

## PLANT GENETICS AFFECTS ARTHROPOD COMMUNITY RICHNESS AND COMPOSITION: EVIDENCE FROM A SYNTHETIC EUCALYPT HYBRID POPULATION

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**Abstract.**—To examine how genetic variation in a plant population affects arthropod community richness and composition, we quantified the arthropod communities on a synthetic population of *Eucalyptus amygdalina*, *E. risdonii*, and their F<sub>1</sub> and advanced-generation hybrids. Five major patterns emerged. First, the pure species and hybrid populations supported significantly different communities. Second, species richness was significantly greatest on hybrids (F<sub>1</sub> > F<sub>2</sub> > *E. amygdalina* > *E. risdonii*). These results are similar to those from a wild population of the same species and represent the first case in which both synthetic and wild population studies confirm a genetic component to community structure. Hybrids also acted as centers of biodiversity by accumulating both the common and specialist taxa of both parental species (100% in the wild and 80% in the synthetic population). Third, species richness was significantly greater on F<sub>1</sub>s than the single F<sub>2</sub> family, suggesting that the increased insect abundance on hybrids may not be caused by the breakup of coadapted gene complexes. Fourth, specialist arthropod taxa were most likely to show a dominance response to F<sub>1</sub> hybrids, whereas generalist taxa exhibited a susceptible response. Fifth, in an analysis of 31 leaf terpenoids that are thought to play a role in plant defense, hybrids were generally intermediate to the parental chemotypes. Within the single F<sub>2</sub> family, we found significant associations between the communities of individual trees and five individual oil components, including oil yield, demonstrating that there is a genetic effect on plant defensive chemistry that, in turn, may affect community structure. These studies argue that hybridization has important community-level consequences and that the genetic variation present in hybrid zones can be used to explore the genetic-based mechanisms that structure communities.

**Key words.**—Community genetics, *Eucalyptus*, generalists, herbivores, hybrid, specialists, species richness, terpenoids.

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Although genetically controlled plant traits are known to affect the survival and the distribution of diverse herbivores and pathogens (e.g., Maxwell and Jennings 1980; Fritz and Simms 1992), the community-level consequences of these same traits are poorly understood (but see Fritz et al. 1987; Maddox and Root 1987, 1990; Fritz and Price 1988; Linhart 1989; Fritz 1992; Whitham et al. 1994, 1999; Dickson and Whitham 1996). Plant hybrid swarms represent ideal systems to examine the mechanisms of plant-herbivore interactions and the community-level consequences of trait variation because they exhibit a large amount of variation in morphological (Potts and Reid 1985), chemical (Orians and Fritz 1995), and phenological traits (Floate et al. 1993) that are known to affect herbivores and higher trophic level interactions (Whitham et al. 1999).

Several recent studies have examined how hybridization among plants in the wild affects diverse herbivore communities and demonstrated apparent hybrid susceptibility (Fritz et al. 1994; Whitham et al. 1994), dominance (Messina et al. 1996), and additive responses (Aguilar and Boecklen 1992; reviewed in Strauss 1994 and Fritz 1999). For example, in a study of a wild hybrid swarm and adjacent pure stands of *Eucalyptus amygdalina* and *E. risdonii*, the hybrid zone was a center of species richness (Fig. 1; Whitham et al. 1994). Of 38 insect and two fungal taxa examined in the study by

Whitham et al. (1994), the average hybrid tree supported 53% more species than either eucalypt species growing in pure stands. Even though individual taxa exhibited all possible responses to hybrids, the overall community response was that hybrids as a group accumulated both insects and fungi that were otherwise unique to each parental species.

Although the pattern of increased species richness on wild hybrids shown in Figure 1 may be genetically based, the lack of either a known pedigree or a common-garden setting meant that such studies in the wild confounded genetic, environmental, and spatial factors and their interactions. To discriminate between these alternative factors, we performed controlled crosses of *E. amygdalina* and *E. risdonii* to generate a synthetic population of pure and hybrid trees of known pedigree. These seedlings were then planted in a common garden in a replicated randomized block design and their associated arthropod communities were censused three years later.

For a subset of this synthetic population, 31 different leaf terpenoids (essential oils) were assayed to determine how these oils might play a defensive role and affect species distributions among cross types. Terpenoids are thought to play a defensive role in *Eucalyptus* (Edwards et al. 1990, 1993; Stone and Bacon 1994) and the variation of some of these compounds are known to be under strong genetic control

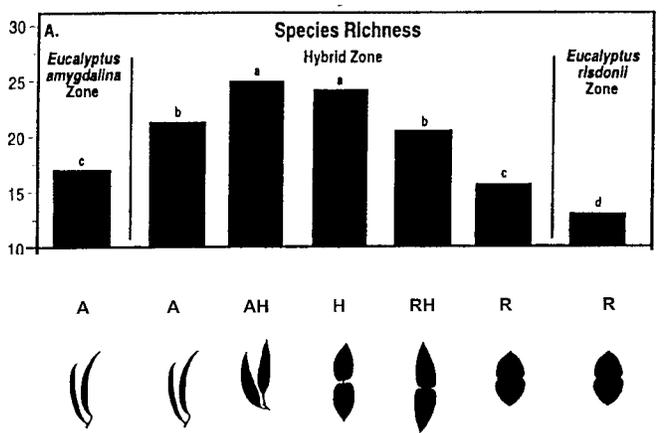


FIG. 1. Average species richness (the number of insect taxa per individual tree) for the wild population as determined by Whitham et al. (1994) for 38 insect and two fungal taxa. Significant differences at  $P \leq 0.05$  are indicated by different letters. Cross types are: A, *Eucalyptus amygdalina*; R, *E. risdonii*; H, intermediate hybrid phenotype; AH, hybrid phenotype tending toward A; RH, hybrid phenotype tending toward R.

