Are plant hybrid zones centers of vertebrate biodiversity? A test in the *Quercus grisea × Quercus gambelii* species complex

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Abstract. The plant-hybrid-zones-as-centers-of-biodiversity (hereafter, PHZCB) hypothesis posits that plant hybrid zones represent areas of elevated biodiversity, and supports the inclusion of plant hybrid zones in conservation efforts. Support for the PHZCB hypothesis is limited to a handful of cases involving insect and fungal species and to two studies involving higher trophic levels. The PHZCB hypothesis requires further testing before plant hybrid zones can be established with any certainty as centers of biodiversity. We test whether the PHZCB hypothesis holds for higher trophic levels by examining the community structure of birds and reptiles associated with the *Quercus grisea × Quercus gambelii* species complex. Specifically, we compare patterns of species richness and abundance of these taxa in 10 hybrid zones and 11 contact zones (i.e., zones where both parental species occur but hybrids do not). In contrast to predictions of the PHZCB hypothesis, contact zones supported significantly more species of birds and reptiles than did hybrid zones. Species abundances exhibited idiosyncratic responses to zone type, but were higher generally in the contact zones.

Key words: biodiversity, birds, community, hybridization, oak, plant hybrid zones, *Quercus gambelii*, *Quercus grisea*, reptiles

Introduction

There is much recent interest among plant–herbivore ecologists in plant hybrid zones and their attendant effects on herbivore community structure and population dynamics (reviewed by Strauss 1994; Fritz et al. 1999; Whitham et al. 1999). More than a decade of study has revealed that herbivores are quite variable in their responses to hybrid host plants; hybrid plants may support higher (Whitham 1989; Floate et al. 1993; Fritz et al. 1994; Whitham et al. 1994; Graham et al. 1995; Floate et al. 1997), intermediate (Aguilar and Boecklen 1991; Fritz et al. 1994; Hanhimäki et al. 1994; Preszler and Boecklen 1994; Gange 1995; Graham et al. 1995; Gaylord et al. 1996), or lower (Boecklen and Spellenberg 1990; Boecklen and Larson 1994) densities of herbivores than do parental hosts. In addition, patterns of herbivore species richness

also appear to be variable with respect to host plant hybridization. For example, Whitham et al. (1994) found hybrid hosts to support significantly more species of insects and fungi than did parental hosts in a *Eucalyptus amygdalina* × *Eucalyptus risdonii* hybrid zone. Similar results were obtained in the *Eucalyptus obliqua* × *Eucalyptus baxteri* and *Eucalyptus caliginosa* × *Eucalyptus stellulata* species complexes (Morrow et al. 1994). In contrast, Boecklen and Spellenberg (1990) observed that hybrid hosts supported significantly fewer species of leaf-mining moths and gall-forming wasps than did parental hosts in *Quercus depressipes* × *Quercus rugosa* and *Quercus emoryi* × *Quercus coccolobifolia* hybrid zones.

The potential of plant hybrid zones to harbor increased levels of insect diversity has attracted the attention of conservation biologists and has led to the plant-hybrid-zones-as-centers-of-biodiversity (hereafter, PHZCB) hypothesis (Whitham et al. 1994). The PHZCB hypothesis posits that plant hybrid zones represent concentrated areas of elevated biodiversity that could play an important role in conservation planning. Studies supporting the PHZCB hypothesis (Whitham et al. 1991; Morrow et al. 1994; Whitham et al. 1994; Floate et al. 1997) have contributed to a movement to preserve plant hybrid zones (see Whitham et al. 1991; Whitham and Maschinski 1996) and warrant the protection of plant hybrids under the United States Endangered Species Act, despite the Act's 'Hybrid Policy' (O'Brien and Mayr 1991) that excludes hybrids on the grounds that they are not genetically distinct species.

The PHZCB hypothesis recently has been extended to birds that use hybrid plants as foraging or nesting substrates. Martinsen and Whitham (1994) examined a cottonwood hybrid zone (*Populus fremontii* × *Populus angustifolia*) in northern Utah, and reported greater densities of bird nests and greater abundances of birds in the hybrid zone than in allopatric zones; within the hybrid zone, they found greater densities of nests in hybrid trees than in parental trees. Martinsen and Whitham (1994) attributed these patterns to the birds' responses to the altered architecture of hybrid trees and to increased aphid abundance in the hybrid zone (see Whitham 1989). Subsequently, Dickson and Whitham (1996) demonstrated that, within hybrid zones, birds do spend more time foraging on *Populus* hybrids than on parental trees, and that birds concentrate their foraging in response to increased gall densities.

An open question is the extent to which the PHZCB hypothesis holds for species that do not depend directly on hybrid plants for nesting or foraging (T.G. Whitham pers. comm.). In other words, are plant hybrid zones centers of biodiversity in general, or do they represent special cases for particular subsets of species? Because studies at lower trophic levels have yielded mixed results, there is reason to believe that there will be a variety of patterns existing at higher trophic levels as well. If the effects of plant hybridization on associated herbivore populations are variable, then so too could be the effects on higher trophic levels. Thus, the PHZCB hypothesis requires further testing before plant hybrid zones can be established generally as centers of biodiversity for higher trophic levels.

Hybrid zones in the *Quercus grisea* × *Quercus gambelii* species complex are an appropriate experimental system for testing the PHZCB hypothesis at higher trophic levels. First, the pattern of hybridization in the *Q. grisea* × *Q. gambelii* species complex in central New Mexico has been described as a mosaic hybrid zone (Howard et al. 1997). Mosaic hybrid zones consist of localized areas of hybridization within broader geographic areas where parental species are sympatric (Harrison 1986). Within the larger areas of sympatry, it is possible to find hybrid zones and areas where both parental taxa are present but little or no hybridization occurs (hereafter, contact zones). These types of areas are often quite similar, differing mainly in the presence or absence of hybrids. Of course, hybrid zones and contact zones may differ in subtle ways, and some of these may have fascilitated hybridization in the first place. Nevertheless, comparisons of contact and hybrid zones still may represent the most robust experimental system for testing the PHZCB hypothesis in natural systems.

Second, the influence of deciduous trees on breeding bird community composition in conifer forests has been well documented (Johnston and Odum 1956; Dickson and Segelquist 1979; Johnson and Landers 1982; Morrison and Meslow 1984; Dickson et al. 1995). Oaks, in particular, have been shown to be inordinately important when they occur in coniferous forest communities. In spite of their secondary abundance, the presence of oaks has a disproportionate effect on foraging behavior of birds, such that many bird species use oaks much more than would be expected based on its availability (Balda 1969; Szaro and Balda 1979). The presence of oaks in an otherwise coniferous forest can also affect the composition of the bird community. For example, Brawn and Balda (1988) found nearly all insectivorous bird species to be more abundant on a study plot with higher Gambel oak density, compared to another plot with similar ponderosa pine live tree and snag densities but fewer oaks. Likewise, Rosenstock (1998) showed that pine–oak stands of northern Arizona supported a more distinct species composition and more species of Neotropical migrants, ground nesters, primary cavity excavators and secondary cavity users than pure pine stands.

Oaks may be a higher quality foraging substrate for foliage gleaning birds, because oak foliage supports more insect species (Southwood 1961) and greater insect biomass/unit foliage volume than pines (Clary 1978). The additional foliage layers afforded by the presence of oaks can also increase potential nest sites and thereby increase species diversity (Martin 1988). Additionally, oaks provide an alternative cavity nesting substrate that may increase the diversity and abundance of cavity nesting species (Cunningham et al. 1980; Rosenstock 1996).

Here, we examine patterns of species richness and species abundances of birds and reptiles in the *Q. grisea* × *Q. gambelii* species complex. We examine contact and hybrid zones to determine the effects of hybrid plants on vertebrate community structure and to test the generality of the PHZCB hypothesis with regards to vertebrates.

