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## Changes in interactions between juniper and mistletoe mediated by shared avian frugivores: parasitism to potential mutualism

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**Abstract** Although mistletoe is typically viewed as a parasite of juniper in a two-way interaction, its role may become neutral or even mutualistic when their common avian seed dispersing agents are considered as a three-way interaction. In the study area, wintering avian frugivores forage on both one-seed juniper (*Juniperus monosperma*) berries and on the fruit of its associated mistletoe (*Phoradendron juniperinum*). Three major findings emerged from our studies that support a three-way interaction and the hypothesis of conditional interactions. First, mistletoes provide a stable resource for shared avian seed dispersers; junipers do not. Whereas juniper berry production varied 10- to 15-fold over the 3 years of our study, mistletoe fruit abundance did not vary significantly. Second, the abundance of avian seed dispersal agents, such as Townsend's solitaires (*Myadestes townsendi*), is strongly tied to the abundance of juniper berries in most years and mistletoe fruits in all years. In fact, the best overall predictor of their common avian seed dispersal agents was the abundance of mistletoe; stands with mistletoe attracted up to 3 times more avian frugivores than stands with little or no mistletoe. Thus, mistletoe berries can serve as the main attractor for birds that disperse juniper berries. Third, in agreement with the hypothesis that mistletoe can benefit junipers by attracting and supporting greater populations of avian seed dispersal agents, the number of juniper seedlings was more than 2-fold greater in stands with high mistletoe density compared with stands that had little or no mistletoe. Results suggest that the occurrence of a three-way interaction, in the presence of environmental variation (in this case, annual variation in juniper berry crops),

may change the ecological roles of associated species. A conceptual model is presented to illustrate how the role of mistletoe may range from parasitic to mutualistic, while the role of avian seed dispersers may conversely range from mutualistic to parasitic, the latter by acting as vectors for the spread of mistletoe.

**Keywords** Avian frugivores · Mistletoe · Mutualism · One-seed juniper · Parasitism

### Introduction

Species interactions have been shown to vary from antagonistic to mutualistic in response to biotic and abiotic conditions (Thompson 1988; Cushman and Beattie 1991; Bronstein 1994). Factors influencing the outcomes of such interactions include the physical, genetic, and life history traits of hosts (Thompson 1988; Cushman and Whitham 1989; Saikonen et al. 1998); other interacting species (Smith 1968; Glynn 1976; Davidson et al 1985; Palumbi 1985; Dungan 1986; Clay et al 1993; Gehring and Whitham 1994; Gehring et al. 1997); and abiotic environmental conditions (Palumbi 1985; Thompson 1988; Johnson et al. 1997; Saikonen et al. 1998). These studies suggest that complex interactions and different or changing environmental conditions can result in non-intuitive relationships among associated species. Parasitism, commensalism, and mutualism are better viewed as points along a continuum from negative to positive effects, rather than as well-defined and discrete classifications that can be consistently applied to sets of interacting species (Bronstein 1994). More importantly, the ecological roles of species may shift along this continuum in response to environmental variation and the influence of other interacting species. Here we examine how, under variable environmental conditions, a three-way interaction between juniper, mistletoe, and birds confounds traditional interpretations based only on direct, two-way interactions.

Mistletoes have typically been characterized as parasites on their host plants (Kuijt 1969; Calder 1983;

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Ehleringer et al. 1985). In the western United States, mistletoes (*Arceuthobium* and *Phoradendron* spp.) are considered "pests" that should be controlled (Cain et al. 1990; but see Bennetts et al. 1996). Mistletoe, by functioning as a sink for water and nutrients, can negatively affect host plant condition by reducing host growth and reproduction, and increasing susceptibility to pathogens (Ferrell 1974; Hawksworth 1983; Knutson 1983). The mistletoe (*Phoradendron juniperinum*) found on junipers (*Juniperus* spp.) obtains water, carbon, and other nutrients from the xylem of its host plant (Ehleringer et al. 1986; Marshall and Ehleringer 1990; Marshall et al. 1994) and can cause branch dieback, increased host plant water stress, and reduced growth (Johnsen 1962; Knutson 1983).

The otherwise clear parasitic relationship of mistletoe on juniper is confounded because both share common seed-dispersing mutualists. The relationships between avian frugivores and many flowering plants have been extensively studied both in tropical and temperate regions and exemplify classic examples of mutualism (Snow 1971; Jordano 1987; Wheelwright 1988; but see Cushman and Beattie 1991). Avian frugivores obtain nutritional benefits while dispersing the seeds of flowering plants. Junipers (*Juniperus monosperma* and *occidentalis*) in the western United States produce crops of "berries" (i.e., modified cones) that represent an important food source for wintering avian frugivores (Lederer 1977; Salomonson and Balda 1977; Poddar and Lederer 1982; Balda 1986). While the birds obtain nutritional value from the berries, junipers benefit by having their seeds dispersed. Similarly, the relationship between some species of mistletoe and avian frugivores has also been described as a mutualism. The fruits of most mistletoe species are consumed almost exclusively by birds and the seeds are subsequently dispersed through defecation or regurgitation (Kuijt 1969; Calder 1983; Del Rio et al. 1996; Larson 1996).

