

Arthropod community diversity and trophic structure: a comparison between extremes of plant stress

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Abstract. 1. Previous studies have shown that plant stress and plant vigour impact the preference and performance of many insect species. Global climate-change scenarios suggest that some regions such as continental interiors may become increasingly subject to severe drought. In combination, these two issues suggest that drought-driven plant stress may impact insect communities on a landscape scale. While there have been many population studies relating plant stress to the life history of individual herbivore species, far less is known about how plant stress affects entire communities.

2. To study the effect of plant stress on arthropod communities, arthropods were sampled from the canopies of pinyon pines (*Pinus edulis*) growing at sites with a history of chronically high environmental stress (e.g. lower water potentials, soil moisture, and reduced growth rates), and those growing under more favourable conditions. Sampling in these environments yielded >59 000 arthropods, representing 287 species from 14 orders and 80 families, and revealed three major community patterns.

3. First, chronic stress significantly altered community composition. Second, trees growing under high stress supported about 1/10th the number of arthropods, and roughly half the species as trees growing under more favourable conditions. Third, of the 33 abundant herbivore species that exhibited a significantly skewed distribution towards either high- or low-stress trees, 73% were skewed with higher numbers on low-stress trees.

4. The pattern of potentially reduced arthropod diversity and abundance on stressed pines observed in this study may further compound the loss of species resulting from the recent, landscape-scale drought-induced mortality of pines in the southwestern USA.

Key words. Arthropod community, climate change, community structure, diversity, pinyon pine, plant stress, plant vigour.

Introduction

The coming century is predicted to bring increased temperatures, as well as increased risk of more frequent and severe droughts, particularly in continental interiors (IPCC, Working Group I, 2001). As a landscape-scale disturbance, drought is of particular interest because of its capacity for producing rapid, long-lasting (Allen & Breshears, 1998), and large-scale shifts in

the distributions of dominant plants (Ogle *et al.*, 2000; Breshears *et al.*, 2005; Mueller *et al.*, 2005; Gitlin *et al.*, 2006; Parmesan, 2006), particularly in arid and semi-arid systems (Hanson & Weltzin, 2000). Because dominant woody species provide much of the habitat, structure, and resource base for the associated biota in woodland systems, stress agents that impact long-lived woody species will have cascading effects on the associated communities (Brown *et al.*, 2001) including microbial (Kuske *et al.*, 2003) and mycorrhizal mutualist (Swaty *et al.*, 2004) communities. While there have been numerous studies that examine the impact of plant stress on herbivore species (Waring & Cobb, 1992; Koricheva *et al.*, 1998), and feeding guilds

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(Inbar *et al.*, 2001), there has been little study of the impact of plant stress on arthropod communities including herbivores, predators, and parasites.

The spectrum of expected herbivore responses to plant stress spans two extremes, the plant stress and plant vigour hypotheses. Briefly summarised, the plant stress hypothesis (White, 1976, 1984) states that some herbivores will respond positively (increased survivorship/fecundity) to increased plant stress, and is based on the observation that in some plants as stress increases, available nitrogen increases, while plant defences are often negatively correlated with stress. Supportive evidence of these patterns has been shown in both natural (e.g. Whitham & Mopper, 1985) and agricultural systems (e.g. White, 1976, 1984). The other extreme is described by the plant vigour hypothesis (Price, 1991), which states that herbivores will exhibit increased performance (fecundity/survival) when feeding on rapidly growing plants or parts of plants, as vigorously growing plant tissues may have increased nutritional content (Inbar *et al.*, 2001), and/or less lignin, making the material easier to digest. Although there is a wealth of supportive observational and experimental data for both hypotheses (Waring & Cobb, 1992; Watt, 1994; Koricheva *et al.*, 1998), little is known about how naturally occurring communities of herbivores and their associated predators and parasites collectively respond to plant stress (but see Schowalter *et al.*, 1999).

