

ORIGINAL PAPER

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Plant hybrid zones as centers of biodiversity: the herbivore community of two endemic Tasmanian eucalypts

Received: 5 August 1993 / Accepted: 20 December 1993

Abstract We found the hybrid zone between *Eucalyptus amygdalina* and *Eucalyptus risdonii* to be a center of insect and fungal species richness and abundance. Of 40 taxa examined, 73% were significantly more abundant in the hybrid zone than in pure zones, 25% showed no significant differences, and 2% were most abundant on a pure host species. The average hybrid tree supported 53% more insect and fungal species, and relative abundances were, on average, 4 times greater on hybrids than on either eucalypt species growing in pure stands. Hybrids may act as refugia for rare species: 5 of 40 species were largely restricted to the hybrid zone. Also, 50% of the species coexisted only in the hybrid zone, making for unique species assemblages. Although hybrids support more species and greater abundances, all hybrids are not equal: 68% of the 40 taxa examined were significantly more abundant on one hybrid phenotype than another. While herbivore concentrations on F1 type intermediates were rare, concentrations were common on phenotypes resembling backcrosses either to *E. amygdalina* or *E. risdonii*. For specialist herbivores, the hybrid phenotype most heavily utilized appears to be determined by its phenotypic affinity to its host species. Generalists exhibit an overall greater abundance on hybrids, but are less likely to utilize one hybrid phenotype over another. Mechanistic explanations for these distributions are numerous and probably species specific, but are likely to include: increased genetic susceptibility of hybrids due to hybrid breakdown; increased stress in

the hybrid zone resulting in greater plant susceptibility; and a greater diversity of resources in the hybrid zone which could support more species. Seed capsule production by hybrids and their parental species is negatively correlated with herbivory. However, it is difficult to determine whether herbivores cause this pattern as hybrids may have inherently lower sexual reproduction. Laws enacted to protect rare and endangered species do not include hybrids. We argue that a re-examination of our current "hybrid policy" is warranted. Plant hybrid zones are centers of plant evolution and speciation, sources of economically important plants and potential biocontrol agents, and, as our study suggests, also provide essential habitats for phytophagous communities.

Key words Biodiversity · *Eucalyptus*
Hybrid conservation · Phenotypic affinity hypothesis
Plant/herbivore interactions

Introduction

Herbivore and parasite responses to hybrid hosts are variable. Compared to pure host species, herbivore and parasite populations on hybrid plants and mammals, respectively, were smaller (Heaney and Timm 1985; Boecklen and Spellenberg 1990), intermediate (Manley and Fowler 1969; Aguilar and Boecklen 1991), or greater (Drake 1981; Sage et al. 1986; Dupont and Crivelli 1988; Whitham 1989; Barker 1990; Floate and Whitham 1993; Floate et al. 1993; Ericson et al. 1993). Furthermore, some organisms appear to be dependent upon their hybrid host habitat. The hybrid and overlap zone of two *Populus* species supported 85–100% of the populations of a specialist gall-forming aphid and a generalist leaf-feeding beetle (Whitham 1989; Floate et al. 1993).

Recent community level studies of diverse organisms have shown mixed responses to hybrid plants. Most species were more abundant on hybrids, while others

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were less abundant, intermediate or showed no differences (Fritz et al. 1994; Morrow et al. 1994; this paper). These mixed responses within the same system offer great potential for examining the genetic (Fritz et al. 1994) and non-genetic mechanisms (Paige and Capman 1993; Floate et al. 1993) involved in host use, host specificity, host shifting, and herbivore evolution (Moran and Whitham 1988; Floate and Whitham 1993; Morrow et al. 1994). Such studies can provide insights into other important issues, including pest management (Manley and Fowler 1969; Whitham 1989; Barker 1990; Ericson et al. 1993), conservation of plants and their dependent communities (Whitham et al. 1991; Martinsen and Whitham 1994) and mutualisms (Floate and Whitham 1994).

We sought to examine the potential generalities and differences that might be characteristic of hybrid zones by studying hybrids in the Australian genus *Eucalyptus* (Myrtaceae). This genus has an ecology and an evolutionary history (Pryor 1976, 1981) very different from the systems examined in North America and Scandinavia. *Eucalyptus* is a species-rich group (500+ species, Pryor and Johnson 1971) known for its propensity to hybridize (Griffin et al. 1988; Duncan 1989) and for its abundant herbivore fauna (Fox and Morrow 1983, 1986; Morrow and Fox 1989).

We examined the phytophagous community associated with a natural hybrid swarm between *Eucalyptus risdonii* Hook.f. and *Eucalyptus amygdalina* Labill, and adjacent pure stands of each species, near Hobart, Tasmania. Extensive analyses of the patterns of hybridization at our site (Potts and Reid 1985, 1988; Potts 1986) provided the taxonomic base for the present study. Both species are endemic to Tasmania and exhibit extreme differences in morphology which enabled us to classify individual trees to one of five possible phenotypes (pure *E. amygdalina*, backcrosses to *E. amygdalina*, F1-type intermediates, backcrosses to *E. risdonii* or pure *E. risdonii*).

These trees were used to address four questions. First, within the hybrid zone, how are insects and fungi distributed across the two pure and three hybrid phenotypes of trees? Because both hybrid and parental trees grow side by side, differences in species richness and abundance among phenotypes are most likely to be due to differences in host genetics rather than environmental effects.

Second, how are insects and fungi distributed in the hybrid zone versus adjacent pure host stands? Although site and host genotype effects are mixed in this comparison, it allows us to examine the distribution of phytophagous species at two levels: within the hybrid zone, and across pure and hybrid zones.

Third, do the distributions of generalist and specialist phytophagous species exhibit different patterns of hybrid and pure host use?

Fourth, is there an association between sexual reproduction by the different tree phenotypes and herbivore load? If the phytophagous community shows patterns

of concentration on specific tree phenotypes, then plant fitness may be affected.