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Methods

Study sites and plant hybrid complex

Quercus grisea (Liebm.) and *Q. gambelii* (Nutt.) are members of different subsections of the white oaks (Nixon 1993). They are distributed throughout the southwestern states of Utah, Colorado, Arizona and New Mexico. The range of *Q. grisea* extends north from central Mexico to New Mexico and Arizona, while that of *Q. gambelii* extends from northern Mexico to Utah and Colorado.

Individuals of *Q. grisea*, *Q. gambelii*, and hybrids are readily distinguishable on the basis of leaf morphology (see Aguilar and Boecklen 1991). *Quercus grisea* has small, entire, ovoid, grayish-pubescent, evergreen or drought deciduous leaves (Tucker 1961). In contrast, *Q. gambelii* has medium-sized, moderately to deeply lobed, deciduous leaves that are commonly glossy green above (Tucker 1961). The F1 hybrids, 'Q. undulata', have leaf shapes intermediate to either parental species; they have obovate to oblong, slightly lobed to serrate dull green leaves with undulate margins. Classifications of individuals as hybrids and parental species on the basis of leaf morphology are highly correlated with classifications based on molecular genetic (RAPD) markers (Howard et al. 1997).

We tested the PHZCB hypothesis in the San Mateo and Magdalena mountain ranges of central New Mexico (Figure 1). In these mountain ranges, *Q. grisea* varies in growth form from a small tree in the pinyon–juniper zone to a shrub at higher elevations. *Quercus gambelii* occurs at higher elevations and more mesic sites than *Q. grisea*, where it grows in small clones of shrubs to moderately sized trees. Hybrids are usually low shrubs with densities varying from sparsely distributed to thick undergrowth at some sites. *Quercus grisea* and *Q. gambelii* meet over an elevational gradient, but the pattern of hybridization is not clinal. Rather, it is a mosaic hybrid zone (Harrison 1986; Howard et al. 1997), meaning there are relatively small and patchily distributed areas of hybridization that occur throughout the zone of overlap of the two species.

We identified two types of sympatric zones: ones in which both parental species occur and hybridize (hybrid zones), and ones in which both parental species occur without (or with very limited) hybridization (contact zones). Identification of contact and hybrid zones was based on the proportion of oaks that were hybrids, as determined by leaf morphology: hybrid zones averaged 49% (17–100%), whereas contact zones averaged 1% (0–6%). In all, we haphazardly sampled 10 hybrid zones and 11 contact zones. The locations of these 21 zones can be roughly divided into four regions: the Magdalena Mountains, and the south, central and northern San Mateo Mountains. Each of these regions contained both zone types, but the number of hybrid zones and contact zones were not equally distributed in each region. Within the regions, both types of zones occured in a variety of habitat types, ranging as low as the pinyon–juniper vegetational belt (1370 m) and up to the fir–aspen belt (2895 m).
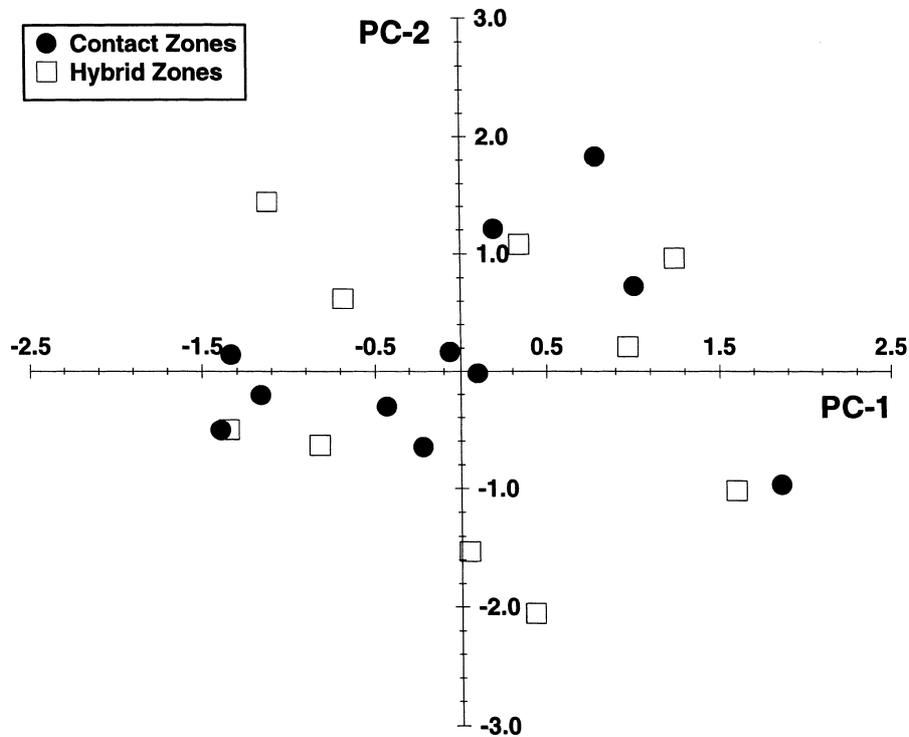
Figure 1. Principal components analysis of 21 habitat and vegetation characteristics measured in 11 contact and 10 hybrid zones.

Habitat structure of contact and hybrid zones

The vegetation in each of the 21 sites was characterized using two 0.04 ha (11.28 m radius) circular plots (James and Shugart 1970) placed at random distances ($\leq$89 m) and directions from the centers of each site. Within each vegetation plot, species, frequency, and diameter-at-breast-height (dbh) were recorded for all trees (woody stems with dbh > 7.62 cm). From these measurements, total basal area (BA) was calculated, as were BA's separately for oaks (OBA), pines (PBA), junipers (JBA), firs (FBA), and snags (SBA). Trees were sorted into four size classes based on dbh: 7.62–15.24 cm (A Trees), 15.24–22.86 cm (B Trees), 22.86–38.1 cm (C trees), and greater than 38.1 cm (D Trees). BA's were calculated for each size class (A BA, B BA, C BA, and D BA, respectively). Additionally, the height of each tree was recorded by a clinometer. We examined the distribution of tree heights and found no natural categories by which to create height classes. Wiens (1989) warns about the use of height classes without any a *priori* reason for establishing them because the correlation between vertical vegetation structure and bird diversity can be strengthened depending on how the vertical structure is partitioned. Instead, we

used the average tree height (TH) and the standard deviation (SDTH) of the tree heights in each site.

The frequency of shrub species (Shrubs) was measured by counting the number of woody stems less than 7.62 cm in dbh intercepted by two perpendicular, outstretched arms width (1.7 m) transects across each circle. Likewise, canopy cover (CC) and ground cover (GC) were estimated by taking presence/absence sightings through the cross hairs of an ocular tube on alternate steps of perpendicular transects. Because hybrids occur in the GC, the woody species in this stratum were also recorded.

The densities of rocks (Rocks) and logs (Logs) were estimated by the number of rocks and logs that were higher than 25 cm within two perpendicular transects of outstretched arms width. These variables were recorded mostly for correlation with reptile and amphibian data, since they provide perching sites and shelter. However, they may also be useful predictors for bird distribution patterns since these two variables are related to GC and CC.

The vegetation data were collected from 2 August to 25 October 1996. Although this period did not coincide with that of the bird censusing, these data still provide a close representation of the habitat at the time of censusing. Most of the bird censuses were conducted after leaf flush, so the differences in the habitat from the two periods are negligible.

Avian community structure of contact and hybrid zones

Species richness and densities of birds in each zone were determined using circular plots (Reynolds et al. 1980; Hutto et al. 1986). Circular plots were chosen over transects because: (1) being stationary at each point allowed the observer to devote full attention to detecting birds rather than having to concentrate on travel over the rough terrain (Reynolds et al. 1980; Dawson 1981); (2) the relatively small size of the zones of interest precluded the effective use of transects; and (3) since the identification of habitat determinants of the bird community is an objective of the study, point counts are especially suitable because habitat variables within the circle can be directly associated with the distribution and abundance of bird species (Reynolds et al. 1980; Bibby et al. 1992).