In pinyon-juniper woodlands in northern Arizona, a three-way interaction exists between one-seed juniper, mistletoe, and wintering avian frugivores. Mistletoe (*P. juniperinum*) grows on one-seed juniper and produces fruits, which are available in the same season as the berries of its host plant. Field observations by the authors, analysis of stomach contents (M. Guntert, unpublished data), and past studies (Salomonson and Balda 1977; Balda 1986) have found that the most abundant wintering frugivores in these woodlands feed on both juniper berries and mistletoe fruit. These include the Townsend's solitaire (*Myadestes townsendi*), western bluebird (*Sialia mexicana*), American robin (*Turdus migratorius*), and cedar waxwing (*Bombycilla cedrorum*). Salomonson (1978) suggested that Townsend's solitaires were an important seed disperser of one-seed juniper in northern Arizona. Johnsen (1962) found that *J. monosperma* seeds from bird and other animal droppings germinated faster than those that did not pass through an avian or mammalian gut. He also found that seeds left in berries had a 10-fold lower germination percentage compared

with seeds removed from berries, emphasizing the importance of physical separation of the seed from the berry by dispersal agents.

The objective of this study was to examine how the presence of a three-way interaction and annual variation in food resources for avian frugivores can potentially affect the functional relationships between one-seed juniper, its associated mistletoe, and their shared avian seed dispersers. To examine the nature of the interactions and their possible outcomes, three major inquiries were made: (1) What is the variability in juniper berry and mistletoe fruit abundance over time? (2) How is bird abundance related to the abundance of juniper berries and mistletoe fruit? (3) What is the pattern of juniper seedling abundance relative to the presence of mistletoe? Our findings argue that in this three-way interaction, mistletoe may shift from having parasitic to neutral or even positive effects on one-seed juniper. These findings also argue for a more holistic approach that encompasses greater complexity to understand ecological processes.

## Materials and methods

The study took place in pinyon (*Pinus edulis*) and juniper (*Juniperus monosperma*) woodlands on the Colorado Plateau in northern Arizona, USA. Study sites were located within an area approximately 20 km wide by 30 km long, directly north, northeast, and east of Flagstaff, at an elevational range of about 1,600–2,000 m above mean sea level. Data on juniper berry, mistletoe fruit, and avian frugivore abundance were collected at 17 sites over a 3-year period. The sites, separated by a minimum of 0.8 km, were selected non-randomly to obtain a continuum ranging from no mistletoe present to high mistletoe density. In the second year of the study, avian frugivore abundance and vegetation data were collected along transects at ten sites with high mistletoe density ("mistletoe-infected": estimated mistletoe density, mean $\pm$ 1SE=2,129.8 $\pm$ 671.79 plants/ha) and ten sites where mistletoe was absent or rare ("mistletoe-free": estimated mistletoe density=46.7 $\pm$ 32.71 plants/ha). As an estimate of the success of juniper reproduction, juniper seedling abundance was recorded at these same 20 sites in the third year of the study.

To determine the variability in juniper berry production, the number of berry-producing junipers were recorded along six randomly selected 100 $\times$ 30 m belt transects at each of the initial 17 sites in November and December 1994, 1995, and 1996. In 1994, numbers of junipers with high berry crops (estimate of >30% of visible foliage layer composed of berries) were recorded. In 1995 and 1996 few trees met this classification and only the numbers of junipers with any visible berries were recorded. For each site, transect data were pooled to obtain an estimated number of berry-producing junipers per ha. The mean number of berry-producing junipers per site was compared among the three study years using a Kruskal-Wallis test.

An assessment of annual variability in mistletoe fruit production was made at one of the study sites. The number of mistletoe fruits on randomly selected plants along two randomly determined 500 m transects were recorded in October and November of 1994, 1995, and 1996. Each fall, a total of 16 mistletoe plants were randomly selected and sampled at 30 m intervals along the same two transects. Selected mistletoe plants were removed from the trees and destructively sampled to obtain a fruit count. Data from the two transects were pooled and the mean number of fruits per mistletoe plant was compared across the three study years using a Kruskal-Wallis test and a Tukey's post hoc test.