Methods

Tree classification and measurement of sexual reproduction

We used the same study site as Potts and Reid (1985, 1988) and Potts (1986). Following their example, phenotypes were subjectively classified into five phenotypic classes. Trees were designated as (A) if they resembled pure *E. amygdalina* and (R) if they resembled pure *E. risdonii*. Hybrids were classified as backcrosses to *E. risdonii* (RH) if phenotypes deviated towards *E. risdonii*, backcrosses to *E. amygdalina* (AH) if phenotypes deviated towards *E. amygdalina*, and intermediate or F1-type hybrids (H) if they resembled a single known F1 hybrid which resulted from an experimental cross.

Our subjective classification was corroborated, and the continuous nature of the variation in the hybrid zone quantified, by calculating hybrid index scores for each individual sampled. The hybrid index is a discriminant function calculated to differentiate between the pure stand samples of *E. risdonii* and *E. amygdalina* using the DISCRIM procedure of SAS (1988). The analysis is based on 15 morphological traits measured from the juvenile and adult leaves, seed capsules, and a subjective glaucousness score (see Potts and Reid 1985 for details). The scores on this discriminant function were then calculated for plants sampled from the hybrid zone, and following Potts and Reid (1985), the discriminant function was rescaled so that pure stand samples of *E. amygdalina* and *E. risdonii* have a mean of 0 and 1 respectively. On this scale a known F1 hybrid has a value of 0.51.

To determine if there is an association between plant reproduction and herbivore loads, seed capsule production was quantified. The entire capsule loads of individual trees were counted in 1990 and 1992 by two scorers. The results from these two replicates were averaged to give an estimate of sexual reproduction. These data were also compared to capsule production data collected in 1980 (Potts 1986).

Insect and fungal classification, censusing and data analysis

We identified 38 insect taxa from diverse orders (Homoptera, Diptera, Hymenoptera, Coleoptera and Lepidoptera) and two fungal taxa. All produce distinctive sessile, persistent structures such as galls and mines which facilitated accurate quantification. While relatively few taxa were identified to species, taxonomists confirmed that 36 of the 40 taxa examined were likely to be good species and in only 4 instances was it likely that a taxon included more than a single species. Taxonomic studies of many of these groups are lacking and many species are undescribed.

We censused the insects and fungi on 135 mature multi-stemmed trees that were 3–4 m in height. The stems were of approximately the same age as a result of coppice regeneration from a 1980 fire (Potts 1986). Along a transect we examined 15 trees for each of the five phenotypes in the hybrid zone. To reduce site effects, all trees within the hybrid zone were blocked in groups of 5, with each group containing one each of A, AH, H, RH and R (the diameter of a block did not exceed 20 m). Within each pure zone, we censused trees every 3–4 m along two transects; the 1st transect was approximately 100 m from the nearest hybrids and the 2nd transect was approximately 150 m from the nearest hybrids. Along each transect, 15 trees were haphazardly selected for sampling. Because only specific taxa were examined along the second transect in each pure zone, some figures show data for both transects while other figures show data for only the first transect. Also, data from these second transects were excluded from species-richness calculations as the full complement of species was not censused.

Using ladders, we examined all sides and heights of each tree.

For common species, two observers recorded all individuals that could be counted during a 2 min period. Rarer species were censused by collecting all the galls, lerps, mines, etc. that could be found during a 12-min period, and were later sorted in the lab. Altogether we recorded 22,192 insects and fungal lesions (tree mean = 200, range = 51–617). Searches were thorough: with the exception of the most abundant species, we obtained total counts per tree.

All data were standardized into 'per minute' counts and log transformed to normalize the data. Analyses of variance followed by least squares significant differences (if the former was significant at $P < 0.05$) were undertaken using the GLM procedure of SAS (1988), and were employed to examine potential differences among various pure and hybrid categories. Additionally, relative abundance values for each tree were calculated. This was accomplished by standardizing the log transformed counts/minute, for each of the 40 taxa to have a total standard deviation of 1 and a mean of 0.5 across all the data. We then summed these standardized values for each tree. This prevented common species from swamping the abundances of less common species in our relative abundance analysis, allowing general response patterns to be summarized.

We examined the patterns of hybrid utilization by generalist and specialist insects and fungi. We defined a species as being a specialist if it was found on only one plant species and/or was significantly more abundant on one plant species than on the other. Insects and fungi were classified as being generalists if there were no significant differences in abundance between the tree species. For each group we then examined their use of hybrids. Insect concentrations on F1 phenotypes were rare in this study (there was only one example in which $H > RH$ and AH) so we reduced the number of possible outcomes by considering only the more common cases in which the abundance of a herbivore fell into one of three classes (AH significantly $> RH$; RH sig. $> AH$; $RH = AH$).

Results

Identification of pure and hybrid trees

Trees from pure stands of either *E. risdonii* or *E. amygdalina* show no overlap in their basic morphologies. *E. risdonii* has glaucous, sessile opposite leaves that are fused around the stem, while *E. amygdalina* has green, alternate, petiolate and lanceolate leaves. The distribution of hybrid indices based upon 15 morphological traits also shows no overlap between either species when each is growing in pure stands (Fig. 1).

In the hybrid zone, however, the distribution of hybrid indices shows trees indistinguishable from pure *E. risdonii* and pure *E. amygdalina*, as well as a continuum of intermediates (Fig. 1). This hybrid zone is approximately 100 m across, and forms a ribbon where the parental species come into contact (see Potts 1986). Five phenotypic classes were recognized (pure *E. amygdalina* = A, backcrosses to *E. amygdalina* = AH, intermediate or F1-type = H, backcrosses to *E. risdonii* = RH, and pure *E. risdonii* = R). Figure 1 shows the distinctive leaf silhouettes of trees in each of these five phenotypic categories, with a known F1 hybrid having the H phenotype. This continuum also indicates that the pattern of introgression is bidirectional (i.e. fertile F1 hybrids backcross with either parental species), as opposed to unidirectional introgression (e.g. Keim et al. 1989).