A single circular plot was centered in each of the 10 hybrid zones and 11 contact zones in order to maximize the distance between the observer and the outer edge of the zone. The centers of the circular plots were all located a minimum of 250 m from one another in order to ensure statistical independence of the plots and hence the zones (Reynolds et al. 1980; Ralph et al. 1992). Within each circular plot, bird species were identified aurally and visually, and their distance from the observer was estimated. Although we recorded the distances of all birds observed, we excluded from the analysis those birds that were recorded greater than 100 m from the observer. We only considered birds within this 100 m radius circle, because of the relatively small size of the zones and because restricting our analysis to a 100 m radius around

the observer made it more likely that the birds recorded were in the zone of interest. We included birds that flushed within the circular plot when walking to its center, as well as birds that flew directly overhead during the census period (e.g. Violet-green Swallows or White-throated Swifts) since they may have been feeding on insects from the zones.

Counts at each station were 10 min in duration (Scott and Ramsey 1981; Ralph et al. 1992) following a 1 min adjustment period. This length of time allowed for most of the species in the area to be recorded, since species accumulate with time spent censusing (Hutto et al. 1986; Scott and Ramsey 1981). Censusing was conducted between sunrise and 10 h and 00 min, since during this period the rate of calling is relatively stable (Robbins 1981a; Hutto et al. 1986; Ralph et al. 1992). Censusing was not conducted on rainy or windy mornings due to decreased activity and detectability of birds (see references in Robbins 1981b; Verner 1985).

Each census station was visited four times between 14 June and 20 July in 1995 and five times between 25 May and 19 July in 1996 by a single observer (Campbell), thus no variability was introduced with additional observers. Repeated visits ensured an adequate sample size and accounted for the phenologies of the different species (Morrison et al. 1981). However, repeated visits also made it very likely that the same birds were present in different visits.

Reptile community structure of contact and hybrid zones

In each of the four regions (see above), a hybrid zone and a contact zone that roughly resembled each other in habitat were selected from among the set used in the vegetation and avian analyses described above. Species richness and relative abundance of reptiles were measured by the use of drift fences. The arrangement of each drift fence array consisted of four 7.6 m lengths of 50 cm high aluminum flashing buried 10–15 cm in the ground in an intersecting pattern with a central separation of 15 m (see Campbell and Christman 1982). They were used in conjunction with pitfall traps with funnel rims and funnel traps made of 0.635 cm (1/4 in.) hardware cloth. The drift fence arrays were placed so that their centers approximately coincided with the center of the circular plots used in the bird censusing and so that the arms ran parallel and perpendicular to the slope.

Because of the rocky soil, 3.78 l buckets were used as pitfall traps instead of the 18.9 l buckets as in Campbell and Christman (1982). Using these smaller pitfall traps may have biased the size of the trapped individuals (63.4% of the pitfall trap captures were juveniles), since larger individuals may have been able walk across the pitfall opening or escape if they have the ability to jump (i.e. *Sceloporus undulatus* and *Urosaurus ornatus*). Even so, some of the larger species, such as *Eumeces multivirgatus* or *Elgaria kingii*, are unable to escape once in the trap. The funnel traps, which were employed primarily for the capture of snakes, also served to catch those larger individuals that the pitfalls could not.

Drift fence arrays were opened from 20 August to 27 October in 1995 and 23 June to 8 November in 1996 and checked weekly during these periods. Captured individuals were identified to species and released. Individuals that were observed while at the study site were recorded also. No attempt was made to mark individuals. Thus, there exists the possibility of the same individuals being caught or observed more than once.

Statistical analysis

We characterized variation in habitat structure among the 21 zones with principal components analysis based on the correlation matrix of mean values (averaged over the two 0.04 ha plots in each zone) for the 21 variables described above. We did not use discriminant function analysis using zone types as groups since the number of zones within a type was rather small, and since the number of variables was as large as the number of zones. We also compared contact and hybrid zones directly with 1 factor, univariate analyses of variance on the zone means.

To compare avian community structure between contact and hybrid zones, we conducted a repeated-measures (years) analysis of variance on the average number (averaged over census periods) of species at a site in 1995 and 1996. Blocking by region had no effect on the analyses and was not incorporated into the experimental designs. We also examined community-wide variation in mean frequencies (individuals/census) of each species among the 21 zones in 1995 and 1996 using principal components analyses, and we tested for differences in species densities between zone types in 1995 and 1996 with 1 factor, univariate analyses of variance.

We compared mean species richness (averaged over census periods) and mean number of individuals of reptiles and amphibians in contact and hybrid zones with 1 factor, univariate analyses of variance. We restricted the analyses to the 1996 data since initiation of trapping late in the 1995 field season resulted in small sample sizes for that year. No attempt was made to do separate analyses for reptiles and amphibians since only one species of amphibian (*Ambystoma tigrinum*), represented by one individual, was captured.

Results

Habitat structure of contact and hybrid zones

Variation in habitat structure among the 21 zones produced seven principal components with eigenvalues greater than 1.0 that collectively explained about 89% of the variation among zones. The first principal component accounted for approximately 29% of the variation and represented increasing total BA, pine BA, BA of medium-sized trees (15.24–38.1 cm dbh), frequencies of medium and large-sized

Table 1. Habitat and vegetation characteristics measured in 11 contact and 10 hybrid zones, univariate tests for differences between zone types, and factor loadings for the first (PC 1) and second principal component (PC 2).

	Hybrid zones		Contact zones					
Variable	Mean	St. Err.	Mean	St. Err.	*F*	*P*	PC 1	PC 2
TBA	0.65	0.11	0.65	0.08	0.00	0.989	0.90	0.04
OBA	0.10	0.03	0.04	0.01	2.65	0.120	0.08	0.53
PBA	0.28	0.09	0.35	0.09	0.30	0.588	0.83	−0.20
JBA	0.14	0.06	0.12	0.05	0.08	0.777	−0.07	0.11
FBA	0.01	0.01	0.09	0.04	2.75	0.114	0.39	−0.11
SBA	0.04	0.03	0.04	0.02	0.05	0.827	0.15	0.09
A Trees	9.50	1.51	11.70	2.11	0.74	0.400	0.18	0.75
B Trees	4.09	1.01	5.05	1.38	0.33	0.575	0.68	0.54
C Trees	4.00	0.85	2.65	0.54	1.70	0.208	0.78	−0.05
D Trees	0.86	0.21	1.25	0.28	1.22	0.283	0.63	−0.48
A BA	0.09	0.02	0.10	0.02	0.19	0.671	0.29	0.79
B BA	0.11	0.03	0.14	0.04	0.48	0.499	0.67	0.52
C BA	0.26	0.06	0.17	0.04	1.51	0.234	0.76	−0.13
D BA	0.18	0.06	0.23	0.05	0.32	0.577	0.37	−0.36
Shrubs	11.32	2.43	57.45	15.36	9.68	0.006	−0.43	−0.16
GC	0.40	0.05	0.39	0.04	0.03	0.865	−0.24	−0.37
CC	0.22	0.04	0.22	0.03	0.01	0.921	0.78	0.20
Rocks	3.27	1.73	3.20	1.47	0.00	0.975	−0.33	−0.13
Logs	1.77	0.56	1.35	0.37	0.38	0.547	0.08	0.04
TH	7.02	0.90	9.48	1.46	2.14	0.160	0.71	−0.58
SDTH	3.76	0.67	7.38	2.35	2.38	0.140	0.47	−0.66
					Eigenvalue		6.09	3.46
					Percent of variation		29.01	16.48

($>$38.1 cm dbh) trees, CC, and TH (Table 1). The second principal component explained roughly 16% of the variation and corresponded to increasing BA of oaks, frequencies and BA's of small (7.62–15.24 cm dbh) and medium-sized trees (15.24–22.86 cm dbh) and decreasing TH and variation in TH. There was no clear separation of zone types in a space created by the first two principal components (Figure 1), indicating that the overall habitat structure of contact and hybrid zones were quite similar for the measured variables.