(e.g., 1,8-cineole in *E. camaldulensis*,  $h^2 = 0.52$ ; Doran and Matheson 1994). In apparent response to these defenses, herbivores have evolved behavioral and physiological mechanisms to avoid and/or detoxify these oils (Morrow et al. 1976; Morrow and Fox 1980; Foley et al. 1987; Ohmart and Larsson 1989). We examined how oils were distributed among *E. amygdalina*, *E. risdonii*,  $F_1$ , and  $F_2$  hybrids in this common-garden trial and then quantified how the distributions of arthropods were correlated with these oils.

Studies of this hybrid system are of added interest because both species are endemic to Tasmania, Australia, and *E. risdonii* is listed as rare and endangered (Pryor 1981). Furthermore, because studies of the wild population suggested that the small, 100-m wide hybrid zone provided important habitat for some insect species (Whitham et al. 1991a,b, 1994), from a conservation perspective it was important to ascertain the relative contributions of genetic and/or site effects on the distributions of these insects.

## METHODS

### Synthetic Population Field Trial

The pure species *E. amygdalina* and *E. risdonii* and first ( $F_1$ ) and second generation ( $F_2$ ) hybrids between the two species were grown in an experimental field trial near Nugent in southeastern Tasmania, Australia ( $42^\circ 46'S$ ,  $147^\circ 43'E$ ). The trial, which originally contained more than 1100 trees (953 of which were available for analysis), was established in June 1991 at a eucalypt forest site that had been cleared. *Eucalyptus amygdalina* was previously by far the dominant eucalypt on this site, but *E. tenuiramis* (closely related to *E. risdonii*; Chippendale 1988), *E. globulus*, and *E. ovata* were also growing nearby. Apart from the *Pinus radiata* plantation that surrounded the trial site, *E. amygdalina* was also the dominant eucalypt both in the remnant areas left after planting and in the surrounding local vegetation. Spacing was 3 m within rows and 4 m between rows. The trial comprised

16 randomized blocks, with 72 trees per block. Families were randomly assigned to single tree plots. Where there were greater than 16 individuals per family, extra progeny were equally partitioned between blocks and randomly allocated to unfilled block positions.

Controlled crosses in the trial included: (1) two *E. amygdalina*  $\times$  *E. amygdalina* full-sib families and nine polycross families; (2) two *E. risdonii* full-sib and 10 polycross families; (3) seven  $F_1$  hybrid families, five of which were polycross families and two of which were full-sibs from reciprocal crosses; and (4) one  $F_2$  hybrid family. Four of the five *E. risdonii* parents and five of the seven *E. amygdalina* used as females in the crosses mentioned above were further represented by open-pollinated progeny collected from the trees in the field. All the crosses represented in the trial, except the  $F_2$ , were from crosses done in situ in and around a natural hybrid zone at Government Hills, near Risdon, Tasmania (Potts and Reid 1985). The single  $F_2$  family was of unrelated pedigree and originated from the selfing of a putative  $F_1$  hybrid found in open-pollinated seed collected from a pure *E. risdonii* female from a nearby population. In addition, five advanced-generation hybrid families were included in the trial; these families were derived from open-pollinated seed collected from intermediate,  $F_1$  type phenotypes from the hybrid zone studied by Whitham et al. (1994).

For pooled analyses across cross types, all pure species progenies from controlled crosses and open pollination were pooled into either *E. risdonii* (R) or *E. amygdalina* (A) categories. All  $F_1$  hybrids from full-sib or polycross families were pooled into one  $F_1$  hybrid cross type. All advanced-generation hybrid families from open-pollination were pooled into one cross type ( $F_{1op}$ ) and the single  $F_2$  family was also considered as a separate cross type.

### Community Response

The community of dependent taxa on each tree in the synthetic population was assessed by scoring the presence (1) or absence (0) of 30 insect taxa from diverse orders (Hymenoptera, Coleoptera, Lepidoptera, Hemiptera; Table 1). Initially, the presence or absence of 24 insect taxa was determined on each tree in early March 1994. In addition, the presence or absence of another six taxa were included from abundance scores at different times in the same season: presence of a hymenopterous leaf gall (February); damage caused by the autumn gum moth *Mnesampela privata* (September); double-ended lepidopteran leaf miners (October); two lepidopteran leaf tiers (tier 1, tier 2, November); and damage caused by the scarab beetle, *Heteronyx* sp. (December). Species identifications were undertaken following CSIRO (1991), Whitham et al. (1994), and by using the reference collections of Forestry Tasmania with the assistance of specialists.

Following Minchin (1987), the compositional dissimilarity of dependent communities on hybrid and pure species families in the trial were summarized using the nonlinear ordination technique of global nonmetric multidimensional scaling (GNMDS). This technique was applied to the dissimilarity matrix calculated among families using the Bray-Curtis dissimilarity coefficient (see Greig-Smith 1983; Faith et al.

TABLE 1. Description of the 30 insect taxa scored for their presence or absence in the *Eucalyptus amygdalina* × *E. risdonii* experimental field trial and a summary of their responses observed in the synthetic population. Insect taxa were divided into either specialist (followed by preferred host species) or generalist categories (see Methods) and then were further classified under hybrid response as exhibiting one of additive (A), susceptible (S), or dominant (D) responses (see Methods for definitions) to the hybrid taxa. In the last column, comparisons of the susceptibility of hybrids only are made (first generation hybrids [F<sub>1</sub>] vs. F<sub>2</sub> vs. advanced generation hybrids [F<sub>1</sub>op]); the most susceptible cross is given, followed by the significance level (\**P* = 0.05; \*\**P* = 0.01; \*\*\**P* = 0.001). Only significant different comparisons are given in this last column.