The relative abundance of mistletoe fruit was estimated at each of the 17 sites in the fall of 1995. While recording the number of

berry-producing junipers, the number of fruit-bearing mistletoe clumps 12 cm in diameter or greater were also recorded along the same 100×30 m transects. For each site, transect data were pooled to obtain an estimated number of fruit-bearing mistletoe per ha.

The relative abundance of an important seed disperser, the Townsend's solitaire, was estimated at each of the 17 sites in the fall of 1994, 1995, and 1996, and correlated with the number of junipers with high berry crops (1994 only), the number of berry-producing junipers (1995 and 1996), and the number of fruit-bearing mistletoe (all three years). The number of vocalizing solitaires detected in a 5-min sampling period was recorded in November 1994, December 1995 to early January 1996, and in November 1996. Mean numbers of solitaires per site were obtained from censuses on five separate days in the 1994 and 1995 seasons and from censuses on two separate days in the 1996 season. Each site was sampled twice each census day.

The abundance of all avian frugivores was compared between mistletoe-infected and mistletoe-free sites in the second year of study to determine the relationship between avian seed disperser abundance and mistletoe abundance when juniper berry crops were low. At each of the ten mistletoe-infected and mistletoe-free sites, one 800 m transect was established in a random direction and censused for birds in October and November 1996. Each transect was surveyed twice (consecutively) in one day on two separate days. All birds were recorded by species to a maximum distance of 150 m on either side of the transect line. Mean numbers of avian frugivores per ha in mistletoe-infected and mistletoe-free sites were compared using a Mann-Whitney U-test.

Data were collected to determine whether differences existed in juniper seedling recruitment between mistletoe-infected and mistletoe-free stands. Juniper seedling densities were estimated by recording the number of junipers less than 15 cm in height in eight 2,500 m<sup>2</sup> quadrats along each of the ten previously established 800 m transects in mistletoe-infected and mistletoe-free areas from August 1996 to March 1997. Junipers under 15 cm in height generally average 10 years or less in age (Blackburn and Tueller 1970). Based on an established aging technique (Dawson et al. 1990), mistletoe plants in the study area were found to range between 1 and 12 years old, with the greatest proportion of plants in the 7- to 10-year age class. This suggests that mistletoe was present at the time these juniper seedlings germinated.

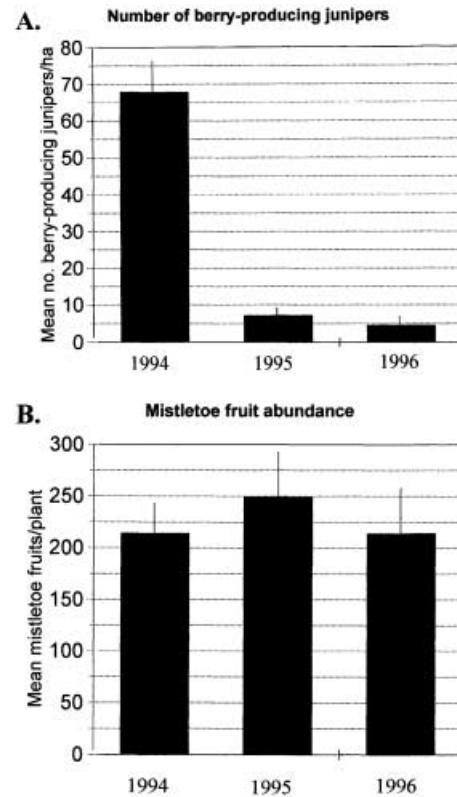
The number of juniper seedlings per quadrat was pooled to obtain an estimate of seedling density per site. The mean number of seedlings per ha were compared between mistletoe-infected and mistletoe-free sites using a Mann-Whitney U-test. To account for stand differences, the number of reproductive adults within 5 m of each transect line was recorded. Mean numbers of reproductive adults per hectare were compared between mistletoe-infected and mistletoe-free sites using a Mann-Whitney U-test.

## Results

### Seed production

The number of berry-producing junipers in the study area varied significantly among years. The mean number of berry-producing junipers was nearly 10-fold greater in 1994 (mean±1SE=67.8±8.33 trees/ha,  $n=17$  sites) when compared to 1995 (7.1±1.29 trees/ha,  $n=17$  sites) and was 15-fold greater when compared to 1996 (4.5±1.19 trees/ha,  $n=17$  sites, Kruskal-Wallis  $\chi^2=29.91$ ,  $P<0.001$ , Fig. 1A). High variability in one-seed juniper berry crops between years has also been documented by others (Salomonson and Balda 1977).