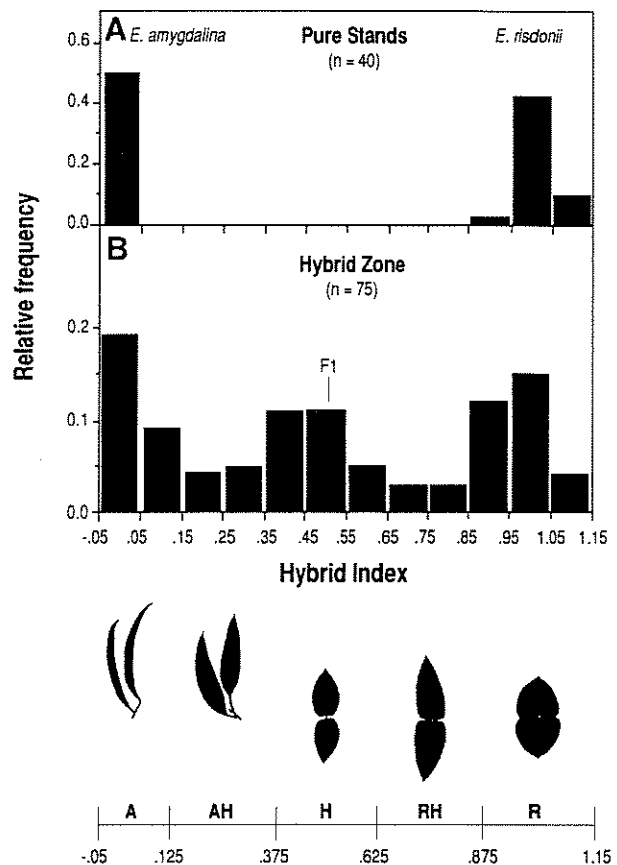


Fig. 1A, B Silhouettes of leaves, illustrating some of the distinctive traits used to classify trees into phenotypic classes (A pure *Eucalyptus amygdalina*, AH backcrosses to *E. amygdalina*, H intermediate or F1 type, RH backcrosses to *Eucalyptus risdonii*, R pure *E. risdonii*). A shows that trees from pure stands exhibit no overlap in the frequency distributions of hybrid indices. *E. risdonii* has glaucous, connate leaves (opposite leaves fused around the stem), while *E. amygdalina* has green, alternate and lanceolate leaves. B shows that trees in the hybrid zone exhibit a continuum of hybrid indices from pure *E. risdonii* to pure *E. amygdalina*. The bottom line marks the boundaries of each phenotypic class used in our analyses (see text), and the position of a single known F1 hybrid is indicated.

Response patterns of hybrid use

Concentrations on F1 hybrid phenotypes

Larvae of the wood-boring beetle *Hesthesis cingulata* (Coleoptera) are concentrated on F1 phenotypes at levels approximately 10 times greater than on either eucalypt species (Fig. 2A). The distinctive spiral galleries of this species result in severed stems that appear to have been cut with a saw. The leaf miner *Eupselia* sp. (Lepidoptera) showed a similar pattern of concentration on F1 phenotypes (Fig. 2B). This pattern of hybrid utilization was rare: of the 40 taxa examined, only with *Eupselia* sp. was abundance on H significantly greater than both AH and RH.

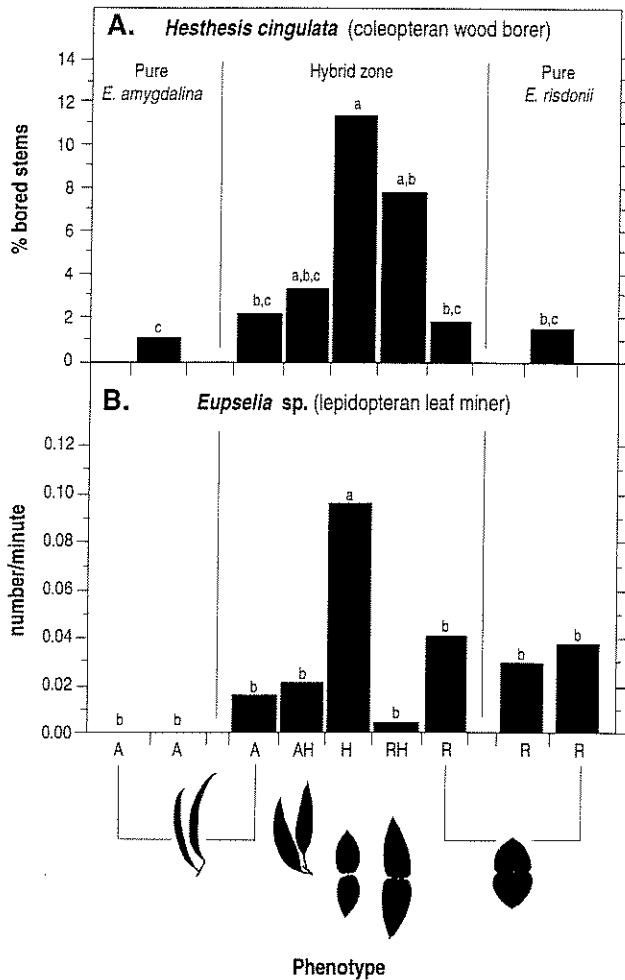


Fig. 2A, B Herbivore numbers are highest on intermediate phenotypes: **A** shows the distribution of larvae of the wood boring beetle *Hesthesis cingulata*. **B** shows a similar pattern for *Eupselia* sp., a lepidopteran leaf miner. Significant differences at the 0.05 level are indicated by a change in letters. Note that *Eupselia* sp. was censused along two transects in each pure zone while *H. cingulata* was censused along one transect in each pure zone. See Fig. 1 for definitions of phenotypic classes