Taxa	Identification	Specialist or generalist	Preferred species	Hybrid response	Hybrid preferred (F <sub>1</sub> vs. F <sub>1</sub> op vs. F <sub>2</sub> )
Hymenopterous gall	Hymenoptera 1	specialist	<i>amygdalina</i>	D	ns
Flat hymenopterous gall	Hymenoptera 2	specialist	<i>amygdalina</i>	A	ns
Large psyllid gall	Psyllidae	—	—	—	—
Spherical hymenopterous gall	Hymenoptera 3	—	—	—	—
Miner 1	Lepidoptera 1	—	—	—	—
Miner 2	unidentified 1	specialist	<i>amygdalina</i>	D	F <sub>2</sub> > F <sub>1</sub> op*
Miner 3	Lepidoptera 2	specialist	<i>amygdalina</i>	D	ns
Double-ended mine	Lepidoptera 3	generalist	—	S***	F <sub>1</sub> > F <sub>1</sub> op*** F <sub>2</sub> > F <sub>1</sub> op*
Autumn gum moth damage	<i>Mnesampela privata</i>	specialist	<i>risdonii</i>	A	F <sub>1</sub> op > F <sub>2</sub> *** F <sub>1</sub> op > F <sub>1</sub> ***
Basket moth	<i>Hypertropha</i> sp.	specialist	<i>amygdalina</i>	D	ns
Tier 1	<i>Strepsicrates ejectana</i>	generalist	—	S***	F <sub>1</sub> > F <sub>1</sub> op*** F <sub>2</sub> > F <sub>1</sub> op***
Tier 2	<i>Chlorodes boisduvalaria</i>	specialist	<i>amygdalina</i>	S**	F <sub>1</sub> > F <sub>2</sub> * F <sub>1</sub> > F <sub>1</sub> op*
Tier 3	<i>Acrocercops</i> sp.	generalist	—	S**	ns
Adult tier 1 moth	<i>Strepsicrates ejectana</i>	—	—	—	—
Weevil damage	<i>Gonipterus scutellatus</i>	generalist	—	S***	ns
Gum tree scale	<i>Eriococcus</i> spp.	specialist	<i>risdonii</i>	S**	F <sub>1</sub> > F <sub>2</sub> *
Terminal gall	Hymenoptera 4	—	—	—	—
Mite gall	Psylloidea	specialist	<i>amygdalina</i>	D	ns
Stem galls	Hymenoptera 5	—	—	—	—
Bud galls	Hymenoptera 6	specialist	<i>risdonii</i>	D	ns
Chrysomelid 1	<i>Chrysophtharta decolorata</i>	specialist	<i>amygdalina</i>	D	ns
Chrysomelid 2	<i>Chrysophtharta aurea</i>	specialist	<i>amygdalina</i>	D	F <sub>1</sub> > F <sub>1</sub> op**
Chrysomelid 3	<i>Chrysophtharta nobilitata</i>	specialist	<i>amygdalina</i>	D	ns
Chrysomelid 4	<i>Chrysophtharta</i> sp. 14	—	—	—	—
Chrysomelid 5	<i>Paropsis porosa</i>	generalist	—	—	ns
Chrysomelid 6	<i>Paropsis tasmanica</i>	—	—	—	—
Scarab beetle	<i>Heteronyx</i> sp.	specialist	<i>amygdalina</i>	D	F <sub>2</sub> > F <sub>1</sub> op*** F <sub>1</sub> > F <sub>1</sub> op***
<i>Amorbus</i> damage	<i>Amorbus obscuricornis</i>	specialist	<i>risdonii</i>	D	ns
Leafhopper	<i>Eurymela fenestrata</i> ( <i>Eurymelidae</i> )	—	—	—	—
Helena gum moth	<i>Opodiphthera helena</i>	generalist	—	S***	F <sub>1</sub> > F <sub>1</sub> op*

1987), based on family data standardized such that the abundance of each taxa had a unit maximum. GNMDS was fitted in one to six dimensions and a two dimensional solution was chosen as an adequate representation of the dissimilarities between families based on the inspection of the stress levels (a measure of the fit of the input dissimilarities to the distances in the reduced subspace). Only families with three or more individuals were included in the analysis. Cross type differences in community composition were tested with ANOSIM (Warwick et al. 1990) using the same dissimilarity matrix as the GNMDS. ANOSIM uses bootstrap analyses to test for differences among groups based on 1000 random reassignments of the data to groups and determines whether the group structure of the dissimilarity matrix were significantly different from the group structures obtained through chance alone (Warwick et al. 1990).

#### Species Richness

The richness of the dependent community was calculated by summing the presence (1) or absence (0) of all 30 insect

taxa at the individual tree level. Differences among cross types in the richness of the community on individual trees were tested using PROC MIXED of SAS (SAS Institute 1990) using the model: species richness = block + cross type + family(cross type) + error, where block refers to the fixed effect of the complete blocks in the trial; cross type to the fixed effects of A, R, F<sub>1</sub>, F<sub>2</sub> or F<sub>1</sub>op; and family(cross type) to the random variation between families within cross types. The families within cross types term was used as the error term to test the differences between cross types and test specific contrasts.

#### Individual Species Responses

Using methods of Whitham et al. (1994), insect taxa were classified as specialists if the frequency of infested plants of *E. amygdalina* and *E. risdonii* differed significantly or as generalists if no significant differences (*P* < 0.05) were detected. Following Fritz et al. (1994) herbivore response types to hybrid trees were classified as susceptible (i.e., herbivores attacked a significantly higher proportion of hybrids than

either parental species), resistant (i.e., a significantly lower proportion of hybrids were attacked than either parental species), additive (i.e., an intermediate proportion was attacked and significantly differed from both parents), and dominance (i.e., the proportion of attacked hybrids significantly differed from one parent, but not the other). Taxa that did not differ significantly between either parent and the hybrids supported the null hypothesis proposed by Strauss (1994). All individual responses of common insect taxa to host cross type were analyzed using the NPAR1WAY procedure of SAS (Mann-Whitney *U*-test; SAS Institute 1990).