Previously, these hypotheses have been compared at larger scales by tabulations (e.g. Waring & Cobb, 1992; Watt, 1994) or meta-analyses (e.g. Koricheva *et al.*, 1998) of the literature. While these do provide information on how many species respond to plant stress, compilations of species-level studies do not describe community-level responses, since the collection of species in the literature represents varied, typically un-associated herbivore species from disparate ecosystems. This study seeks specifically to examine the impact of soil-induced plant stress on a herbivore community, as well as the extended community of arthropod predators and parasitoids found in the canopy of pinyon pine (*Pinus edulis* Engelm.).

Pinus edulis is a dominant of the pinyon–juniper woodland, the third largest vegetation type in the continental USA (West, 1984). Because it is a dominant tree with a large biogeographic distribution, changes in stress experienced by this tree are likely to affect many species at large landscape scales. Using the diverse canopy arthropod community, including both rare and common species from multiple trophic levels, the effect of variation in plant stress was quantified in 178 trees, in which 90 grew in cinder soils characterised by high chronic stress, and 88 grew under more favourable growing conditions provided by a sandy–loam soil. Previous published works have documented the stress experienced by these trees, and so in the interest of brevity, more complete discussions of these conditions are left to previously published work (Whitham & Mopper, 1985; Cobb *et al.*, 1997; Gehring *et al.*, 1998; Swaty *et al.*, 1998; Brown *et al.*, 2001; Kuske *et al.*, 2003). Summarised briefly, long-term studies comparing these high- and low-stress environments have shown that trees growing at high-stress sites suffer greater water stress, grow more slowly, suffer higher rooting zone soil temperatures, and produce fewer cones (Table 1). This system was utilised to address three key hypotheses: (i) How does water and nutrient

Table 1. Multiple studies have documented the high stress conditions associated with the cinder soils of Sunset Crater, AZ, U.S.A. Cinder soils provide a chronic water stress environment.

Parameter	High stress (cinder soils)	Low stress (sandy-loam soils)
Soil temperature (°C)	17.2	13.8
Soil moisture (%)	5.61	9.39
Soil NO ₃ Min. (µg per g soil per day)	0.015	0.147
Soil phosphate (µg g ⁻¹)	4.45	12.20
Average cone production during masting event	20	50

Min., Mineralization.

Data from summary by Gehring *et al.* (1998), Swaty *et al.* (1998), Christensen and Whitham (1993), and Ogle *et al.* (2000).

stress relate to the abundance and richness of the canopy arthropod community supported by *P. edulis*? (ii) What impact does high plant stress have on community structure and composition? and (iii) How does plant stress impact the abundance and distributions of individual species of herbivores, predators, and parasites?

Because there is a paucity of studies assessing the community level response to plant stress, and because there are no general predictions about how the entire arthropod community (with the inclusion of predators and parasitoids) will respond to variation in plant stress, the expected community-level response in this system were modelled on the general findings of Waring and Cobb (1992). In their review, Waring and Cobb (1992) found that, for studies focused on conifers, >90% of the herbivores studied responded positively to increased plant stress, and previous studies with two of the most common insect herbivores in this system support these findings (e.g. Whitham & Mopper, 1985; Cobb *et al.*, 1997). However, it is important to note that the patterns produced by the literature survey of Waring and Cobb are general patterns in the literature, rather than generalised ecological patterns. Comparisons between the canopy arthropod community of the pinyon pine, and general patterns in the literature are used as a starting point for discussion rather than a strict operating hypothesis.

Methods

Site descriptions

Six sites for arthropod sampling were selected within the pinyon juniper woodlands of northern Arizona, across two soil types. The first soil type is located on cinder soils known to be deficient in water and nutrient availability (Table 1). These high-stress cinder soils are the result of a series of eruptions from Sunset Crater, which ended around AD 1260 (Krutch, 1974). The cinder and ash ejected by this eruption formed an island of hotter, drier abiotic conditions surrounded by a more benign environment (Whitham & Mopper, 1985; Gehring & Whitham, 1994; Cobb *et al.*, 1997; Gehring *et al.*, 1998; Swaty *et al.*, 1998; Brown *et al.*, 2001; Kuske *et al.*, 2003). The three high-stress sites, designated High A–C, range in elevation from 1798 to 1889 m, at ~35°09'N, 111°W. These sites have had limited anthropogenic disturbance