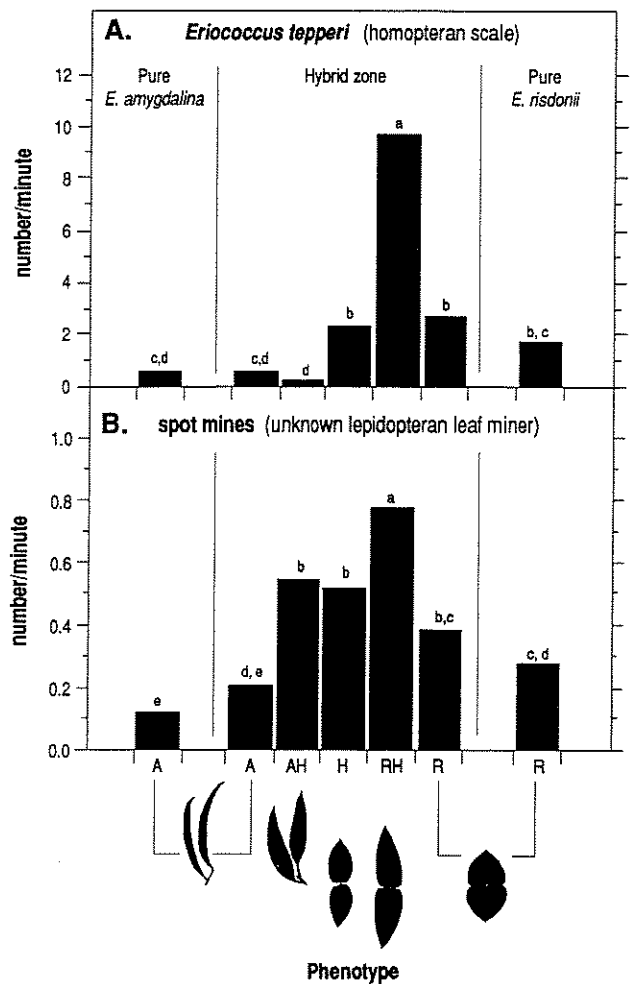


Fig. 3A, B Herbivores are concentrated on backcross phenotypes to *Eucalyptus risdonii*: **A** shows the distribution of the homopteran, *Eriococcus tepperi*, a scale insect found on leaves. A similar distribution is exhibited by an unknown species of lepidopteran leaf miner (**B**). Significant differences at the 0.05 level are indicated by a change in letters. See Fig. 1 for definitions of phenotypic classes

Concentrations on backcrosses to E. risdonii

Eriococcus tepperi (Homoptera) is a sap feeding insect that produces a brownish-white, waxy, egg-like scale on leaves (Fig. 3A). While there was a significant 87-fold difference in density among hybrid class phenotypes (8.7/min on RH vs 0.1/min on AH), no significant differences were observed between the two parent species (i.e. 0.6/min on A vs 1.5/min on R in pure stands). This is not an isolated example and demonstrates that the differences in herbivore densities among hybrid classes can be greater than those observed between pure species. An unknown leaf miner (Lepidoptera) that produces distinctive spot-like mines also shows its greatest concentrations on backcross phenotypes to *E. risdonii* (Fig. 3B).

Concentrations on backcrosses to E. amygdalina

Eriococcus coriaceus (Homoptera) is a scale insect found on stems (Fig. 4A). This species is one of five that is virtually restricted to the hybrid zone. A similar distribution was found with yellow leaf spot, a fungus that produces distinct necrotic spots associated with the immature stage (Fig. 4B).

Declines in abundance across hybrid classes

A few species exhibit gradual declines across hybrid classes, such that their densities on hybrids are intermediate between two parental host species. For example, four species of leaf tiers that we were unable to separate (*Acropolitis* sp., *Stepsicrates* sp., *Protolechia* sp. and *Garrha* sp.: Lepidoptera) gradually declined in abundance from *E. amygdalina* to *E. risdonii* (Fig. 5A). Their

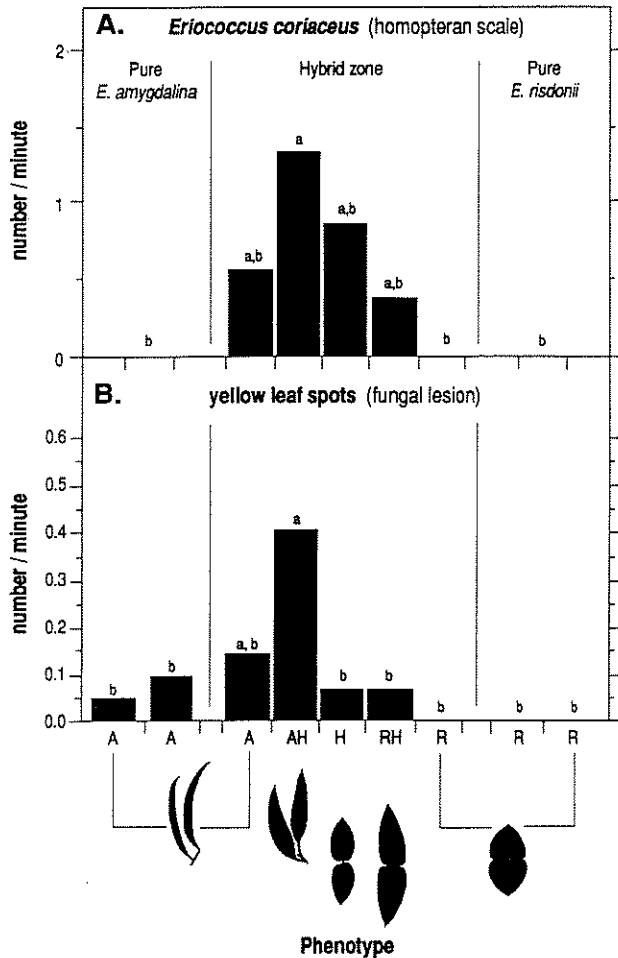


Fig. 4A, B Herbivores are concentrated on backcross phenotypes to *Eucalyptus amygdalina*: **A** shows the distribution of the homopteran, *Eriococcus coriaceus*, a scale insect found on stems. **A** fungus caused yellow leaf spot shows a similar distribution **B**. *E. coriaceus* (**A**) is one of five species that is almost restricted to the hybrid zone and its distribution is the opposite of its close relative, *Eriococcus tepperi* (Fig. 3A). Significant differences at the 0.05 level are indicated by a change in letters. See Fig. 1 for definitions of phenotypic classes. Note that *E. coriaceus* was censused along one transect in each pure zone while yellow leaf spot was censused along both transects in each pure zone