Direct comparisons of contact and hybrid zones on the basis of individual habitat variables also indicated remarkable similarity between zone types (Table 1). Both the contact zones and hybrid zones had an average total tree BA of 0.65 m^2. The seven most abundant species: ponderosa pine (*Pinus ponderosa*), alligator juniper (*Juniperus deppeana*), pinyon pine (*Pinus edulis*), gambel oak, snags, Douglas fir (*Pseudotsuga menziesii*), and grey oak (*Q. grisea*) collectively represented 89 and 97% of the BA in the contact and hybrid zones, respectively. None of these species showed significant differences in BA between contact zones and hybrid zones.

There were also no significant differences between the zone types when tree frequencies were examined by diameter classes (Table 1). Both zone types were

dominated by smaller trees (7.62–15.24 cm); their average frequency was more than twice that of any of the remaining three size classes. Although on average there were relatively few large trees (>38.1 cm) at a site (roughly 5% of trees), they still represented 28 and 35% of the total BA in contact zones and hybrid zones, respectively.

Percent CC and GC were virtually identical in contact zones (22 and 40%, respectively) and hybrid zones (22 and 39%, respectively), as were the frequencies of rocks and logs (Table 1). The average number of rocks and logs greater than 25 cm above the ground were 3.27 and 1.77 in contact zones, and 3.20 and 1.35 in hybrid zones, respectively. The average TH and corresponding average standard deviations were less similar between contact and hybrid zones, but were not significantly different.

The only significant difference in vegetation structure between hybrid zones and contact zones was shrub density ($F_{1,19} = 9.68$, $P = 0.006$). There was an average of five times more shrubs in hybrid zones than in contact zones (Table 1). In both zone types, oaks represented 48% of the shrubs counted; however, the proportions of parental oaks and hybrids were not the same. The shrubs in contact zones were, on average, 22% gambel, 25% grey and 0.8% hybrid oaks. In the hybrid zones, the proportions were 18, 8, and 22%, respectively.

Although there were few structural differences between contact and hybrid zones, the species compositions of the vegetation were somewhat different (see Appendix A). There were a total of 15 tree species observed in the contact zones and 12 species in the hybrid zones, but the average number of tree species in contact zones and hybrid zones were quite similar (5.73 and 5.70, respectively). In the shrub level, both zone types supported 15 species, but the average number of shrub species in hybrid zones (6.4 shrubs) was significantly greater ($F_{1,19} = 5.32$, $P = 0.0324$) than that in contact zones (4.3 shrubs). Finally, hybrid zones supported 12 species in the GC level, while contact zones supported 10 species. The average number of species in the GC was significantly greater ($F_{1,19} = 7.54$, $P = 0.0129$) in hybrid zones (4.5 species) than in contact zones (2.9 species).

Contact zones occurred, on average, at significantly ($F_{1,19} = 39.68$, $P = 0.0001$) lower elevations (2266 m) than did hybrid zones (2536 m). This difference corresponded with the locations of the zone types; contact zones generally occurred in or near canyon bottoms, whereas hybrid zones typically occurred on canyon slopes or ridges.

Avian community structure in contact and hybrid zones

In all, 54 species of birds were observed: 41 species in 1995 and 50 species in 1996 (see Appendix A). In 1995, 40 species and 372 bird encounters were recorded in the contact zones, and 24 species and 288 bird encounters were recorded in the hybrid zones. Only one species, MacGillivray's Warbler, was observed only in the hybrid zones. Conversely, 17 of the 41 species were observed only in the contact zones. In 1996, 47 species and 479 bird encounters, and 27 species and 304 bird

encounters occurred in contact zones and hybrid zones, respectively. Hybrid zones supported only three unique species in 1996: Cassin's Kingbird, Townsend's Solitaire, and Pine Siskin. In contrast, 23 species occurred exclusively in the contact zones.

Contact zones typically contained more species than did hybrid zones. Repeated-measures analysis of variance indicated significant differences between zone types in average number of species recorded ($F_{1,19} = 6.88$, $P = 0.017$). Contact zones averaged 6.05 species in 1995 and 6.13 species in 1996; hybrid zones averaged 4.60 and 4.16 species in 1995 and 1996, respectively. Separate analyses indicated significantly greater species richness in contact zones for both years ($t_{19} = 2.21$, $P = 0.040$ in 1995; and $t_{19} = 2.81$, $P = 0.011$ in 1996).

Principal components analysis on the average abundances of species accounted for 91% of the variation among sites with 13 principal components (eigenvalues > 1.0) in 1995, and for 94% of the variation among sites with 14 components (eigenvalues > 1.0) in 1996. The first principal component accounted for 16.8 and 14.6% of the variation among sites in 1995 and 1996, respectively (Table 2). In both years, the first principal component primarily represented increasing abundances of all species and largely separated the two zone types (Figure 2). However, in 1995, the first principal component also corresponded with decreasing abundances of Dark-eyed Juncos, Red-faced Warblers, Steller's Jays, and Townsend's Solitaire; in 1996, it also corresponded with decreasing abundances of Red-faced Warblers (Table 2). The second principal component explained 12.4 and 11.8% of the variation in average abundance of bird species among sites in 1995 and 1996, respectively. This component largely represented mixed responses of species (Table 2) and did not contribute much to the separation of the two zone types in either year.

The separation of contact zones from hybrid zones along the first principal component also reflected the distribution patterns of rare species (five observations or less in a year), which represented 15 and 21 species in 1995 and 1996, respectively. These species occurred with not only a much higher frequency in the contact zones (14 in 1995 and 18 in 1996) than in the hybrid zones (4 in 1995 and 5 in 1996), but the occurrence of many of these species was restricted to the contact zones (11 in 1995 and 16 in 1996).

Although there were clear differences overall between the bird communities of hybrid and contact zones for both years, the densities of individual species exhibited mixed responses with respect to zone type and year (Figure 3). In 1995, six species showed strong ($P < 0.05$) differences in abundance between contact zones and hybrid zones; the Steller's Jay, Townsend's Solitaire, Red-faced Warbler and Dark-eyed Junco were more abundant in the hybrid zones, while the Ash-throated Flycatcher and the Chipping Sparrow were more abundant in the contact zones (Table 3). In addition, nine species exhibited relatively weak ($0.05 < P < 0.10$) differences between zone types; the Purple Martin, Solitary Vireo, Western Wood-Pewee, Acorn Woodpecker, White-Breasted Nuthatch, Scrub Jay, American Robin, Brown-Headed Cowbird, and

Table 2. Principal components analysis of bird species abundances in 11 contact and 10 hybird zones in 1995 and 1996.

1995			1996		
Species	PC 1	PC 2	Species	PC 1	PC 2
MODO	0.29	0.40	TUVU	−0.02	−0.36
BTHU	−0.34	−0.25	MODO	0.10	0.35
NOFL	0.27	0.63	WTSW	0.49	0.28
ACWO	0.53	0.46	BTHU	−0.21	−0.37
HAWO	0.27	0.11	NOFL	−0.07	0.47
CAKI	0.39	0.60	ACWO	0.69	0.49
ATFL	0.77	0.03	HAWO	−0.31	−0.01
WEWP	0.50	0.26	CAKI	−0.30	0.01
GRFL	0.28	−0.32	ATFL	0.43	−0.21
COFL	−0.30	−0.03	WEWP	0.47	0.45
VGSW	−0.07	0.16	GRFL	0.19	−0.52
PUMA	0.38	0.69	COFL	−0.42	0.14
SCJA	0.55	−0.48	VGSW	0.68	−0.31
STJA	−0.69	0.05	PUMA	0.11	0.53
PLTI	−0.13	0.17	SCJA	0.18	−0.62
BRTI	0.38	−0.52	STJA	−0.36	0.05
MOCH	−0.37	0.16	CLNU	0.25	0.02
COBU	−0.14	0.06	CORA	−0.12	0.35
WBNU	0.68	0.22	MOCH	−0.27	0.16
PYNU	−0.05	0.20	COBU	−0.09	−0.28
HOWR	0.39	0.60	WBNU	0.64	0.19
BEWR	−0.05	−0.08	PYNU	0.09	0.71
BGGN	0.38	−0.39	HOWR	0.36	0.63
WEBL	−0.20	0.23	BEWR	0.18	−0.25
TOSO	−0.58	0.09	CAWR	0.04	0.41
HETH	0.24	−0.37	ROWR	0.04	0.41
AMRO	0.51	0.61	RCKI	0.38	0.47
SOVI	0.45	−0.52	BGGN	0.23	−0.48
WAVI	0.52	−0.25	WEBL	0.56	0.11
YRWA	−0.14	0.02	TOSO	−0.37	0.02
GRWA	0.21	0.05	HETH	0.71	−0.12
MGWA	−0.29	−0.05	AMRO	0.38	0.45
RFWA	−0.58	0.19	SOVI	0.72	0.15
BHGR	0.14	0.01	WAVI	0.64	−0.13
RSTO	−0.27	−0.02	VIWA	−0.30	−0.23
RCSP	0.30	−0.52	YRWA	−0.27	0.18
CHSP	0.50	−0.51	BTYW	0.21	−0.60
BCSP	0.38	−0.52	GRWA	0.43	0.00
DEJU	−0.61	−0.01	WIWA	0.04	0.41
BHCO	0.55	0.41	RFWA	−0.65	0.34
WETA	0.42	−0.33	BHGR	0.14	0.05
			RSTO	0.08	−0.30
			VESP	−0.02	−0.36
			CHSP	0.53	−0.42
			BCSP	0.48	−0.30
			DEJU	−0.45	0.24