due to their proximity to a wilderness area, and do not have a known history of fire disturbance. The division of the trees into three separate sites was based on field logistics and stand size, rather than an attempt to capture within-soil inter-stand variation in community structure. The low-stress sites were located approximately 29 km from the high-stress sites, near Winona, Arizona. These sites, designated Low A–C, ranged in elevation from 1930 to 1940 m. Their disturbance regime is similar to that of the high-stress sites, based on the presence of tyre tracks, evidence of fuel wood harvesting, and other signs of anthropogenic impact.

Arthropod sampling

Within each of the three sites, 30 trees were haphazardly selected after controlling for canopy size. Canopy size was standardised to control for the proportion of the canopy sampled, as well as potential ontogenetic effects by the tree on the arthropod community (Kearsley & Whitham, 1989; Boege & Marquis, 2005). The arthropod community was sampled by placing a canvas sweep net over a pinyon branch, to the point that the end of the branch touched the end of the inside of the sweep net (net dimensions are 56 cm depth, 38 cm diameter opening, bottom 16 cm wide), and vigorously shaking the branch for 15 s. This was repeated for a total of 10 branches per tree. Branches were selected randomly by both height and direction within the canopy (canopies were typically about 3 m tall); the samples from each tree were pooled, placed in sealed plastic bags, and stored in a freezer.

Sampling was conducted from 12 to 18 May 1993 on the cinder soils, and from 23 to 31 May 1993 on the sandy-loam soils. The differences in collection periods reflect differences in the phenology of the trees. Trees growing on the warmer cinder soils are usually ~10 days ahead of those on sandy-loam soils. The longer sampling period in the sandy-loam soils reflects a delay of several days needed to allow the phenology of the last sites to coincide. To standardise the phenology among sites, the maturation of the male strobili was used as a metric.

Samples were later sorted by hand. Reference specimens of soft-bodied arthropods were placed in vials with 70% EtOH; hard-bodied arthropods were mounted. Individuals were identified to family and, while it was possible to identify some to genus and species, many were classified into morphospecies, as described by Wimp *et al.* (2005). Previous work (Oliver & Beattie, 1996; Siemann *et al.*, 1998) has shown that morphospecies classifications are acceptable for the description of the richness and composition of communities. The total collection included >59 000 arthropods, representing 14 orders, 80 families, and 287 species and morphospecies. Example specimens of all species and morphospecies (hereafter simply species for simplicity) have been archived with the Colorado Plateau Museum of Arthropod Biodiversity at Northern Arizona University, and are available for reference. A species list is provided in the Appendix.

Analyses

Sampling yielded measures of abundance for 287 species, from 178 trees, 90 in high stress soil, and 88 from low-stress

soil, respectively (two low-stress samples were lost to freezer-thaw). Comparisons of community compositions between high and low-stress soil types were made using non-metric multidimensional scaling ordination (NMDS). NMDS has shown itself to be a robust tool for analysis of arthropod communities (e.g. Dungey *et al.*, 2000; Wimp *et al.*, 2005), as it compares community composition based on both the presence and abundance of individual species. Statistical separation of communities was demonstrated using the analysis of similarity (ANOSIM), and the associated *R*-value. High *R*-values indicate very different groups; smaller *R*-values indicate more similar groups. Ordinations and ANOSIM analyses were conducted with the software package DECODA, courtesy of Peter Minchin (DECODA: Database for Ecological Community Data, version 3.00 beta supplied by Peter R. Minchin, Edwardsville, Illinois, U.S.A.). Within the NMDS and ANOSIM analyses, samples were separated by site as a *post hoc* analysis to determine the similarity of species composition among the apparently similar sites within a soil. Because of its *post hoc* nature, these comparisons are provided as a point for discussion, rather than a hypothesis test.

