance (J. O'Reilly-Wapstra, *unpublished data*), as well as the negative effects of pathogens on tree growth (Carnegie and Ades 2005, Milgate et al. 2005*a*). At a broader level, there is also the intriguing possibility of a "hotspot" of coevolution among the southern races of *E. globulus*. This interaction involves the Swift Parrot, *Lathamus discolor*, which is a very effective pollinator of *E. globulus* (Hingston et al. 2004*a*, *b*). The parrot migrates onto the island of Tasmania, where it is largely dependent on flowers of *E. globulus* as a food source to rear its offspring, and has evolved morphological characteristics associated with this diet (Gartrell et al. 2000, Hingston et al. 2004*a*). *Eucalyptus globulus* in turn has evolved atypically large flowers in the southern part of its geographic range, which produce copious nectar (Jordan et al. 1993, Hingston et al. 2004*a*).

The present study represents an essential first step toward demonstrating the existence of (co)evolution involving the foundation tree species and canopy community members, having demonstrated that the dependent community is responsive to genetic variation within our foundation species. Future studies using reciprocal common gardens within the geographic range of each race are important to determine the stability of this genetic mosaic and the community response, as well as its significance relative to abiotic factors that also drive species distributions and adaptation (Johnson and Stinchcombe 2007). An important issue is whether local communities show preference for, or genetic covariance with, the local *E. globulus* race and have feedbacks on the local race that differ from nonlocal races. As such studies will involve multispecies interactions with the genetics of a foundation species, the specific pairwise interactions between each organism and the foundation species may vary across the geographic mosaic in terms of both their existence (i.e., "hotspots and coldspots" of coevolution, Benkman 1999, Thompson 2005) and type (i.e., in the specific strategies deployed in "arms race," mutualistic, or commensalistic interactions; Berenbaum and Zangerl 1998, Martin et al. 2008). All of these interactions will be influenced heavily by their abiotic environments and the community in which they are embedded (Thompson 2005, Johnson and Stinchcombe 2007, Wade 2007).

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