Table 2. Continued.

1995			1996		
Species	PC 1	PC 2	Species	PC 1	PC 2
			BHCO	0.72	−0.03
			WETA	0.07	0.02
			PISI	−0.22	0.06
			LEGO	−0.02	−0.36
Eigenvalue	6.88	5.08		7.30	5.88
Percent of variation	16.78	12.38		14.60	11.75

Values associated with species codes are factor coefficients.

Hairy Woodpecker were all more abundant in the contact zones than in the hybrid zones.

In 1996, six species exhibited strong differences between zone types. The Cordilleran Flycatcher, Red-Faced Warbler, and Dark-Eyed Junco were more abundant in hybrid zones; the Ash-Throated Flycatcher, Violet-Green Swallow, and American Robin were more abundant in contact zones (Table 3). Four species exhibited relatively weak differences between zone types; the Acorn Woodpecker, Brown-Headed Cowbird, and Western Bluebird were more abundant in contact zones, while the Virginia's Warbler was more abundant in hybrid zones.

The Ash-Throated Flycatcher, Dark-Eyed Junco, Red-Faced Warbler, American Robin, Acorn Woodpecker, and Brown-Headed Cowbird exhibited consistent differences between zones types over the 2 years (Table 3). In contrast, the Stellar's Jay, Chipping Sparrow, Townsend's Solitaire, Purple Martin, and Solitary Vireo exhibited significant differences between zones types in 1995 but not in 1996, while the Cordilleran Flycatcher and Violet-Green Swallow exhibited significant differences between zone types in 1996 but not in 1995.

Reptile communities in contact and hybrid zones

A total of 10 species of reptiles and one species of amphibian (*A. tigrinum*), represented by 93 observations, were recorded in 1996 (see Appendix A). All 11 species were encountered in the contact zones, while only five species were recorded from the hybrid zones (Figure 4). The average number of species in contact zones was 4.25, while hybrid zones averaged 2.5 species. There was a significant difference in average species richness between zone types ($t_6 = 3.13$, $P = 0.020$). None of the 11 species exhibited significant differences in average abundance between zone types.

Relationships between habitat structure and bird and reptile communities

The vegetation of the sites as measured in this study was essentially unrelated to the distribution of the bird species. The BA of the oak species, when examining all sites
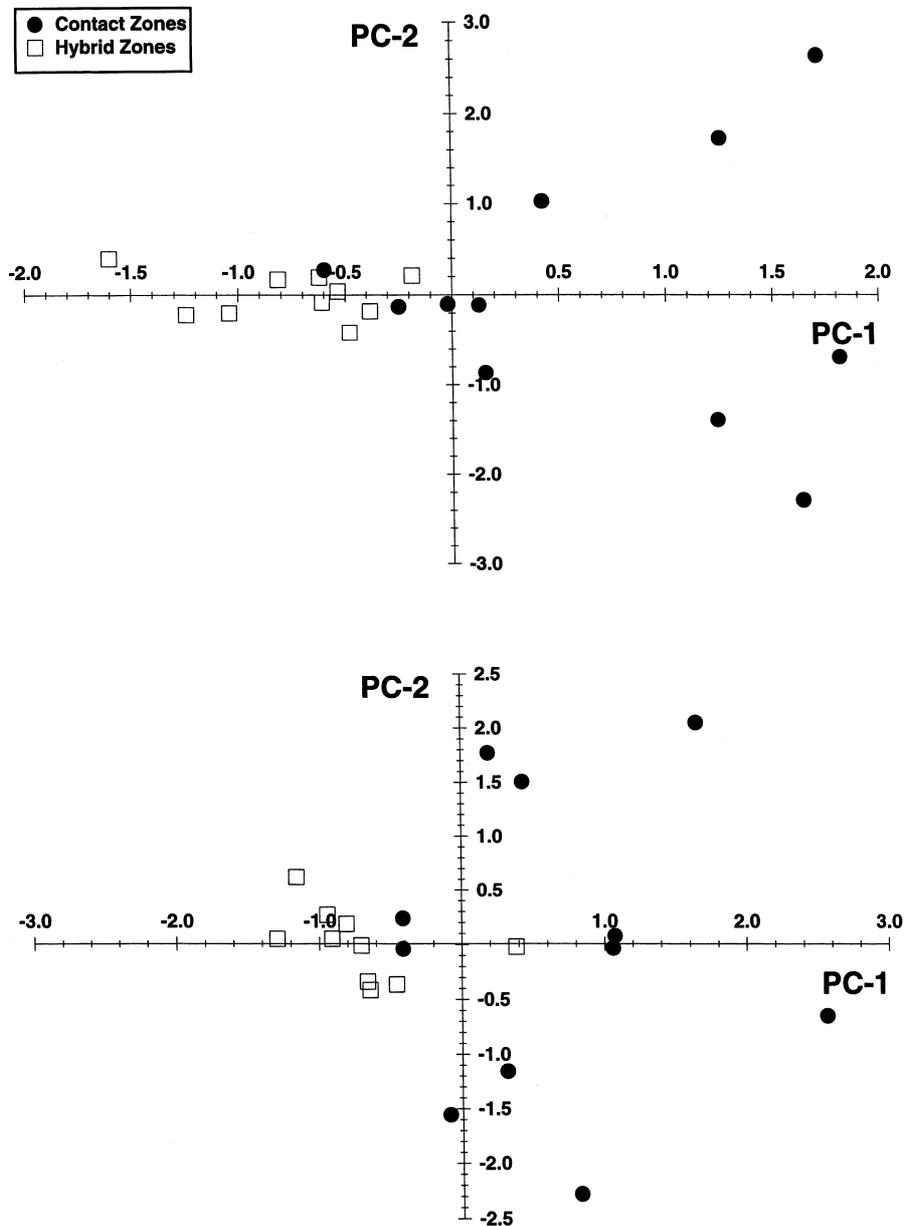
Figure 2. Principal components analysis of bird species abundances in 11 contact and 10 hybrid zones for 1995 (top) and 1996.