Distributions of richness and abundance values for each of the three feeding groups across the two soil types were checked for normality using a Kolmogorov–Smirnov test. Because herbivore, predator, and parasite abundances in sandy soils, and herbivore and parasite richness and abundances demonstrated distributions that deviated significantly from normal, sample distributions for the two stress levels were compared using the two-tailed Kolmogorov–Smirnov *Z* statistic. The same analysis was used for comparisons of herbivore:predator ratios between soil types.

To determine whether individual species responded positively or negatively to plant stress, abundances on all trees between stress types were compared using a two-tailed *t*-test. Those species with a significantly skewed distribution towards high or low stress in either direction were tabulated, and the total numbers of skewed species were then compared using the χ^2 statistic to determine whether a greater than expected portion of the overall community (number of species) responded positively or negatively to increased plant stress, assuming a random (even) distribution. Implicit in the assumption of a random distribution is the assumption that rare and common species are found with equal probability between the two soil types, an important point since a statistically significant soil bias might be more difficult to detect in rare species. To test this assumption, a threshold of 10 individuals was assigned, above which species were classified as abundant. The number of species in either pool (rare or abundant) was compared between the two soil types using a χ^2 statistic. Statistical significance was defined at the 0.05 level, and analyses were conducted using SPSS V14.

Results

Effect of stress on community composition, abundance, and richness

Pinyon pines growing in high- and low-stress conditions support different arthropod community compositions, as is shown

by the ordination in Fig. 1, where each point represents a tree, with the position of the point determined by the entire community on that tree ($n = 88$ low-stress and 90 high-stress trees). Table 2 provides the ANOSIM results for comparisons between soil types, and the *post hoc* comparison among the three sites within each soil type. Overall, the distribution of points demonstrates two key patterns. First, there is a strong divergence in community composition between trees growing on high- and low-stress sites, with no overlap in ordinal space between these two groups. Second, although samples (trees) growing within a stress level fall out very closely to each other, the three sites in each stress level (i.e. three high and three low-stress sites) were also significantly different (Table 2). This was unexpected as the sites were selected based on their proximity to each other, as well as their apparent similarity, and indicates undocumented heterogeneity that merits further study.

In addition to changes in the community composition, arthropod abundance was negatively associated with increased plant stress (Fig. 2a). Contrary to expectations based on population level studies in the literature (Waring & Cobb, 1992), total median arthropod abundance was nearly twice as high on low-stress trees than on high-stress trees (low-stress median arthropod abundance = 23 arthropods per tree, high-stress = 12 arthropods per tree, $P < 0.001$, Kolmogorov–Smirnov $Z = 3.776$). Furthermore, analyses for each trophic level shows the same pattern; on low-stress trees, median herbivore, predator, and parasitoid abundances were 12.7, 1.5, and 2.7 times greater, respectively, than on high-stress trees [Fig. 2a, Kolmogorov–Smirnov Z statistic for herbivore abundance = 5.628 ($P < 0.001$), predators = 1.786 ($P < 0.004$), parasites = 2.298 ($P < 0.001$)], suggesting a multi-trophic effect.

Similar to the observed patterns of abundance, median species richness on a per tree basis was nearly twice as high on low-stress trees as compared to high-stress trees (low-stress median richness = 10 species per tree, high-stress median

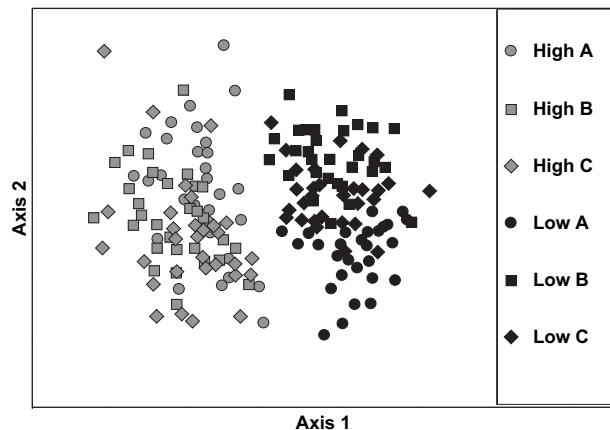


Fig. 1. Canopy arthropod community composition differs significantly between high- and low-stress sites. Black symbols represent high-stress sites, grey symbols represent low-stress sites. Note that there is no overlap in ordinal space between the groups. The ordination shown is based on abundance data in which abundance has been adjusted to unit maxima. The use of presence/absence data resulted in the same pattern.