### Leaf Oils

To examine how these potential plant defenses might systematically differ both between host species and in a segregating population, we assessed oils in a subset of families: *E. amygdalina* (A1 polycross), *E. risdonii*, (R2 polycross), their reciprocal  $F_1$  hybrids ( $A1 \times R2$ ,  $R2 \times A1$  using the same parents from which the pure species polycrosses were obtained), and the single  $F_2$  family where traits were most likely to be segregating. Ten individuals were randomly sampled from these families as well as all the surviving individuals of the single  $F_2$  family. To eliminate potential quantitative and/or qualitative differences that might arise by sampling leaves at different times, all leaf collections were made in mid-January 1995. All leaves for the oil analysis were selected randomly from the new seasons' growth, over the entire canopy. Sample preparation, oil extraction and analysis, and details of the 31 components assayed are presented in Li et al. (1995).

To summarize variation in the percentage oil composition, we used GNMDS as described previously. Vectors were fit to determine the compositional trends revealed by the GNMDS ordination (Bowman and Minchin 1987; Minchin 1987). The correlation between the fitted vector and the samples indicates the goodness of fit of the independent variable in the ordination space. The significance of the correlation was tested based on 1000 randomizations of the data. We then investigated the association between the oil components and insect taxa by calculating the rank correlation in the non-parametric NPAR1WAY procedure in SAS (Mann-Whitney *U*-test, SAS Institute 1990) between insect presence/absence or abundance scores where available, and each of the 31 separate oil components and total oil yield (percent oil/dry weight of leaf). Associations detected at the cross type level may be fortuitous and confounded with general genetic differences between the species that have no direct causality. We therefore restricted our comparison to the single large  $F_2$  family in which we would expect some segregation of the many traits differentiating the two parent species. Sequential Bonferroni adjustments (Rice 1989) were made to significance levels in all cases. These analyses were repeated after grouping a number of the oil components: ( $\alpha$ - and  $\beta$ -pinene;  $\alpha$ - and  $\beta$ -phellandrene; cis and trans-menth-2-en-1-ol, cis- and trans-piperitol with piperitone;  $\gamma$ -terpinene, terpinolene, terpinen-4-ol, and  $\alpha$ -terpine-ol; and  $\gamma$ -,  $\alpha$ -, and  $\beta$ -eudesmol. We also fitted the individual oil components and the major axes derived from the GNMDS ordination of these components into the community space derived from GNMDS or-

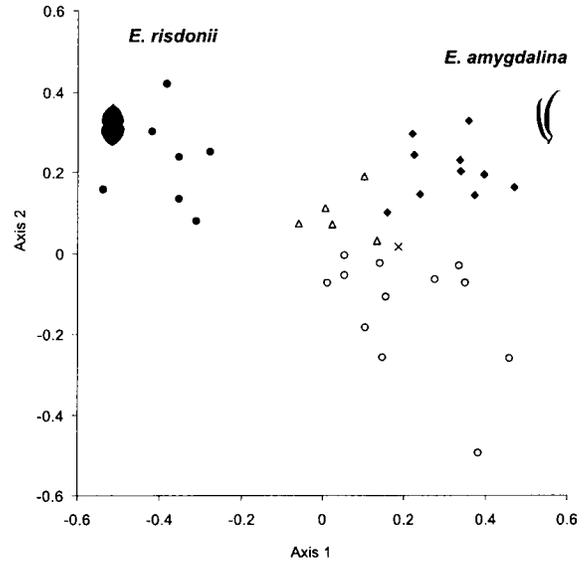


FIG. 2. A summary of the compositional dissimilarity of different families from the presence of 30 insect taxa on *Eucalyptus amygdalina* ( $\blacklozenge$ ), *E. risdonii* ( $\bullet$ ), their  $F_1$  hybrid ( $\circ$ ),  $F_{1op}$  ( $\triangle$ ), and the  $F_2$  hybrids ( $\times$ ) based on the first two dimensions (axis 1 and axis 2), of a six-dimensional, global, nonmetric multidimensional scaling (GNMDS).

dination of individual  $F_2$  plants using vector fitting as previously described.

### Leaf Toughness

To test the hypothesis that the mechanical difference in the leaf toughness among the species and their hybrids affects the distributions of insect taxa, we quantified leaf toughness for the same trees used in the oil analyses. In mid-January 1995, five leaves from each of three leaf types from the current growing season were selected at random across the canopy of each individual and measured for toughness. Leaf types were: (1) oldest fully expanded leaf; (2) the youngest fully expanded leaf; and (3) the youngest leaf, immediately behind the bud. All leaf toughness measurements were made using a portable penetrometer (after Sands and Brancatini 1991). Analysis on individual leaf type means was undertaken using a repeated measures model in the GLM procedure of SAS (SAS Institute 1990), treating the leaf classes as dependent and cross type as independent. The association between the presence/absence of the 30 insect taxa and leaf toughness was calculated for the host  $F_2$  genotypes in the trial as previously described.