In contrast to high variability in juniper berry crops, no difference was found in average mistletoe fruit production among years. The mean number of mistletoe fruits per plant in 1994 (mean±1SE=213.9±29.00 fruits/



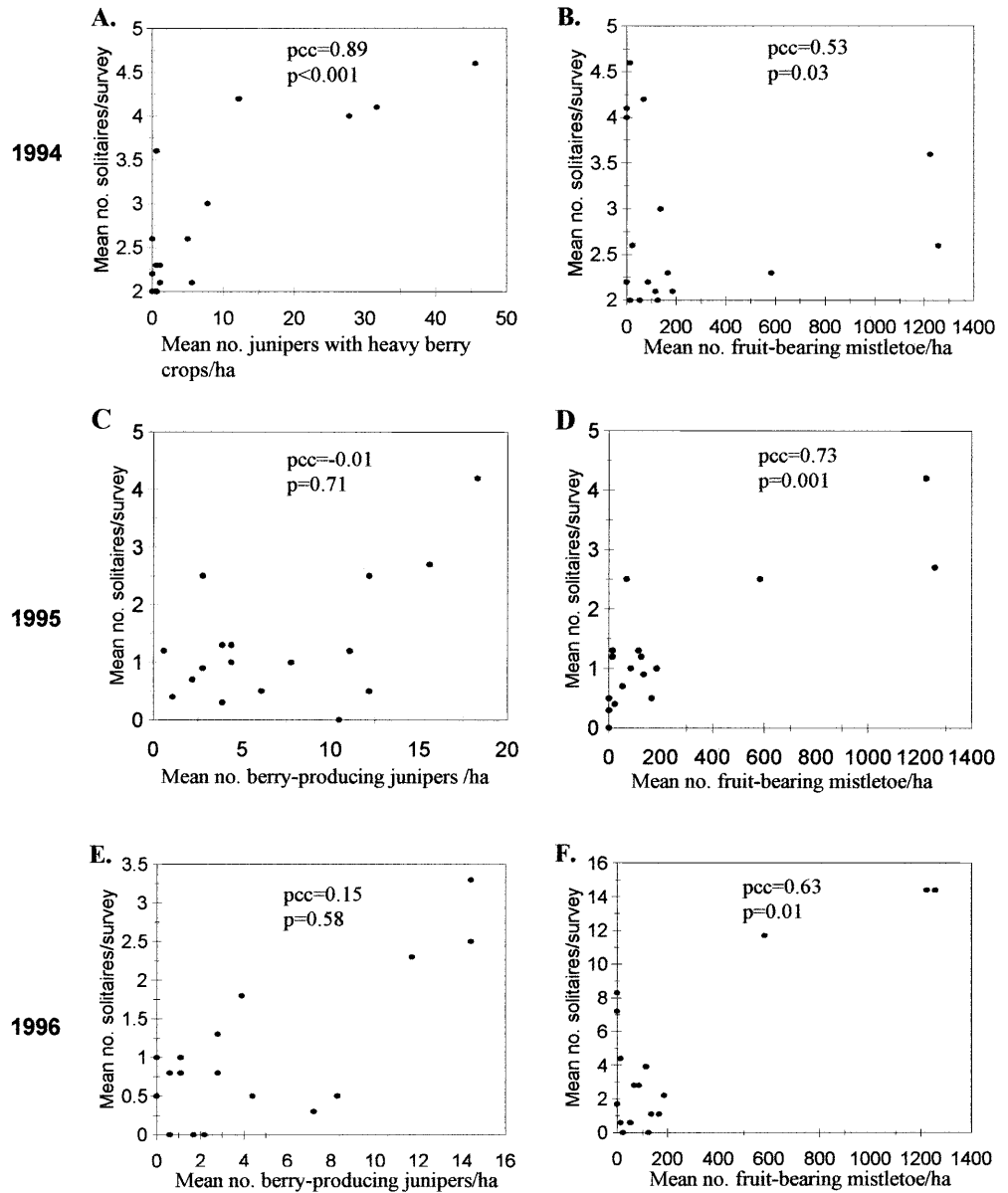
**Fig. 1A, B** Juniper (*Juniperus monosperma*) berry crops vary greatly from one year to the next, but mistletoe (*Phoradendron juniperinum*) fruits remain relatively constant. **A** Mean (±1SE) numbers of berry-producing junipers per ha recorded at 17 sites in 1994, 1995, and 1996. **B** Mean (±1SE) numbers of fruits per mistletoe for 16 different female mistletoe plants along the same two transects over the same time period. Differences in means were considered significant at  $P\leq 0.05$

plant,  $n=16$  plants) was not statistically different from the number per plant recorded in 1995 (249.1±42.58,  $n=16$  plants) or 1996 (214.0±47.44,  $n=16$  plants, Kruskal-Wallis  $\chi^2=0.44$ ,  $P=0.81$ , Fig. 1B). Similarly, Larson (1996) found that overall fruit production did not vary significantly between years for *Phoradendron californicum* in southern Arizona. These data sets demonstrate that juniper berry production fluctuates, whereas mistletoe berry production is relatively constant, which in combination could affect the distributions of avian seed dispersal agents.