richness = 6 species per tree, Kolmogorov–Smirnov $Z = 4.765$, $P < 0.001$). This pattern of increased species richness was again consistent across the three trophic levels, with low-stress trees supporting median herbivore, predator, and parasitoid richness of 1.7, 1.6, and 2 times that of high-stress trees, respectively [Fig. 2b, Kolmogorov–Smirnov Z statistic for herbivore richness = 4.354 ($P < 0.001$), predators = 3.423 ($P < 0.001$), parasites = 3.3 ($P < 0.001$)]. This pattern of increased richness across trophic levels suggests the differences in abundance are a function of multiple species and feeding groups, rather than a single hyper-abundant species or trophic level (e.g. a single highly common herbivore), and agrees with the separation in community composition shown in Fig. 1.

More predators and parasitoids in low-stress sites

While the patterns across each trophic level are the same, the magnitude of the differences are not. The disproportionate change in herbivore species abundances results in a large change in the herbivore:predator ratios across these stress levels. The median ratio of herbivores to predators among low-stress trees was 17.8:1 while in the high-stress sites the ratio dropped to 1.7:1 (Kolmogorov–Smirnov $Z = 5.675$, $P < 0.001$). This order-of-magnitude shift in ratios indicates a change not only in composition, but in the trophic structure in which predators may feed on other predators more often in these high-stress sites.

Negative effects of plant stress on both common and rare species

In contrast to the general patterns of population level studies in the literature that tend to emphasise very common or outbreak species (e.g. Waring & Cobb, 1992), these results show that of all the species sampled (both common and rare), 24% showed a statistically significant, negative response to plant stress, while only 7% responded positively. Of those species that responded significantly, 73, 74, and 92% of herbivore, predator and parasitoid species, respectively, responded negatively to plant stress (Fig. 3).

Comparing populations of both rare and common species suggests that both typically respond negatively to plant stress in the pinyon pine system (Fig. 4). These findings suggest that the general pattern of negative responses by species to increased stress [which stands in contrast to the general trends in the literature, see Waring and Cobb (1992)], are not driven by the inclusion of rare species, but instead represent a community-wide response. It is important to note, however, that disproportionately more common species respond significantly to variation in stress (in either direction), although this may be a statistical artefact stemming from the higher numbers of individuals associated with common species which facilitate the detection of statistical significance.

It is also important to note that even though nearly the same number of trees were sampled in high- and low-stress sites (i.e. 90 high-stress trees, and 88 low-stress trees) most of the individuals were found in the low-stress sites. Thus, many of the

Table 2. Separation among pairwise communities. Values are ANOSIM R ($P <$).

	High stress				
Low stress	0.6409 (0.0000)				
	High A	High B	High C	Low A	Low B
High B	0.1776 (0.0000)				
High C	0.1633 (0.0000)	0.0428 (0.0330)			
Low A	0.7679 (0.0000)	0.8102 (0.0000)	0.7166 (0.0000)		
Low B	0.6789 (0.0000)	0.7782 (0.0000)	0.7040 (0.0000)	0.4826 (0.0000)	
Low C	0.6532 (0.0000)	0.7592 (0.0000)	0.6995 (0.0000)	0.3186 (0.0000)	0.2184 (0.0000)

species found in the high-stress areas may not have been abundant enough to detect a statistically significant response to increased stress. To aid in addressing the issue of sampling effort, the numbers of species with restricted distributions, defined as a species that was observed within only one stress type, regardless of the total number of individuals observed, were compared. This analysis shows that of the total number of sampled herbivore species, nearly half (38 of 81 total herbivore species) were found in only one stress type. Of the 38 species with restricted distributions, 19 were unique to sandy-loam soils, and 19 were unique to cinder soils. This apparently balanced mix of species with shared and restricted distributions suggests that while spe-

cies richness may be biased towards low-stress trees, biodiversity at the stand or landscape scales are maximised with the inclusion of some high-stress trees. Current studies exploring landscape heterogeneity and landscape-scale biodiversity in this system are in progress, and will follow this work.