## RESULTS

### Community Response

After allowing insects to naturally colonize our synthetic population for three years, we found consistent differences among the arthropod communities on the families of each eucalypt species and their hybrids (Fig. 2). We found no significant differences between the herbivore communities of  $F_1$  and  $F_{1op}$  families ( $P = 0.246$ ; ANOSIM). However, both  $F_1$  and  $F_{1op}$  families differed significantly from *E. risdonii*

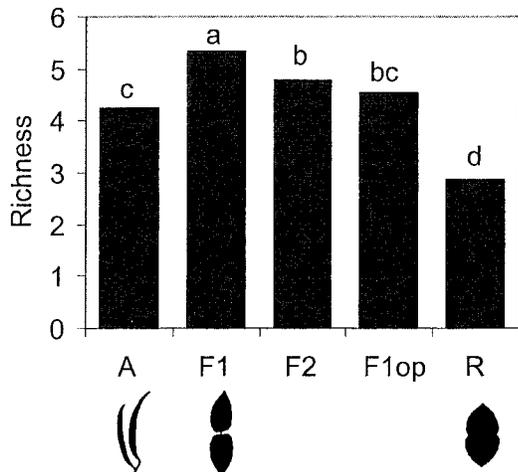


FIG. 3. Average species richness within the *Eucalyptus amygdalina* × *E. risdonii* synthetic population, for the number of insect taxa per individual tree, for 30 insect taxa (see Methods). Different letters indicate significant differences at the 0.05 level. Cross types are: A, *E. amygdalina*; R, *E. risdonii*, F<sub>1</sub>, first generation hybrids; F<sub>2</sub>, second generation hybrids (F<sub>1</sub> hybrid selfed); F<sub>1op</sub>, advanced generation hybrids.

( $P < 0.001$ ; ANOSIM) and *E. amygdalina* ( $P < 0.001$ ,  $P < 0.021$ , respectively; ANOSIM). The single F<sub>2</sub> family did not have a herbivore community that differed significantly from that on the *E. amygdalina* families ( $P = 0.708$ ), but did differ significantly from that on the *E. risdonii* families ( $P < 0.001$ , Fig. 2). Although the herbivore community of F<sub>1</sub> hybrids differed from both parent species, it was closest in affinity to the community on *E. amygdalina* (Fig. 2). However, rather than appear intermediate between the communities on the parent taxa, the community on the F<sub>1</sub> hybrids varied in a different direction (negative on axis 2), suggesting that the community on this cross type had unique components.

#### Species Richness

The patterns of species richness on crosses of known pedigree suggest that the underlying genetic structure of the plant population is a major determinant of species richness. In analyses of the number of species found on individual trees, insect species richness was significantly greatest on hybrids and least on individuals of either parental species ( $F_1 > F_2 > E. amygdalina > E. risdonii$ ;  $P < 0.05$  between F<sub>1</sub> and F<sub>2</sub> cross types;  $P < 0.001$  in other contrasts; Fig. 3). Open-pollinated F<sub>1</sub>s (i.e., F<sub>1op</sub>) were intermediate but not significantly different from either F<sub>2</sub> or *E. amygdalina* genotypes.

In comparisons of insect species richness on trees from controlled crosses in a common garden (Fig. 3) with trees of unknown pedigree in the wild, which were classified based on morphological traits (Fig. 1), we found remarkable agreement (F<sub>1</sub> types = backcross types to *E. amygdalina* > backcross types to *E. risdonii* = *E. amygdalina* > *E. risdonii*). Two major similarities were apparent. First, in both wild and synthetic populations, individual hybrid trees supported significantly greater species richness than the parental tree species. Second, in both wild and synthetic populations, *E. amygdalina* supported more species than *E. risdonii*. Because the

pool of species available to colonize hybrids is derived primarily from *E. amygdalina*, this species should exhibit a disproportionate influence on the pattern of species acquisition by hybrids and may explain their similarity in insect communities.

#### Individual Species Responses

Three major patterns emerged from examination of the responses of the individual arthropod taxa to the different cross types. First, the distributions of most insects were significantly affected by the pure and hybrid status of their host plants. Of 24 insect taxa common enough for individual analyses (i.e., six of 30 total taxa were eliminated due to rarity), 21 exhibited significant differences in host use among *E. amygdalina*, *E. risdonii*, and hybrids. In three cases, we accepted the null hypothesis of no response (Strauss 1994) in which the proportion of trees colonized among cross types did not differ significantly (Table 1).

Second, specialist insects are most likely to exhibit a dominance response to F<sub>1</sub> hybrids. Of 15 specialist insects that were identified, 11 fed significantly more on *E. amygdalina* than *E. risdonii* and four fed significantly more on *E. risdonii* than on *E. amygdalina*. Eleven of these 15 specialists showed a dominance response to the F<sub>1</sub> hybrids, where the proportion of plants on which they fed did not differ significantly ( $P > 0.05$ ) between the F<sub>1</sub> and one of the parental species.

Third, generalist insects exhibited a very different response in which hybrids were generally classified as being susceptible. Six taxa were easily classified as herbivore generalists as they showed no significant differences in feeding on either *E. amygdalina* or *E. risdonii*. Of these generalists, five were significantly more likely to feed on F<sub>1</sub> hybrids than either parental species and only one exhibited no significant differences. The above three general patterns are consistent with those observed in the wild (Whitham et al. 1994; Fig. 1).

#### Leaf Oils

Observations of the GNMDS ordination showed that *E. amygdalina*, *E. risdonii*, and their hybrids had clear differences in their leaf oil composition (Fig. 4A). Both F<sub>1</sub> and F<sub>2</sub> hybrids were intermediate and fell outside the range of their parental species, and the F<sub>2</sub> plants appeared to be more variable than individuals from the two F<sub>1</sub> families. Vector analyses showed that all the oils tested contributed significantly to the GNMDS ( $P < 0.001$ ) except for myrcene ( $P = 0.128$ ) and a small group of other unidentified compounds ( $P = 0.663$ ). The oils that contributed the most to the differentiation of the parental species and their hybrids are given in Figure 4B.