### Responses of avian dispersal agents

The relative abundance of avian seed dispersers varied among years relative to the estimated abundance of mistletoe fruit and the number of berry-producing junipers. Although relatively constant among years within a site, mistletoe fruit abundance varied significantly among sites. The number of fruit-bearing mistletoes varied from none to over 1,200 per ha (min=0.0±0.00 plants/ha, max.=1,257±207.99 plants/ha), with significant differences occurring among sites (Kruskal-Wallis,  $\chi^2=37.83$ ,  $P=0.002$ ).

**Fig. 2A–F** Avian seed disperser abundance is positively correlated with mistletoe abundance in all three years, but positively correlated with juniper berry abundance only in the first (“mast”) year. **A–F** show the relationship between juniper berry abundance and mistletoe abundance for 1994 (**A, B**), 1995 (**C, D**), and 1996 (**E, F**). Partial correlation coefficients show the influence of one food source when the other is held constant. Partial correlations were considered significant at  $P \leq 0.05$

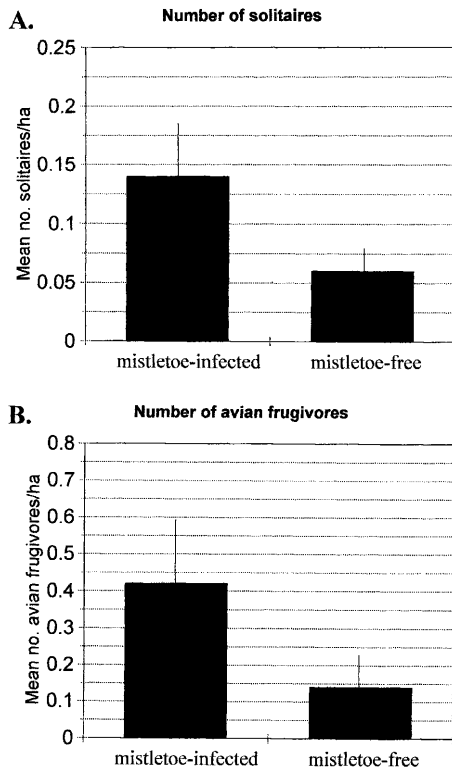


In the 1994 “mast” year, the number of junipers with high berry crops explained a significant proportion of the variability in Townsend’s solitaire numbers when mistletoe fruit abundance was held constant (partial correlation coefficient,  $pcc=0.89$ ,  $P<0.001$ , Fig. 2A). There was also a significant correlation between solitaire numbers and mistletoe fruit abundance when the number of junipers with high berry crops was held constant ( $pcc=0.53$ ,  $P=0.03$ , Fig. 2B). In agreement with these findings, Salomonson and Balda (1977) found that in years when juniper berries were abundant, many male Townsend’s solitaires established small exclusive winter territories. The following year, when juniper berries were not abundant, fewer territories were established and those that were established were larger.

When juniper berry crops were low, avian frugivore abundance was correlated only with mistletoe fruit abundance. In both 1995 and 1996, estimated mistletoe fruit

abundance per site explained a significant proportion of the variability in Townsend’s solitaire numbers when numbers of berry-producing junipers were held constant (1995,  $pcc=0.73$ ,  $P=0.001$ ; 1996,  $pcc=0.63$ ,  $P=0.01$ , Fig. 2D, F). In contrast, there was no significant correlation between solitaire numbers and numbers of berry-producing junipers when mistletoe fruit abundance was held constant (1995,  $pcc=-0.010$ ,  $P=0.71$ ; 1996,  $pcc=0.15$ ,  $P=0.58$ , Fig. 2C, E). Salomonson and Balda (1977) found that solitaires consumed nearly 8-fold more mistletoe berries in a year with low juniper berry abundance, presumably to obtain supplementary water. Mistletoe consumption may also help meet energy needs. Phainopeplas (*Phainopepla nitens*) depend on mistletoe berries (*Phoradendron californicum*) for a substantial portion of their diet (Walsberg 1975; Larson 1996).