decline across hybrid phenotypes to their lowest levels on *E. risdonii* is likely to be due to changes in leaf morphology that make it difficult for caterpillars to tie leaves together to make a shelter. The floppy, alternate and petiolate leaves of *E. amygdalina* are easily tied together. However, the stiff, opposite and sessile leaves of *E. risdonii* are difficult to tie and shelters are only made when branches cross and leaves come into contact. The reverse pattern of decline across hybrid phenotypes is illustrated by an unknown leaf miner (Lepidoptera) that produces oval leaf cutouts (Fig. 5B).

Overall insect and fungal responses to hybridization

Four results show that hybrids significantly influence insect biodiversity. First, hybrid phenotypes support

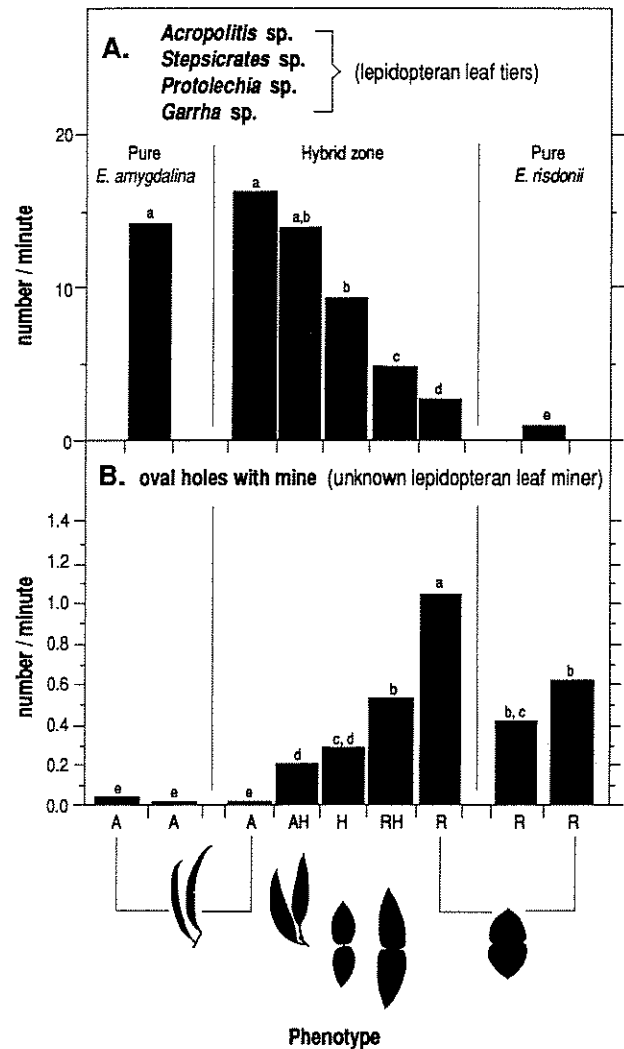


Fig. 5A, B Herbivores are concentrated on a parental species: **A** shows the distributions of four lepidopteran leaf tiers which are difficult to separate in the field (*Acropolitis* sp., *Stepsicrates* sp., *Protolechia* sp., *Garrha* sp.). They decline gradually across hybrid phenotypes, probably due to changes in leaf morphology that make leaf tying difficult on *Eucalyptus risdonii* (see text). The opposite pattern of decline across hybrid phenotypes is exhibited by an unknown lepidopteran leaf miner (**B**); this insect was also the only species we examined that was significantly more concentrated on a parental species than on hybrids or a hybrid class. Significant differences at the 0.05 level are indicated by a change in letters. Note that leaf tiers were censused along one transect in each pure zone while the leaf miner was censused along both transects in each pure zone. See Fig. 1 for definitions of phenotypic classes

more species than their parents (Fig. 6A, Table 1). Two hybrid phenotypes (AH and H) had significantly greater species richness than the parental phenotypes (A and R) growing either in the hybrid zone or in pure stands ($P < 0.05$). The other hybrid phenotype (RH) differed significantly only from the corresponding parental class (R). In pooled analyses, the average hybrid (AH + H + RH) supported 23 species/tree, the average parental type in the hybrid zone (A + R) supported 18, and the average parental in the pure zone (A + R) sup-

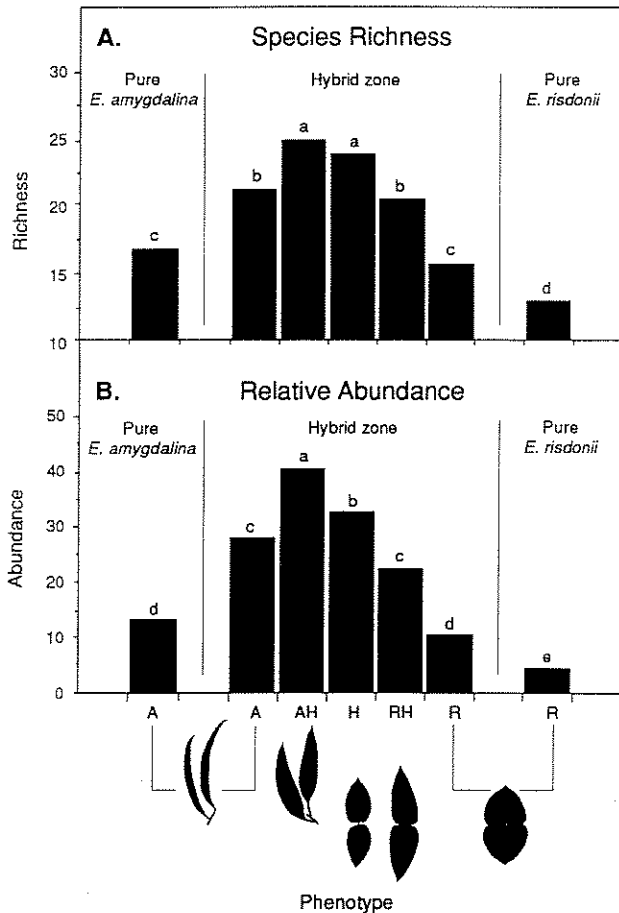


Fig. 6A, B Both species richness (A) and relative abundance (B) of 40 insect and fungal taxa increase on hybrid trees in comparison to pure parental trees growing either in pure stands or inter-mixed with hybrids. Significant differences at the 0.05 level are indicated by a change in letters. See Fig. 1 for definitions of phenotypic classes