combined regardless of zone type, was the only vegetation characteristic positively correlated with the average number of bird species in 1995 ($r = 0.57$, $P = 0.006$) and 1996 ($r = 0.50$, $P = 0.02$). However, these correlations were nonsignificant
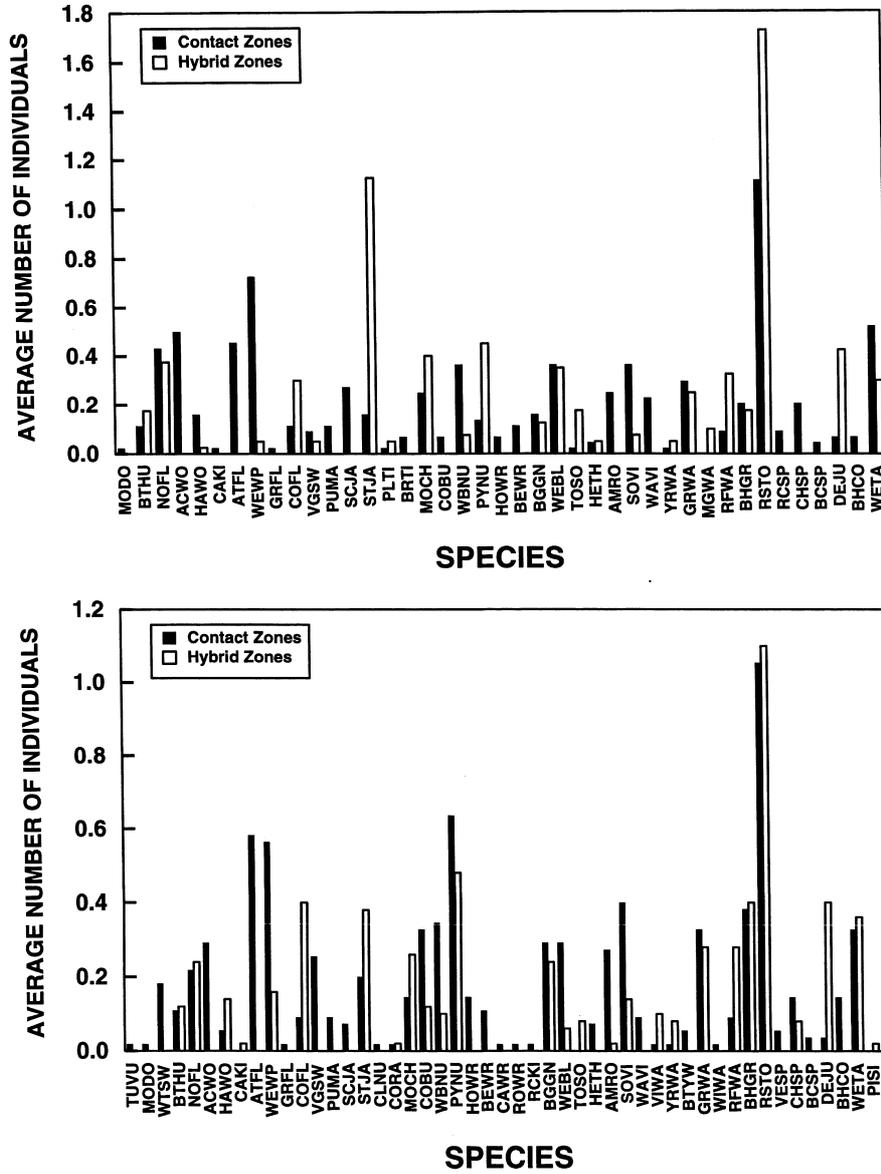
Figure 3. Average number of individuals observed per site visit for bird species in 11 contact and 10 hybrid zones in 1995 (top) and 1996.

when examining the zone types individually, and the addition of OBA as a covariate made no significant contribution in explaining differences between zone types in bird species richness.

There was also relatively little relationship between the vegetation variables and reptile species richness. When the zone types were pooled, there were no significant

Table 3. Mean abundances in contact (Contact) and hybrid zones (Hybrid) for bird species exhibiting strong ($P < 0.05$) and weak ($0.05 < P < 0.10$) differences between zone types in 1995 and 1996.

	1995				1996			
Species	Contact	Hybrid	F	P	Contact	Hybrid	F	P
ATFL	0.45	0.00	11.9	0.003	0.58	0.00	12.59	0.002
DEJU	0.07	0.43	9.10	0.007	0.04	0.40	15.21	0.001
RFWA	0.09	0.33	4.68	0.044	0.09	0.28	5.88	0.025
AMRO	0.25	0.00	3.55	0.075	0.27	0.02	9.11	0.007
ACWO	0.50	0.00	3.90	0.063	0.29	0.00	4.15	0.056
BHCO	0.07	0.00	3.39	0.081	0.15	0.00	3.71	0.069
STJA	0.16	1.13	13.14	0.002	0.20	0.38	1.97	0.177
CHSP	0.20	0.00	5.73	0.027	0.15	0.08	0.31	0.585
TOSO	0.02	0.18	5.27	0.033	0.00	0.08	2.49	0.131
PUMA	0.11	0.00	4.35	0.051	0.09	0.00	1.92	0.182
SOVI	0.36	0.08	4.30	0.052	0.40	0.14	2.62	0.122
WEWP	0.73	0.05	3.92	0.063	0.56	0.16	2.83	0.109
WBNU	0.36	0.08	3.81	0.066	0.35	0.10	2.74	0.114
SCJA	0.27	0.00	3.60	0.073	0.07	0.00	1.54	0.230
HAWO	0.16	0.03	3.03	0.098	0.05	0.14	2.19	0.155
COFL	0.11	0.30	1.37	0.256	0.09	0.40	5.56	0.029
VGSW	0.09	0.05	0.43	0.518	0.25	0.00	4.72	0.043
WEBL	0.36	0.35	0.00	0.946	0.29	0.06	3.42	0.080
VAWA	–	–	–	–	0.02	0.10	3.08	0.095

correlations between any of the vegetation variables and species richness. In the contact zones, the number of reptile species was positively correlated with the BA of juniper ($r = 0.978$, $P = 0.022$), while in the hybrid zones the relationship was negative ($r = -0.963$, $P = 0.037$). The frequency of trees in the 7.62–15.24 cm size class showed a similar relationship, although the correlation coefficient in the hybrid zone was only marginally significant ($r = 0.983$, $P = 0.017$ in contact zones; $r = -0.900$, $P = 0.10$ in hybrid zones).

There were significant, inverse relationships between elevation of a zone and the number of bird species ($r = -0.58$, $P = 0.006$) averaged over both years, and between elevation and the number of reptile species ($r = -0.79$, $P = 0.020$). When adjusted for elevation, contact zones averaged 5.58 species of birds and 3.88 species of reptiles and amphibians, whereas hybrid zones averaged 4.91 and 2.87 species, respectively. Analysis of covariance indicated no significant differences between zone types in bird species richness ($F_{1,18} = 0.52$, $P = 0.14$) or reptile and amphibian species richness ($F_{1,5} = 1.80$, $P = 0.24$).

Discussion

The PHZCB hypothesis (Whitham et al. 1994) is an existential hypothesis (*sensu* Popper 1959); that is, the hypothesis simply states that hybrid zones are centers of
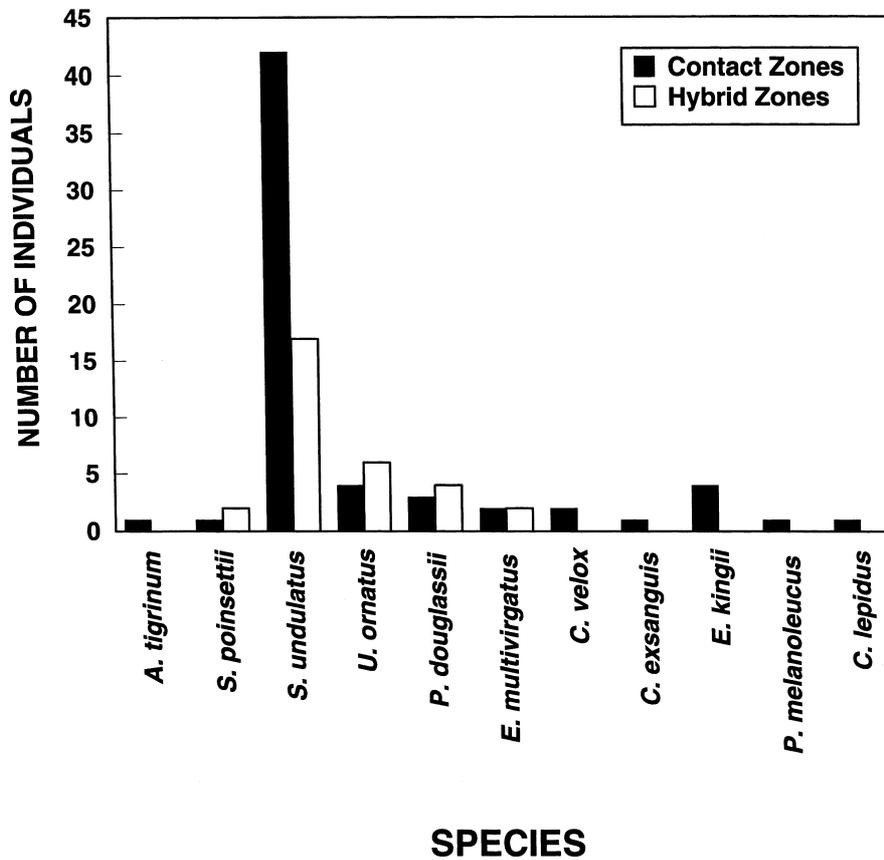
Figure 4. Total number of individuals of reptile and amphibians observed in 1996 in four contact and four hybrid zones.