Consistent with these data, avian frugivores were found to be more abundant at mistletoe-infected sites in

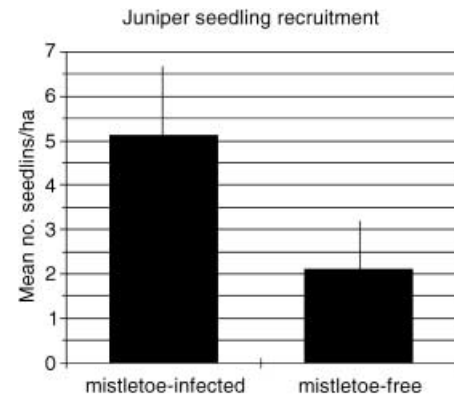


**Fig. 3A, B** When the juniper berry crop is low, Townsend's solitaires and other avian frugivores are most abundant in mistletoe-infected stands of juniper. Mean ( $\pm 1$ SE) densities of **A** Townsend's solitaires and **B** all avian frugivores per hectare at ten sites in mistletoe-infected stands and ten sites in mistletoe-free stands in the 1995 "non-mast" year. Differences in means were considered significant at  $P \leq 0.05$

a year when juniper berry crops were low. Mistletoe-infected stands had more than 2-fold as many Townsend's solitaires (mean  $\pm 1$ SE =  $0.14 \pm 0.04$  solitaires/ha,  $n=10$  transects) as mistletoe-free stands ( $0.06 \pm 0.02$  solitaires/ha,  $n=10$  transects; Mann-Whitney,  $U=24.5$ ,  $P=0.05$ , Fig. 3A). Salomonson and Balda (1977) estimated, based on captive birds, that each territorial solitaire consumes from 42,000 to 84,000 juniper berries per winter. Actual consumption is undoubtedly higher in the wild due to lower temperatures and higher activity levels. Mistletoe-infected stands also had 3-fold more avian frugivores of all species combined (mean  $\pm 1$ SE =  $0.42 \pm 0.18$  frugivores/ha,  $n=10$  transects) compared to mistletoe-free stands ( $0.14 \pm 0.09$ ,  $n=10$  transects; Mann-Whitney,  $U=16.0$ ,  $P=0.01$ , Fig. 3B). These data suggest that mistletoe-infected stands attract more avian seed dispersers than uninfected stands in "non-mast" years.

#### Juniper seedling recruitment

If mistletoes attract and support greater numbers of avian dispersal agents, then the presence of mistletoe might result in greater dispersal of juniper seeds. In agreement with this hypothesis, juniper seedling recruitment was more than 2-fold higher in mistletoe-infected stands



**Fig. 4.** Mistletoe-infected stands had greater than 2-fold more juniper seedlings than mistletoe-free stands. The mean ( $\pm 1$ SE) number of junipers per ha under 15 cm in height in each stand type is shown. Differences in means were considered significant at  $P \leq 0.05$

compared with mistletoe-free stands (mistletoe-infected stands, mean  $\pm 1$ SE =  $5.1 \pm 1.59$  seedlings/ha,  $n=10$  sites; mistletoe-free stands,  $2.1 \pm 1.11$  seedlings/ha,  $n=10$  sites; Mann-Whitney  $U=21.5$ ,  $P=0.03$ , Fig. 4).

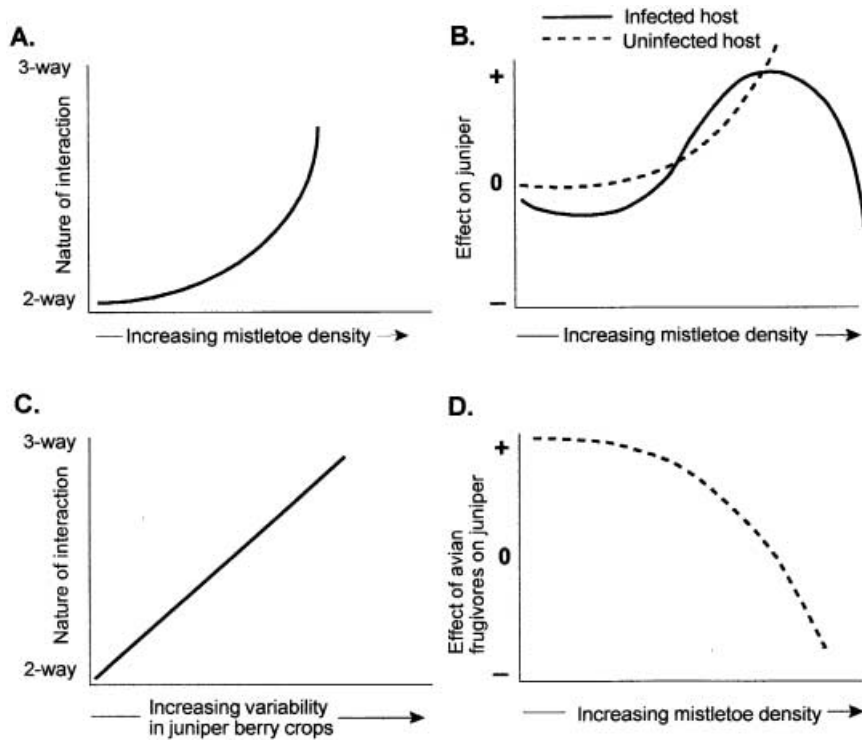
We rejected the alternative hypothesis that the above patterns might be due to differences in stand density between mistletoe-infected and mistletoe-free stands. The number of reproductive adult junipers in mistletoe-infected stands (mean  $\pm 1$ SE =  $110.6 \pm 17.25$  adult trees/ha,  $n=10$  sites) was very similar to that found in mistletoe-free stands ( $101.5 \pm 8.18$  adult trees/ha,  $n=10$  sites; Mann-Whitney  $U=48.5$ ,  $P=0.91$ ). Because these findings are based upon ten mistletoe-free and ten mistletoe-infected stands that are intermixed over 600 km<sup>2</sup>, the observed pattern is likely widespread.