Table 1 ANOVAs for species richness and standardized abundances

Source	df	Mean square	F value	Pr > F
Species richness				
Block	14	13.5	2.4	0.0111
Phenotype	4	202.4	35.7	0.0001
Error	56	5.7		
Standardized abundances				
Block	14	117.5	2.3	0.0137
Phenotype	4	1738.8	34.2	0.0001
Error	56	50.8		

ported 15, with all three groups significantly different ($P < 0.01$). The average hybrid tree supported 28% more species than the average parental type in the hybrid zone and 53% more species than the average parental tree in pure zones.

Second, hybrids are centers of population abundance for most herbivores (Fig. 6B, Table 1). Seventy-three

percent of the species examined were significantly more abundant in the hybrid zone ($P < 0.05$), 25% exhibited no significant differences, and only 2% (one species) was most abundant in a pure zone. Summed over all species, the relative abundance on hybrid phenotypes (AH+H+RH) was 1.7 times greater than on parental phenotypes (A+R) in the hybrid zone, and 4 times greater than on parental phenotypes in pure stands.

Because all five tree phenotypes grow adjacent to one another and were blocked in our analyses, site effects within the hybrid zone could be examined separately. While there were significant block effects both for species richness and relative abundances (Table 1), only 2 of 40 insect and fungal species examined exhibited significant blocking effects. Thus, within the hybrid zone, the block effects are trivial when compared to the effect of hybrid phenotypes on the phytophagous community.

Third, no one species was endemic to the hybrid zone, but some species were found almost exclusively on hybrids. For instance when 60 trees were examined in both pure zones just 7 specimens of one gall-producing chalcid wasp were observed, and these were found on the same leaf. In comparison, 1398 specimens were recorded on 31 of 46 hybrid trees (60% of trees occupied). Thus, this species is 260 times more abundant on the average hybrid than it is on the average parental in pure stands. Because five herbivore species had such restricted distributions (see also Fig. 4A), 13% of the species studied could be impacted by the loss of the hybrid zone.

Fourth, the community supported by hybrid trees is a unique assemblage with the potential for unique interactions and structuring. All the species found in pure stands of both parental trees were found on hybrids, and 50% of the insects and fungi co-existed only on hybrids.

Comparisons of generalists and specialists

Consistent with the notion that generalist and specialist herbivores differ in their use of host species, they also differ in their use of hybrid phenotypes. First, generalists are more likely than specialists to utilize hybrids. In comparing abundances on hybrid phenotypes versus abundances on the parental species in pure stands, 92% of the 12 generalists were significantly more abundant on hybrids than on either parental host species, compared to 50% of the 28 specialists ($\chi^2 = 6.222$, $df = 1$, $P < 0.02$).

Second, for specialists, the hybrid phenotype most utilized is the one phenotypically most similar to its host species. Of the 28 insect and fungal species that were considered to be specialized to either eucalypt species, 19 (68%) were significantly more abundant on the hybrid phenotype closest to their host, 7 were equally abundant on hybrid phenotypes AH and RH, and only 1 was significantly more abundant on the hybrid phenotype least similar to its host species ($\chi^2 = 17.643$, $df = 2$, $P < 0.001$). This concentration of an insect on the hybrid

phenotype most similar to its host species is exemplified by the distributions of two herbivores with different host species. Leaf tiers (Fig. 5A) overwhelmingly use *E. amygdalina* and they utilize the backcross phenotype to *E. amygdalina* (AH) significantly more than RH. In contrast, oval leaf miners specialized to *E. risdonii* utilize the backcross phenotype to *E. risdonii* (RH) significantly more than AH (Fig. 5B). Thus, even though both specialize on different host species, the hybrid phenotype most utilized was the one most similar to their host species.

Generalist species were fairly evenly distributed across hybrid phenotypes. Although there were insufficient cases for statistical analyses, of the 12 generalist species, 8 were equally abundant on hybrid phenotypes (AH and RH), 1 was significantly more abundant on RH, and 3 were significantly more abundant on AH.

There is an overall pattern of greater abundance on hybrids but generalists were relatively more abundant on hybrids than were specialists. Additionally, generalists tended to be equally distributed on hybrid phenotypes while specialists were concentrated on the hybrid phenotype most closely resembling their host species.

Tree sexual reproduction and herbivory

Across a 10-year period, the pattern of reproduction by pure and hybrid phenotypes has remained relatively constant (Fig. 7). Mean capsule production by each phenotype in 1980 is significantly correlated with 1990–1992 capsule production (Spearman Rank, $r_s = +0.857$, $df = 7$, $P < 0.02$, one-tailed test). During both periods of study, hybrids produced fewer seed capsules than their parental species growing in pure stands (except for RH in 1990–1992). Within the hybrid zone, however, pure *E. amygdalina* does not perform better than hybrid phenotypes, but pure *E. risdonii* does. These patterns are consistent with the findings of Potts (1986) which indicate that the superior performance of pure *E. risdonii* has resulted in its invasion of the hybrid zone.