Of 31 different oils that were recovered, the *E. amygdalina* family had 27 oils, the *E. risdonii* family had 29, and the F<sub>1</sub> hybrids had 31. Eleven oil components ( $\alpha$ -thujene,  $\alpha$ -phellandrene,  $\beta$ -phellandrene,  $\gamma$ -terpinene, terpinolene, terpinen-4-ol, piperitone, cis-ocimene, cis-piperitol, unknown 1, geranic acid) were found to have significantly greater concentration in *E. amygdalina* than *E. risdonii*, and seven components ( $\alpha$ -pinene, sabinene, 1,8-cineole,  $\alpha$ -terpinyl acetate, unknown 3,  $\beta$ -pinene, geranyl acetate) plus total oil yield were found to have greater quantities in *E. risdonii* than *E.*

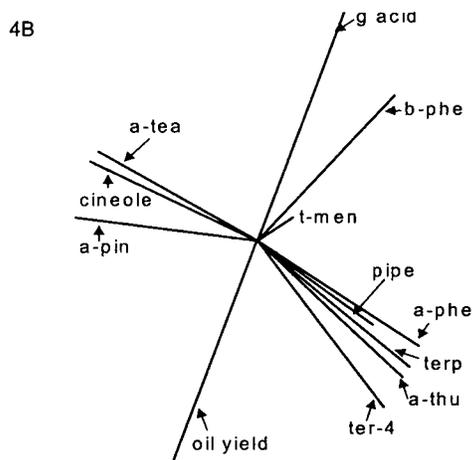
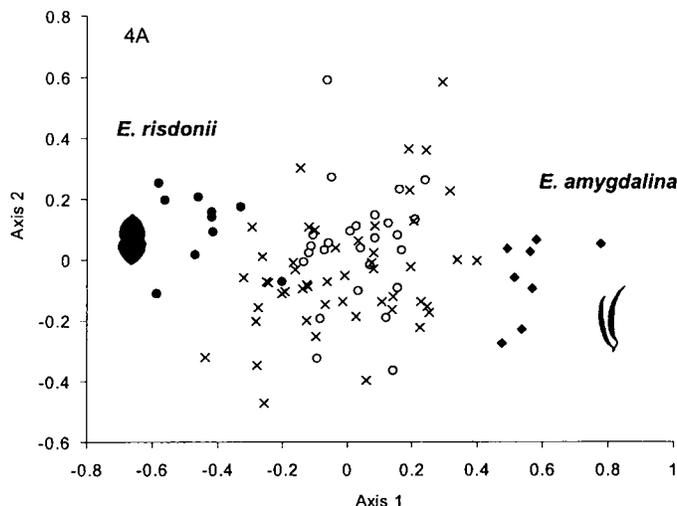


FIG. 4. (A) Multidimensional scaling (GMNDS) axes 1 and 2 based on the oil component content of new seasons' foliage of *Eucalyptus amygdalina* (◆), *E. risdonii* (●), their F<sub>1</sub> hybrid (○), and the F<sub>2</sub> hybrids (×). The most important oil vectors ( $R > 0.75$ ,  $P \leq 0.0001$ ) are given below (B) a-pin,  $\alpha$  pinene; cineole, 1,8-cineole; a-tea,  $\alpha$ -terpinyl acetate; g acid, geranic acid; b-phe,  $\beta$ -phellandrene; t-men, trans-menth-2-en-1-ol; pipe, piperitone; a-phe,  $\alpha$ -phellandrene; terp, terpinolene; a-thu, a-thujene; ter-4, terpinen-4-ol; oil yield, total oil yield %w/w dried leaves.

*amygdalina*. The remaining oil components did not differ between either species.

The F<sub>1</sub> hybrids accumulated all oil components of both parental taxa. Comparing only the two parent species, *E. amygdalina* and *E. risdonii*,  $\beta$ -eudesmol,  $\alpha$ -eudesmol, and one unknown component were found only in *E. risdonii* leaves, but a different unknown component was unique to *E. amygdalina* leaves. The inheritance patterns of individual oils in F<sub>1</sub> hybrids was approximately equally divided among additive and dominance responses. Univariate analyses of each of the 31 oils indicated that there were 10 cases in which the F<sub>1</sub> hybrids had intermediate percentage oil composition between both parental species (i.e., 32% cases showed additive inheritance), eight cases in which they differed from one parent species (four each for *E. amygdalina* and *E. risdonii*) but not the other (i.e., 26% showed dominance). There were

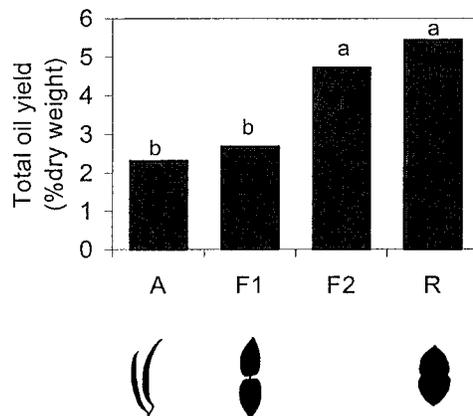


FIG. 5. Average oil yield (%w/w dried leaves) calculated at the individual tree level within the *Eucalyptus amygdalina*  $\times$  *E. risdonii* synthetic population. Different letters indicate significant differences at the 0.05 level.

13 cases in which the percent oil concentrations of F<sub>1</sub> hybrids did not differ from either parental species (i.e., 42% the null hypothesis). There were no cases in which F<sub>1</sub> hybrids had significantly higher or lower individual oil concentrations than both parental species (i.e., 0% better-parent heterosis and 0% negative heterosis relative to the worst parent). F<sub>1</sub> hybrids had one oil component ( $\gamma$ -eudesmol) that was undetected in the pure species in the common garden, but did occur in the field sample of one of the *E. amygdalina* parents used in the original crossing design (unpubl. data). *Eucalyptus risdonii* had significantly higher oil yield than *E. amygdalina* ( $P < 0.01$ ), with the F<sub>1</sub> hybrids not significantly different from *E. amygdalina* (*E. risdonii* = 5.4% of dry weight, F<sub>1</sub> = 2.7%, F<sub>2</sub> = 4.7%, *E. amygdalina* = 2.3%; Fig. 5). In the single F<sub>2</sub> family, oil yields from leaves were almost equal to the higher yielding *E. risdonii*.