An alternative hypothesis for higher numbers of juniper seedlings in mistletoe-infected stands is that the occurrence of mistletoe may be correlated with conditions favorable for juniper reproduction and seedling establishment, such as higher soil moisture. This factor was not investigated in detail, however, mistletoe-infected stands averaged 78 m higher in elevation (mean  $\pm 1$ SE =  $1,900.4 \pm 29.86$  m) than mistletoe-free stands (mean  $\pm 1$ SE =  $1,822.4 \pm 32.96$  m). This difference in elevation was not statistically significant (ANOVA,  $F=3.08$ ,  $P=0.10$ ). The potential effects that elevation, soil moisture, or other site factors had on juniper seedling establishment in the study area are not known.

## Discussion

### Three-way interaction

Greater numbers of juniper seedlings in mistletoe-infected stands confound traditional views on the outcome of this species interaction. A more than 2-fold higher number of seedlings in mistletoe-infected stands relative to mistletoe-free stands is consistent with our hypothesis



**Fig. 5A–D** The outcome of the interaction between both mistletoe and avian frugivores and their shared host plant is expected to vary with mistletoe density and annual variability in juniper berry crops. **A** At low mistletoe densities, avian frugivores interact primarily with junipers and the interaction is two-way. As mistletoe density increases at the individual and stand level, its importance as an alternative food or water resource increases and the interaction shifts to three-way. **B** Low stand mistletoe densities provide no indirect benefits to uninfected junipers and mainly negative physiological effects on infected individuals. Infected and uninfected hosts indirectly benefit at increasing stand mistletoe density. At exceedingly high mistletoe densities on individual hosts, negative physiological effects begin to outweigh indirect seed dispersal benefits. Uninfected or less infected junipers may still benefit. **C** Increased variability in juniper berry crops enhances the role of mistletoe as an alternative resource for avian frugivores, shifting the interaction from two-way to three-way. **D** The relationship between avian frugivores and juniper is mutualistic when the interaction is two-way or three-way, but becomes antagonistic at exceedingly high individual mistletoe densities when birds act as vectors for the continued spread of mistletoe

that the presence of mistletoe can attract seed-dispersing birds that enhance juniper dispersal and germination. Positive correlations between avian frugivore and mistletoe fruit abundance in both “mast” and “non-mast” years provide a mechanism that could account for these observations. Results suggest that, under some conditions, the negative effects of mistletoe on its juniper host may be moderated by indirect positive effects of enhanced host seed dispersal and germination.

#### Conditional outcomes

The roles of mistletoe and avian frugivores relative to their juniper host conceivably change under different, but not necessarily independent, sets of environmental

conditions. First, both the nature of the species interactions and the effects of mistletoe on its juniper host are likely to shift as a function of mistletoe density at the individual and stand level. At low mistletoe densities, avian frugivores interact primarily with junipers. As mistletoe density increases, its importance as an alternative food or water source also increases and the interaction shifts to three-way (Fig. 5A). Thus, at intermediate to high mistletoe densities, the alternative outcomes of the three-way interaction are important to consider.

Increasing mistletoe density at the stand level should affect infected juniper hosts differently than uninfected hosts (Fig. 5B). Several studies show that bird visitation and fruit removal are positively correlated with fruit crop size, both at the habitat level and the individual plant level (Murray 1987; Sargent 1990; but see Davidar and Morton 1986). Del Rio et al. (1996) found that avian seed dispersal of mistletoes was strongly dependent on the prevalence of mistletoe on individual plants. In this system, low stand mistletoe densities attract few avian dispersal agents and mistletoe has mainly negative physiological effects on infected individuals. As mistletoe densities rise to intermediate levels, infected trees may become more efficient foraging areas for avian frugivores, particularly in years when juniper berries are not abundant. Under these conditions, enhanced avian visitation resulting in potentially greater juniper seed dispersal could conceivably outweigh the negative impacts of the mistletoe to have a net positive impact on host tree dispersal and recruitment. As mistletoe density on an individual host juniper increases to higher levels, a point is probably reached where the negative physiological effects begin to outweigh possible seed dispersal benefits and the relationship reverts to antagonistic or parasitic.