Because insect herbivores are known to affect eucalypt productivity (Morrow and LaMarche 1978) and could contribute to the observed patterns of reproduction, we correlated several measures of herbivory (mean species richness, mean relative abundance and mean total abundance) with mean seed capsule production for each pure and hybrid phenotype. We report these three measures of herbivory because none adequately reflects the potential impact of herbivores. For instance, mean total abundance is misleading because it gives equal weight to a small insect that does little damage and a larger insect which can kill a large ramet (e.g. the wood borer, *Hesthesis cingulata*).

The differences in herbivore load are reflected in the pattern of tree reproduction among phenotypic classes. All three measures of herbivory are negatively correlated with 1980 seed capsule production (Table 2). The trend is the same for 1990–1992 capsule production but

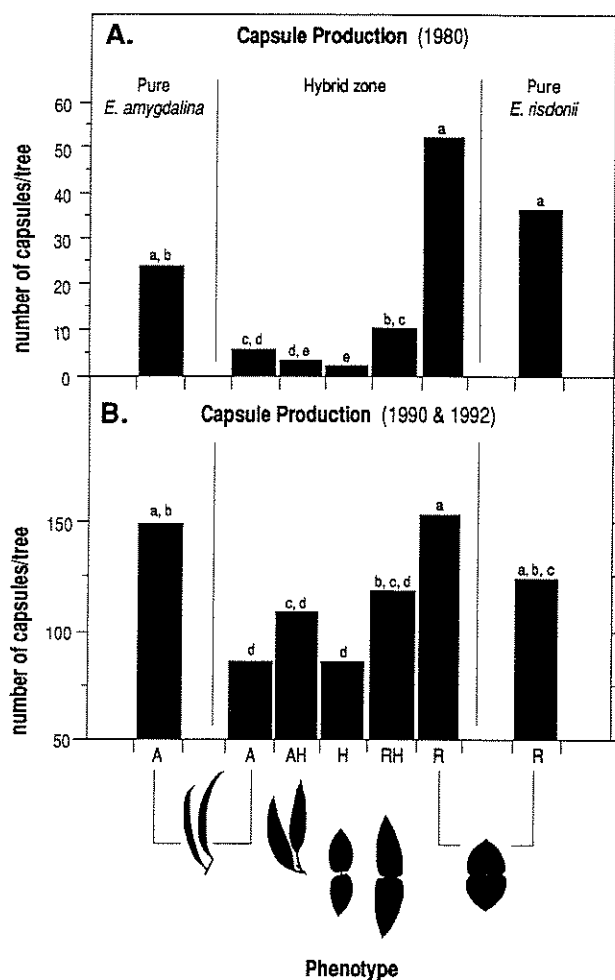


Fig. 7A, B The 1980 mean seed capsule production by hybrids is less than their parental species growing in pure stands (A). Except for AH (see Fig. 1 for definitions of phenotypic classes) the same general pattern was observed 10 years later in 1990–1992 (B). Reproduction by different phenotypes is negatively correlated with herbivore loads (see text). 1980 seed capsule production from Potts (1986)

Table 2 Correlation matrix of three measures of herbivore load and tree reproduction in 1980 and 1990–1992. Shown are Spearman Rank correlations (r_s) of mean species richness, mean relative abundance, and mean herbivore abundance on the mean seed capsule production of pure and hybrid phenotypes. Correlation matrix and one-tailed significance levels are shown ($df = 7$ in all comparisons)

	Seed capsule production	
	1980	1990–92
Species richness	-0.929, $P < 0.01$	-0.768, $P < 0.06$
Relative abundance	-0.929, $P < 0.01$	-0.768, $P < 0.06$
Total abundance	-0.857, $P < 0.02$	-0.643, $P < 0.08$

is only marginally significant. Even in the absence of herbivores, hybrids might produce fewer capsules due to partial sterility (e.g. Grant 1971). As both herbivory and incompatibility may affect reproduction, experiments are needed to establish causality.

Discussion

Potential mechanisms

Our results show that the *E. risdonii* × *E. amygdalina* hybrid zone is a center of biodiversity but the causes of this pattern are less clear. Two likely mechanisms may operate individually or act in concert to produce the observed patterns. First, because plant adaptations against pests are often genetically based (e.g. Maxwell and Jennings 1980; Fritz and Simms 1992), the breakup of co-adapted gene complexes that can occur when two species hybridize (Grant 1971) may result in increased susceptibility.

Second, because hybrid zones are often at the boundaries of their parent species' distributions, plants in hybrid zones may be at the limits of their physiological tolerances (e.g. Bunce et al. 1979; Brussard 1984; McClure 1985). If they are stressed at their distributional limits, plants may be more susceptible to insect and pathogen attack (White 1969, 1976, 1984; Waring and Cobb 1992; Paige and Capman 1993).

Of these two potential mechanisms, the blocking design of our survey should eliminate most site effects. Only 2 of 40 taxa exhibited significant block effects, suggesting that differences in insect and fungal distributions are a result of genetic differences among the five phenotypes. The role of genetics is further supported by the predictable use of specific hybrid phenotypes by specialists (see next section).

Another pattern that may have several causes is the observation that pure *E. risdonii* (R) and *E. amygdalina* (A) in the hybrid zone had significantly more species and greater relative abundances of herbivores than when they occurred in pure stands (Fig. 6, Table 1). At least five mechanisms acting singly or in concert could account for this pattern. First, insects may overflow from hybrids with high herbivore loads to nearby parental types. Second, the close proximity of different plant species with different insect faunas could facilitate the mixing of these faunas. Third, increased stress at species boundaries may make both parental species more attractive to herbivores. Fourth, expanded leafing-out phenologies in a hybrid zone could expand the season that trees can be successfully utilized by herbivores. Fifth, trees classified as pure phenotypes in the hybrid zone may be complex advanced generation hybrids which can be detected by insects but not by our taxonomic methods. With so few experimental tests of these hypotheses (but see Floate et al. 1993), future research needs to focus on specific mechanisms.