#### Phytophage Associations with Oils

When we fitted the oil components as vectors into the GMNDS community space of the single F<sub>2</sub> family, we found an association between the pooled arthropod community and total oil yield ( $P = 0.037$ ),  $\beta$ -phellandrene ( $P = 0.002$ ), linalool ( $P = 0.017$ ), geranyl acetate ( $P = 0.008$ ), geranic acid ( $P = 0.049$ ), and unknown 2 ( $P = 0.009$ ; Rice's sequential Bonferroni adjustment). However, at the individual taxa level, we found only three significant relationships of a possible 930 ( $P < 0.05$  following Rice's sequential Bonferroni adjustment). These relationships involved three oil components and three arthropod taxa (linalool and bud galls [positive]; geranyl acetate and miner 3 [negative]; and unknown 2 and adult tier 1 [positive]). When all cross types were included in the oil vector fitting, oil yield ( $P = 0.027$ ) and three of the five oils significant within the F<sub>2</sub> remained significant ( $\beta$ -phellandrene,  $P = 0.002$ ; geranic acid,  $P = 0.033$ ; and geranyl acetate,  $P < 0.001$ ). Oil yield and the percentage geranic acid were strongly associated with variation along axis 2 in the GMNDS ordination of the oil components (Fig. 4). This direction of variation also was the principal direction that separated individuals within the single F<sub>2</sub> family.

### Leaf Toughness

Leaf toughness differed among the subsample of families used in the oil analysis, but only on the very youngest leaf class ( $P < 0.05$ ). *Eucalyptus amygdalina* had significantly tougher young leaves than *E. risdonii* ( $P < 0.05$ ), and the  $F_1$  and  $F_2$  hybrids were intermediate. No significant association between leaf toughness and the presence/absence of any insect taxa surveyed was found within the  $F_2$  family.

## DISCUSSION

### Genetic Structure of Communities

Our common-garden studies of how 30 insect taxa were distributed on 953 trees of known pedigree showed that genetic variation among cross types significantly affected the structure of this arthropod community. Several major patterns supported this hypothesis. First, distinctive communities developed on each parental species and their  $F_1$  hybrids. Second, the arthropod communities on the  $F_1$  hybrids had unique components when compared to pure species. Third, individual hybrid trees acted as centers of species richness and supported significantly more species of herbivores than their parental plant species (Fig. 3). Fourth, generalist and specialist insects were differentially affected by the underlying genetic structure of our synthetic population. Generalist insects were more common on hybrids than on either parent (i.e., a susceptible response), whereas specialist insects exhibited a dominance response to hybrids. Because our analyses treated all insects the same (i.e., common species were not weighted more than rare species), these patterns were not driven by a few common species, but represent community-wide patterns.

Furthermore, the magnitudes of these patterns are likely conservative because we only censused primary plant consumers. For example, plant genetic-based factors can determine the distribution of a keystone herbivore, which in turn affects the distributions of many other species. In this system, 17 other species of parasites and inquilines (animals that live in the abodes belonging to another) have been identified from galls produced by the hymenopteran, (*Chrysoatomus* spp.; D. Bashford, pers. comm.). In another system, Dickson and Whitham (1996) showed that the resistance traits of individual cottonwood trees affected the distribution of the galling aphid, *Pemphigus betae*, which, in turn, affected the distributions of 42 other taxa from different trophic levels, including birds, fungi, insect predators, and other insect herbivores (see also examples of Fritz 1992; Ericson et al. 1993; Preszler and Boecklen 1994).

The patterns of response observed in our synthetic population in a common garden (Fig. 3) agreed with our observational studies in the wild (Fig. 1). Even though these studies were conducted four years apart at study sites separated by approximately 50 km, and on trees of different ages (i.e., juvenile trees in the common garden and mature trees in the wild), three of the four general patterns described above that were studied in the synthetic population were also found in the wild. In general, the highest species richness was found on the intermediate hybrid types and *E. risdonii* consistently supported the least diverse arthropod community in both the

wild and synthetic populations. By examining both natural and artificial systems, these studies combined the realism of the wild and eliminated a number of alternative hypotheses in a controlled common garden. For the eucalypts studied, wild and synthetic populations appear to be relatively good approximations of one another.

We found one major discrepancy: Trees in the wild supported 40 species (38 insect and two fungal taxa; Whitham et al. 1994), whereas trees in our common gardens supported only 30. Most importantly, average species richness per tree was approximately four times greater in the wild than in the common garden. We suspect that, among other things, these differences were caused in part by the ontogenetic shifts in plant traits as trees phase shifted from small juvenile trees (i.e., the present study) to older and larger trees expressing both juvenile and mature traits (i.e., our observational study in the wild, Fig. 1). Recent studies of other eucalypt species show that these phase shifts are under strong genetic control (Wiltshire et al. 1998) and influence insect herbivores (R. Lawrence, unpubl. data). Similarly, studies on juvenile and mature ramets from the same cottonwood clone growing side by side, showed that per unit of foliage, mature trees supported approximately three times more species than juvenile trees (Waltz and Whitham 1997). Differences in the number of taxa supported per tree between the wild and synthetic population may also be explained in part by the longer time for colonization of the wild population and by the even-aged synthetic population providing a less diverse environment than the natural stand. Although the original trees in the natural stand are likely to be of mixed ages, the stems were even aged and the result of coppice regeneration following wildfire in 1980 (Potts and Reid 1985), allowing 13 years for colonization, whereas the communities in the synthetic population only result from three years of colonization. Future studies should examine how the host age structure and the changing gene expression of trees of known pedigree affects community structure.