biodiversity – no mechanisms are specified. Consequently, falsification of the PHZCB hypothesis only requires a demonstration that hybrid zones do not have elevated levels of biodiversity when compared to other areas. Because the forces that promote hybridization in plants are variable, and because the structure and dynamics of plant hybrid zones are variable also, it is perhaps unreasonable to expect the PHZCB to hold in all cases. The challenge for hybrid zone workers will be to amass a large compendium of case studies so that the generality of the PHZCB hypothesis can be evaluated. The mechanisms by which hybrid zones promote biodiversity also need further examination. Hybrid zones may support elevated levels of biodiversity when compared to pure, monospecific stands owing to increased susceptibility of hybrid plants, the occurrence of hybrid zones in unique habitats, the presence of more than one host species in hybrid zones, or to other factors. These competing mechanisms should be tested in isolation, but are often confounded in natural hybrid zones.

We have found little support for the PHZCB hypothesis for higher tropic levels in the *Q. grisea* × *Q. gambelli* species complex. Hybrid zones had significantly less species of birds and significantly fewer species of reptiles and amphibians than did contact zones. In general, contact zones also supported higher abundances of birds and reptiles than did hybrid zones, although species did exhibit idiosyncratic responses to zone type. Roughly two-thirds of bird species had higher (not necessarily significant) abundances in contact zones, as did approximately 64% of reptile and amphibian species. Our results contrast with those observed in the *P. fremontii* × *P. angustifolia* species complex, where a hybrid zone contained significantly more bird nests than did adjacent pure stands, and where hybrid trees contained more nests than did parental trees within the zone (Martinsen and Whitham 1994). These two results taken together suggest that the responses of higher tropic levels to plant hybridization may be as variable as those observed for herbivores (reviewed by Strauss 1994; Fritz et al. 1999).

Numerous factors associated with plant hybrids and with plant hybrid zones can affect, either indirectly or directly, the distribution and abundance of higher trophic levels. Indirect effects may operate in a bottom-up manner by affecting the abundances of herbivores upon which higher trophic levels may depend. For example, hybrid plants may be more susceptible to herbivores than are parental plants (Whitham 1989; Fritz et al. 1994; Christensen et al. 1995; Floate et al. 1997), and may act as herbivore sinks (*sensu* Whitham 1989). In such cases, hybrid zones may represent superior foraging areas and predators may concentrate their activities there (see Dickson and Whitham 1996). In contrast, hybrid plants may be less susceptible to herbivores than are parental plants (Boecklen and Spellenberg 1990; Boecklen and Larson 1994), or they may be intermediate in their susceptibility (Manley and Fowler 1969; Aguilar and Boecklen 1991; Fritz et al. 1994; Hanhimäki et al. 1994; Preszler and Boecklen 1994; Gange 1995; Graham et al. 1995; Gaylord et al. 1996; Wu et al. 1996). In these cases, predators may not be more abundant in hybrid zones and may actually be less abundant.

Boecklen and Spellenberg (1990) outline several factors that may be important in determining herbivore loads in plant hybrid zones. These include the size of the hybrid zones (see Floate et al. 1997), the location of hybrid zones, taxonomic and morphological relationships of the plants, direction and extent of introgression, and the autecologies of the herbivores themselves. Hybrid zones are not uniform with respect to these factors, and neither are the responses of herbivores to hybrid hosts. It is unlikely, therefore, that plant hybridization will have uniform, indirect effects on higher trophic levels.

Even if higher trophic levels are not foraging on herbivores, but instead on fruit or mast resources, the plant's resistance traits can still indirectly affect their foraging behavior and distribution patterns. If the production of mast or fruit is suppressed by increased levels of herbivores and hybrids are most susceptible (Drake 1981; Christensen and Whitham 1991, 1993; Morrow et al. 1994), then birds may avoid hybrid

trees and even hybrid zones because of reduced foraging efficiency (Christensen and Whitham 1991). On the other hand, if hybrids are least susceptible to herbivores, then the opposite pattern may obtain.

Plant hybridization can directly affect higher trophic levels by providing unique resources in the form of hybrid plants or unique habitats in the form of hybrid zones. Hybrid plants are often architecturally distinct from parental species and may contribute to increased vegetational complexity in hybrid zones. The importance of vegetation structure (MacArthur and MacArthur 1961; Willson 1974; Rotenberry and Wiens 1980; James and Wamer 1982) and species composition (Wiens and Rotenberry 1982; Rice et al. 1984) has been documented in numerous instances for birds. Vegetation structure can influence the distribution of reptiles as well (Pianka 1966, 1967, 1973; Lillywhite 1977; Baltosser and Best 1990, but see Scheibe 1987), however, the influence of the vegetation species composition seems to be relatively unimportant (Pianka 1966, 1967).

The architecture of hybrid plants in the *P. fremontii* × *P. angustifolia* species complex had direct effects on the abundances of nesting birds (Martinsen and Whitham 1994). The architecture of the F1 hybrids was intermediate to that of the parental species, and provided branching characteristics that made the hybrids the most favorable nesting sites (Martinsen and Whitham 1994). In contrast, architectural intermediacy was not the case for the *Q. grisea* × *Q. gambelii* hybrids. Hybrids were predominately shrubs, provided a limited range of heights, and did not provide as diverse a set of nesting sites or foraging sites for birds as did either parental species. The reptiles, which were primarily restricted to the vegetation layers where the hybrids were most common (i.e. shrub and ground cover layers), showed no correlation to the structural features of these layers.

The architecture of hybrid plants can have negative effects on higher trophic levels. Preszler and Boecklen (1994) found intermediate densities of the leaf-mining moth *Phyllonorycter* on *Q. grisea* × *Q. gambelii* hybrids relative to those on parental trees, but a lower density of parasitoids of the moth on hybrids. This pattern was upheld even when controlling for densities of leaf miners, suggesting that the structure of the plant hybrids affected the search behaviors of the parasitoid species.

Location of the hybrid zones can also influence their ability to support higher trophic levels. Mosaic hybrid zones in *Q. grisea* × *Q. gambelii* species complex appear roughly associated with a moisture gradient; hybrid zones occur most often on drier, more exposed slopes, whereas contact zones occur largely in or near more mesic canyon bottoms (Howard et al. 1997). In addition, hybrid zones typically occurred at significantly higher elevations than did contact zones. Adjusting species richness for elevation, showed that differences between zone types could be attributed, in part, to differences in elevation. Thus, there may be factors associated with the location of hybrid zones that are important in their effects on species distributions.