Hybrid zone structure and plant-herbivore interactions

There is great variation in the use of hybrids by phytophages but it is not idiosyncratic. As the distribution of specialist species on hybrids was predictable, we pro-

pose the "phenotypic affinity hypothesis" which states that the most preferred hybrid phenotype will be the one most similar to a species' preferred host. Results from two other eucalypt hybrid swarms (Morrow et al. 1994) support this prediction.

Furthermore, the variation in herbivore loads among hybrids can exceed that observed between species, suggesting that hybrids express novel traits not present in the parent species. For example, *Eriococcus tepperi* shows an 87-fold difference in abundance between AH vs RH, but no difference between A vs R in pure stands (Fig. 3A). At the community level, Morrow et al. (1994) found that for the 33 insect species examined, 52% varied significantly among hybrid phenotypes, while only 24% varied between the parental species. This may be related to some hybrid phenotypes exhibiting increased susceptibility due to hybrid breakdown, while other phenotypes exhibit increased resistance due to heterosis (Grant 1971; Frankel 1983; Mitton and Grant 1984). We predict that hybrid swarms will contain both the most resistant and most susceptible plants.

The great variation that exists in herbivore use of hybrid phenotypes, even by members of the same guild or genus (e.g. Figs. 3A and 4A), also demonstrates that the pooling of hybrid phenotypes and/or insect guilds could be misleading. In their study of hybrid oaks, Boecklen and Spellenberg (1990) pooled all hybrid classes and all insect taxa, and concluded there was a reduced pattern of hybrid use. While their conclusions may still be correct, such pooling may mask important underlying structure.

Evolutionary implications

As plant hybridization can affect host use by diverse insect taxa, future studies need to consider how insect evolution might be affected. For example, in a cottonwood hybrid zone the gall aphid, *Pemphigus betae*, has a complex life cycle involving alternation between cottonwood and a second host. In the pure zone, however, cottonwood is not a host. Experiments show that where aphids have eliminated cottonwoods from their life cycle, the trees are nearly twice as resistant as in the hybrid zone (Whitham 1989). Because these life cycle traits have a genetic component (Moran and Whitham 1988; Moran 1991), it appears that hybridization by plants may influence the evolution of herbivore life cycles.

Hybridization may also influence the evolution of insect host range. The "hybrid bridge hypothesis" (Floate and Whitham 1993), predicts that hybrid intermediates facilitate host shifting by allowing herbivores restricted to one host gradually to experience and adapt to another host's genome via hybrid intermediates. Studies of eight gall-forming species showed that in the absence of hybrid intermediates, no shifting occurred, but in their presence, shifting did occur.

These apparent adaptations by herbivores suggest that plant hybrid zones persist long enough for herbi-

vores to respond ecologically and evolutionarily. Because hybridization has often been tied to periods of environmental disturbance such as glaciation, many current hybrid zones may date back to the Pleistocene or farther (Rattenbury 1962; Grant 1971; Kat 1985). In the present study, the large size of some lignotubers (Potts 1986) suggests that individual hybrids may be 500+ years old (Head and Lacey 1988). Because they reproduce vegetatively from lignotubers, the potential exists for hybrid zones of *Eucalyptus* to persist indefinitely.

Conservation issues

Despite their ecological and evolutionary importance, hybrids have often been maligned. In the United States, the "hybrid policy" advocated by O'Brien and Mayr (1991) is to "discourage hybridization between species" because hybridization may "disintegrate the genetic organization of the species in contact". Hybridization in plants, however, is thought to be of great evolutionary consequence; 30–80% of all plant species are thought to have originated from hybridization events (Stebbins 1950, 1971; Lewontin and Birch 1966; Grant 1971; Lewis 1979, 1980; Levin 1983; Stace 1987; Rieseberg 1991; Wendel et al. 1991). For this reason alone, hybrid zones should be conserved.

If hybrid zones are also centers of biodiversity as suggested by our studies of three different *Eucalyptus* hybrid swarms (Morrow et al. 1994 and present study), they should be conserved as a habitat type for their dependent organisms. Because eucalypts are often endemic (e.g. 59% of 29 species are endemic to Tasmania, Duncan 1989) and frequently hybridize (e.g. 51% of Tasmanian eucalypts hybridize, Duncan 1989), many hybrid zones are likely to exist. Furthermore, because eucalypts support a rich insect fauna (Fox and Morrow 1983, 1986; Morrow and Fox 1989), hybrid trees may provide essential habitats for many species. Although insect conservationists argue that it is especially important to save sites of rich diversity (e.g. Morris et al. 1990), there is unfortunately no current legislation to preserve the habitat of endangered insect species in Australia (Greenslade and New 1990).

Conservation of hybrid zones is important for numerous reasons. Even vertebrate taxa of greater public interest may benefit from plant hybrid zones: in an apparent response to the altered architecture of hybrid trees, we have observed a doubling in bird nest densities in a cottonwood hybrid zone (Martinsen and Whitham 1994). We have argued previously that hybrid zones should be conserved as centers of plant evolution, and as sources of economically important plant varieties and potential biocontrol agents (Whitham et al. 1991). Some argue that hybrids also have been important in animal evolution (Uyeno and Smith 1972; Dowling and DeMarais 1993) and advocate their conservation (Dowling et al. 1992). Hybrids have no protection status

in Australia or the United States. But just as the focus of conservation has shifted from endangered species to the protection of habitat and ecosystem units (e.g. watersheds) so should our focus shift from typological units to evolutionary units (Rojas 1992).

Acknowledgements We thank D. Bashford, J. Cardale, D. Colless, H.J. Elliott, P. Gullan, P. McQuillan, I. Naumann, G. Taylor, K. Taylor, and Y. Yip whose identifications of insects and fungi were crucial to this study; A. Monks for her field and lab assistance; N.S.F. Grants BSR-8918380, BSR-8920709, BSR-9107042 and USDA Grant 91-37302-6224 for financial support; and K.M. Christensen, P. Feinsinger, K.D. Floate, C.A. Gehring, J. Glyphis, J. Maschinski, K.N. Paige, B. Phillips, O.J. Reichman, T. Theimer and K. Whitham for their reviews.

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