### Genetic Mechanisms

Whitham (1989) suggested that the increased susceptibility of hybrids to herbivores may be caused by genetic recombination disrupting co-adapted gene complexes controlling resistance. If this were the case,  $F_2$  hybrids should exhibit greater susceptibility to insect herbivores than  $F_1$  hybrids due to genetic recombination. However, this was not the case in the present study where the  $F_1$  hybrids support more insect taxa than all other cross types including the  $F_2$  family and the advanced generation crosses ( $F_{1op}$ ). Increased susceptibility of the  $F_1$  hybrids could occur through additive inheritance of resistance mechanisms or phenological traits (Fritz et al. 1994; Strauss 1994; Fritz 1999). Additive inheritance of resistance traits could result in increased  $F_1$  susceptibility if, first, resistance is dependent on a threshold response and, second, resistance is conferred by a different mechanism in each host taxon. Under these circumstances, each mechanism (e.g., level of a chemical) is diluted below the threshold required to maintain resistance resulting in host susceptibility. This may help explain why  $F_1$  hybrids were also found to have unique community components when compared to the

other cross types (Fig. 2). Intermediate inheritance of a phenology trait such as foliage flushing time could also result in increased herbivory on  $F_1$  hybrids if they are rarer than either host taxa. Herbivore populations responding to host phenology would then tend to concentrate on the rarer intermediates as they shift hosts through the season. However, this is unlikely to explain the increased species richness on the  $F_1$  hybrids in the present case, because hybrids were not rare in the common garden.

The patterns of oil inheritance are consistent with the additive or threshold hypothesis. In our analyses of 31 essential oils, 32% exhibited additive inheritance, 26% were dominant, 0% better or worse parent heterosis, and 42% showed no response (i.e., the null hypothesis). Thus, while  $F_1$  hybrids accumulated the defenses of both parents and may even have novel oils not previously detectable in the parent species, the concentration of these oils was either intermediate or not different from the parental species. Because the effectiveness of a defense is often dependent upon its concentration, the oils that exhibit intermediate concentrations may reduce the defenses of  $F_1$  hybrids below a critical threshold.

Consistent with a threshold model, at the community level the increase in species richness on  $F_1$  hybrids relative to  $F_2$  hybrids is also associated with a significant decline in total oil yield (Fig. 5). This result, however, is based on a single  $F_2$  hybrid family that is not directly related even though it was derived from the same natural population. Further investigation of arthropod responses to  $F_2$  families that are directly related to the  $F_1$  should provide a critical test of the threshold model.

The effect of these potential defenses on the insect community was dependent on whether the data were analyzed using individual insect taxa or community data. At the most specific level, when we examined the relationships of the presence of individual insect taxa as a function of individual oil components or leaf toughness within the single  $F_2$  family (an ideal genetic model for such analyses), only three significant correlations emerged (linalool and bud galls, geranyl acetate and miner 3, and unknown 2 and adult tier 1). However, at the community level, we found that when all 30 arthropod taxa were pooled, variation in community composition was significantly correlated with total oil yield ( $P = 0.037$ ) and the percentage of  $\beta$ -phellandrene ( $P = 0.002$ ), linalool ( $P = 0.017$ ), geranyl acetate ( $P = 0.008$ ), geranic acid ( $P = 0.049$ ), and unknown 2 ( $P = 0.009$ ).

Two hypotheses may account for these patterns. First, the small number of significant correlations between specific oil components and individual herbivores suggests there are very few one-on-one defenses. Furthermore, the fact that total oil yields (i.e., 31 oils pooled) and five specific oil components were each significantly correlated with the insect herbivore community (i.e., all 30 taxa pooled) suggests that these potential defenses affect many herbivore species. Edwards et al. (1993) found that the concentration of the terpenoid cineole was negatively associated with the defoliation caused by a group of beetles, commonly known as Christmas beetles. However, our study is the first that we know of in which arthropod associations with essential oils have been demonstrated at the community level involving such diverse orders as the Hymenoptera, Coleoptera, Lepidoptera, and He-

miptera in eucalypts. Second, interactions among one or more herbivores may obscure the effects of any one oil on a specific herbivore such that only communitywide correlations yield significant correlations. For example, if different herbivores compete for the same resource (e.g., Denno et al. 1995) and/or if one herbivore induces plant defenses that make the host less palatable for other herbivores (e.g., Karban et al. 1987), plant defenses should be poorly correlated with any one herbivore due to the interactions among herbivores.

### Conclusions

Although other traditional factors such as competition, predation, disturbance, succession, and abiotic factors are widely emphasized as structuring communities (e.g., Pickett and White 1985; Diamond and Case 1986; Ricklefs and Schluter 1993), our results emphasize that the underlying genetic structure of the plant population may also play a major structuring role that is perhaps more proximal than other, better known factors. Because eucalypts represent dominant trees on the Australian landscape and are well known for their propensity to hybridize (Griffin et al. 1988; Williams and Woinarski 1997), these findings may be important at the landscape level. Furthermore, from a conservation perspective, it has long been recognized that the maintenance of genetic variation is crucial to the preservation of individual species. Our study argues that there is another major, but less appreciated benefit of such genetic variation: Preserving genetic variation in the plant population may preserve greater species richness in the dependent community (Whitham et al. 1999). These results also suggest that community genetics, that is the role of genetic variation in directly and indirectly affecting the distribution of species and structuring communities, can make a significant contribution to the understanding of the ecology and evolution of communities.

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