Although half (48 of 81) of the herbivore species sampled did not show a preference (as indicated by statistical differences in mean abundance) for a stress level, it is not yet possible to compare these findings with the general patterns of the literature. Because most publications focus on species that respond significantly to stress or manipulation, non-significant findings may not be commonly published. This lack of information for comparison illustrates the need to study community-level as well species-specific patterns of plant use, as it is only at this level that such patterns may be discernible.

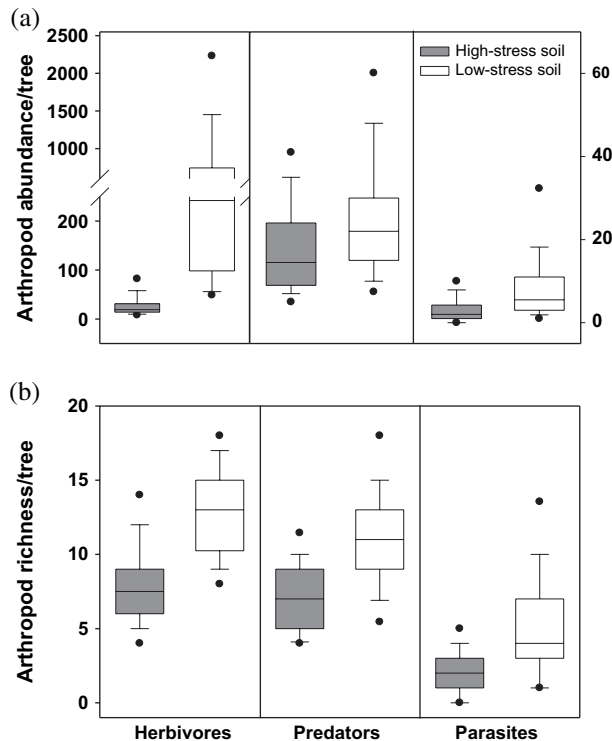


Fig. 2. (a) High-stress soils supported fewer individual canopy arthropods in all three trophic levels. (b) Median per-tree species richness (α diversity) is higher in low-stress trees. Box ends represent the first, second, and third quartiles, whiskers represent two-thirds interquartile range, circles represent 5th and 95th percentiles.

Discussion

Major patterns and implications

This study of the arthropod communities found on pinyon pine in northern Arizona revealed three major patterns. First, increased plant stress greatly reduced the abundance of herbivores, predators, and parasitoids found on pinyon pines. These findings are in contrast to expectations based on the general literature. Although the literature survey by Waring and Cobb (1992) found that $>90\%$ of the studied herbivores in conifer systems had a strong positive response to pine stress, pinyon growing under low-stress conditions supported median abundances of herbivores, predators, and parasites that were 12.7, 1.5, and 2.7 times higher, respectively, than those growing under less favourable conditions.

Second, mean species richness on a per-tree level was negatively associated with high-stress conditions. Trees growing in more favourable conditions supported twice the median number of species as their high-stress counterparts. Of the 33 herbivore species with a significant bias towards either high or low stress, 73% were numerically biased towards low stress, with predators and parasitoids behaving similarly. These patterns among and within species indicate that the loss of herbivore diversity as a function of plant stress may facilitate the loss of predator and parasitoid diversity, thus, as the herbivores go, so will the rest of the community. However, the predator diversity may compensate to some degree through an increase in predator–predator