There have been recent calls for the inclusion of plant hybrids under the United States Endangered Species Act (e.g. Whitham et al. 1991; Whitham and Maschinski

1996; Floate et al. 1997). Many arguments can be made on behalf of inclusion, but among these are that plant hybrid zones are focal points of biodiversity for lower as well as higher trophic levels (Whitham et al. 1991; Whitham and Maschinski 1996; Whitham et al. 1999). The evidence provided by the bird and reptile distribution patterns in this study does not support the PHZCB hypothesis and suggests that higher trophic levels will exhibit idiosyncratic responses to plant hybridization. Further investigation into other hybrid complexes will likely show that the same variety of patterns exist for higher trophic levels as have been found at lower trophic levels (i.e. hybrid zones supporting higher, intermediate or lower species richness and abundance than pure parental stands). A general case cannot be made for distribution patterns of the organisms associated with hybrid zones; rather, hybrid zones will need to be evaluated on a case by case basis, in order to determine their potential to harbor increased levels of biodiversity.

Acknowledgements

Appendix A

List of bird, reptile, amphibian, and plant species observed in 11 contact zones (C) and 10 hybrid zones (H) in 1995 and 1996.

Birds Common name	Scientific name	Code	1995	1996
Turkey Vulture	*Cathartes aura*	TUVU	–	C
Mourning Dove	*Zenaida macroura*	MODO	C	C
White-Throated Swift	*Aeronautes saxatalis*	WTSW	–	C
Broad-Tailed Hummingbird	*Selasphorus platycercus*	BTHU	H, C	H, C
Northern Flicker	*Colaptes auratus*	NOFL	H, C	H,C
Acorn Woodpecker	*Melanerpes formicivorus*	ACWO	C	C
Hairy Woodpecker	*Picoides villosus*	HAWO	H, C	H, C
Cassin's Kingbird	*Tyrannus vociferans*	CAKI	C	H
Ash-Throated Flycatcher	*Myiarchus cinerascens*	ATFL	C	C
Western Wood-Pewee	*Contopus sordidulus*	WEWP	H, C	H, C
Gray Flycatcher	*Empidonax wrightii*	GRFL	C	C
Cordilleran Flycatcher	*E. difficilis*	COFL	H, C	H, C
Violet-Green Swallow	*Tachycineta thalassina*	VGSW	H, C	C
Purple Martin	*Progne subis*	PUMA	C	C

Appendix. Continued.

Birds

Common name	Scientific name	Code	1995	1996
Scrub Jay	*Aphelocoma coerulescens*	SCJA	C	C
Stellar's Jay	*Cyanocitta stelleri*	STJA	H, C	H, C
Clark's Nutcracker	*Nucifraga columbiana*	CLNU	–	C
Common Raven	*Corvus corax*	CORA	–	H, C
Plain Titmouse	*Parus inornatus*	PLTI	H, C	–
Bridled Titmouse	*P. wollweberi*	BRTI	C	–
Mountain Chickadee	*P. gambeli*	MOCH	H, C	H, C
Common Bushtit	*Psaltriparus minimus*	COBU	H, C	H, C
White-Breasted Nuthatch	*Sitta canadensis*	WBNU	H, C	H, C
Pygmy Nuthatch	*S. pygmaea*	PYNU	H, C	H, C
House Wren	*Troglodytes aedon*	HOWR	C	C
Bewick's Wren	*Thryomanes bewickii*	BEWR	C	C
Canyon Wren	*Catherpes mexicanus*	CANW	–	C
Rock Wren	*Salpinctes obsoletus*	ROWR	–	C
Ruby-Crowned Kinglet	*Regulus calendula*	RCKI	–	C
Blue-Gray Gnatcatcher	*Polioptila caerulea*	BGGN	H, C	H, C
Western Bluebird	*Sialia mexicana*	WEBL	H, C	H, C
Townsend's Solitaire	*Myadestes townsendi*	TOSO	H, C	H
Hermit Thrush	*Catharus guttatus*	HETH	H, C	C
American Robin	*Turdus migratorius*	AMRO	C	H, C
Solitary Vireo	*Vireo solitarius*	SOVI	H, C	H, C
Warbling Vireo	*V. gilvus*	WAVI	C	C
Virginia's Warbler	*Vermivora virginiae*	VIWA	–	H, C
Yellow-Rumped Warbler	*Dendroica coronata*	YRWA	H, C	H, C
Black-Throated Gray Warbler	*D. nigrescens*	BTYW	–	C
Grace's Warbler	*D. graciae*	GRWA	H, C	H, C
Mac Gillivray's Warbler	*Oporornis tolmiei*	MGWA	H	–
Wilson's Warbler	*Wilsonia pusilla*	WIWA	–	C
Red-Faced Warbler	*Cardellina rubrifrons*	RFWA	H, C	H, C
Black-Headed Grosbeak	*Pheucticus melanocephalus*	BHGR	H, C	H, C
Rufous-Sided Towhee	*Pipilo erythrophthalmus*	RSTO	H, C	H, C
Vesper Sparrow	*Pooecetes gramineus*	VESP	–	C
Rufous-Crowned Sparrow	*Aimophila ruficeps*	RCSP	C	–
Chipping Sparrow	*Spizella passerina*	CHSP	C	H, C
Black-Chinned Sparrow	*S. atrogularis*	BCSP	C	C
Dark-Eyed Junco	*Junco hyemalis*	DEJU	H, C	H, C
Brown-Headed Cowbird	*Molothrus ater*	BHCO	C	C
Western Tanager	*Piranga ludoviciana*	WETA	H, C	H, C
Pine Siskin	*Carduelis pinus*	PISI	–	H
Lesser Goldfinch	*C. psaltria*	LEGO	–	C

Reptiles and amphibians

Common name	Scientific name	1995	1996
Gopher Snake	*Pituophis melanoleucus*	–	C
Rock Rattlesnake	*Crotalus lepidus*	–	C
Short-horned Lizard	*Phrynosoma douglassii*	C	H, C
Crevice Spiny Lizard	*Sceloporus poinsettii*	H	H,C
Eastern Fence Lizard	*S. undulatus*	H, C	H, C
Tree Lizard	*Urosaurus ornatus*	C	H, C

Appendix. Continued.

Reptiles and amphibians Common name	Scientific name	1995	1996
Many-lined Skink	*Eumeces multivirgatus*	–	H, C
Chihuahuan Spotted Whiptail	*Cnemidophorus exanguis*	–	C
Plateau Striped Whiptail	*C. velox*	–	C
Arizona Alligator Lizard	*Elgaria kingii*	–	C
Tiger Salamander	*Ambystoma tigrinum*	–	C

Plants Common name	Scientific name	Trees	Shrubs	GC
Limber Pine	*Pinus flexilis*	H	H	H
Pinyon Pine	*P. edulis*	H, C	H, C	H, C
Ponderosa Pine	*P. ponderosa*	H, C	H, C	–
Douglas Fir	*Pseudotsuga menziesii*	H, C	H, C	–
White Fir	*Abies concolor*	H	–	–
Alligator Juniper	*Juniperus deppeana*	H, C	H, C	C
One-seeded Juniper	*J. monosperma*	C	C	–
Rocky Mountain Juniper	*J. scopulorum*	H, C	C	–
Arizona Walnut	*Juglans major*	C	–	–
Gambel Oak	*Quercus gambelii*	H, C	H, C	H, C
Wavyleaf Oak	*Q. undulata*	H, C	H, C	H
Grey Oak	*Q. grisea*	H, C	H, C	H, C
Cholla	*Opuntia imbricata*	–	C	–
Prickly Pear	*Opuntia* sp.	–	–	C
Lanceleaf Cottonwood	*Populus acuminata*	C	–	–
Narrowleaf Cottonwood	*P. angustifolia*	C	–	–
New Mexico Locust	*Robinia neomexicana*	–	H	H
Boxelder	*Acer negundo*	C	–	–
Birchleaf Mountain Mahogany	*Cercocarpus betuloides*	H, C	H, C	H, C
Yucca	*Yucca baccata*	–	H, C	H, C
False Mockorange	*Fendlera rupicola*	–	H, C	H, C
Squawbush	*Rhus trilobata*	–	C	H
Wax Currant	*Ribes inebrians*	–	H	–
Broom Snakeweed	*Gutierrezia sarothrae*	–	–	H
Apache Plume	*Fallugia paradoxa*	–	H	–

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