A very different relationship is likely to exist for uninfected junipers in a stand of mistletoe-infected junipers. At low stand mistletoe densities, uninfected junipers gain no indirect benefits and suffer no costs by being associated with infected junipers. However, as mistletoe densities rise and avian dispersal agents increase visitation to the stand, uninfected junipers reap the benefits of increased avian visitation to the “neighborhood”. Sargent (1990) documented enhanced fruit removal from shrubs in neighborhoods of high fruit abundance.

As suggested above, variability in annual juniper berry crops is likely an important influence on the nature and outcome of the interaction between juniper and its associated mistletoe. If juniper berry production was relatively stable between years, the role of mistletoe as an alternative resource would be minimized and the interaction would be primarily two-way. Increased variability in juniper berry crops results in a pattern of “mast” years followed by longer intervals of “non-mast” years. Under these conditions, the importance of mistletoe to avian seed dispersers increases and a three-way interaction predominates (Fig. 5C).

Although we have considered avian frugivores to be mutualists of junipers, it is important to note that this relationship may also shift (Fig. 5D). When the interaction is primarily two-way (i.e., at low stand mistletoe density), avian frugivores are likely mutualists with their juniper hosts. These mutually beneficial effects may continue even as stand and individual mistletoe densities increase, if long-term juniper seed dispersal is enhanced. However, as exceedingly high densities of mistletoe accumulate at the individual and stand level, avian frugivores may begin to exert a negative influence on host trees by serving as vectors for the continued spread of mistletoe. Even within a stand at a particular point in time, it is conceivable that the relationship between birds, mistletoe, and their host plants varies between individual junipers with different levels of mistletoe infection.

#### Conditional outcomes in other systems

Although ecologists tend to emphasize pair-wise interactions for ease of study, in reality such simple systems are rare and exist in a sea of community-level interactions. The outcome of species interactions vary over spatial, temporal, and environmental gradients. Hochberg et al. (2000) suggested that environmental variation may create a geographical mosaic of outcomes, ranging from antagonistic to mutualistic. In a marine intertidal zone, Palumbi (1985) found that the impact of a coralline alga on a co-occurring sponge changed from positive to negative over a distance of just a few meters. He also showed a shift from commensalism to competition depending on the presence and interaction of a herbivorous chiton. Cushman and Whitham (1989) found that the strength and occurrence of a mutualism between ants and membracids varied between years and was dependent on both host age (life stage) and density. Gehring and

Whitham (1995) found that the effects of herbivory on mycorrhizal colonization of pinyon pines varied significantly between two adjacent soil types. In their review of the literature, Saikkonen et al (1998) found that endophyte–plant interactions can vary along a continuum from pathogenic to mutualistic within the lifetime of the endophyte and its host plant. Thompson (1988) suggested that the outcome of interactions between associated species varies with the age, size and genotype of both interacting individuals and their respective populations. In their review of mycorrhizal associations, Johnson et al. (1997) found that mutualistic interactions shifted to parasitic under conditions of high nutrient availability, low light, and high levels of above-ground herbivory. Similar effects between other interacting species has been documented in both marine (Glynn 1976; Dungan 1986) and terrestrial systems (Smith 1968; Davidson et al. 1984; Martinsen et al. 1998).

The outcome of the species interaction between one-seed juniper and its associated mistletoe is also likely to change over time and space and in response to varying environmental conditions. We have presented a simple model that predicts the outcome of the interaction between juniper and mistletoe based on mistletoe density and annual variability in juniper berry crops. However, other factors such as the age of host plants, infection levels on individual junipers, host density and age structure in populations, and edaphic and climatic conditions are also likely to affect outcomes. It is conceivable that a mosaic of outcomes from parasitic to mutualistic occurs at both the individual and stand levels. At any point in time, different individuals within a stand and geographically separated populations are likely to experience a range of costs versus benefits. Over time, the outcomes at both the individual and population level may change along a continuum from antagonistic to mutualistic, and back to antagonistic. This supports the notion that it may be more important to study the distribution of variation in a population, rather than the mean response or outcome (Thompson 1988). Although our results are tentative, we suggest that this classic plant-parasite system has more complex outcomes and is particularly suitable for further research and modeling of variation in species interactions.

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