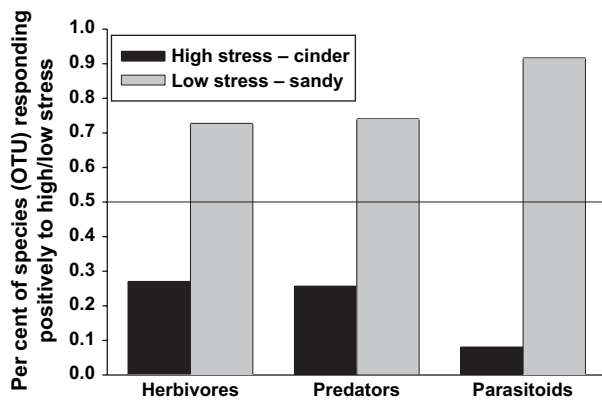


Fig. 3. Of those species that respond significantly to stress, most respond negatively to increased stress (24/33 herbivores, $\chi^2=6.818$, $P<0.009$, 20/27 predators, $\chi^2=6.259$, $P<0.012$, 22/24 parasitoids, $\chi^2=16.667$, $P<0.001$ responded negatively to increased stress), as shown by the figure. If responses to stress were randomly distributed, frequency of responses to stress would be equally distributed between positive and negative (i.e. at the 50% line). OTU refers to use of 'Observational Taxonomic Unit' or Morphospecies.

feeding, as indicated by the change in herbivore : predator ratios between the two environments.

The third major pattern revealed by these data is that stress changes the composition of the arthropod community, as shown by the ordination in Fig. 1. Although increased stress results in the loss of abundance and richness, high-stress sites were not composed of a sub-set of low-stress arthropod species. Because many species appear to have a high fidelity to high or low stress, as indicated by the number of species with restricted distributions, maximum landscape arthropod diversity is supported by a

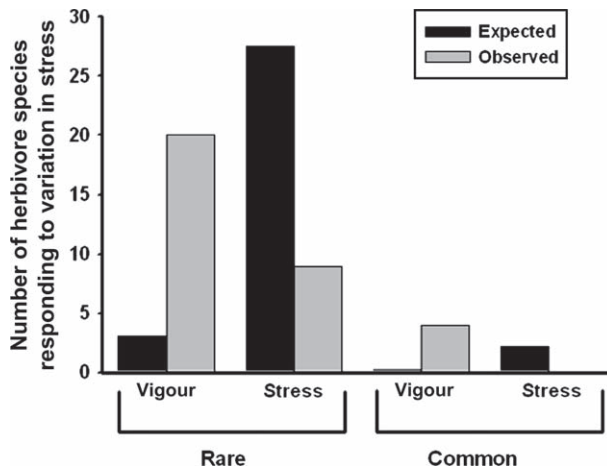


Fig. 4. Across both common and rare species, these results stand in contrast to the general findings of the literature. Although one of the primary differences between this study and the general findings of the literature is the inclusion of less common and rare species, the differences between these results and the general literature is not a function of the inclusion of these species. Both rare and common species appear to exhibit the same pattern in the pinyon system.

heterogeneous landscape. Work is currently under way to examine the scaling relationships between habitat heterogeneity, landscape size, and biodiversity (i.e. patterns of species accumulation) in this pinyon pine system.

Alternative hypotheses

Although the data support plant stress as the factor driving the separation of the arthropod communities, it is possible that differences in community composition between soil types are driven by other undocumented processes. Three lines of evidence, however, support the indication that water and nutrient stress is the driving mechanism.

First, previous studies have shown a strong link between the water stress associated with the cinder soils, and a response by the herbivores and trees. For example, when pinyon pines growing in cinder soils, which were chronically attacked by stem-boring moths (*Dioryctria albovitella*), were experimentally released from stress with supplemental water and nutrients, resin defences increased, tree growth rates increased, and moth attack declined (Cobb *et al.*, 1997). Experimental watering of drought-stressed juvenile pinyon pines by Scudder (2005) has shown that reduced water stress on individual trees within a site significantly altered arthropod abundance, richness, and community composition in patterns similar to those shown here. Experimental studies such as this offer the opportunity to separate direct and indirect impacts of drought-induced plant stress on the associated herbivore community as discussed by Watt (1994), and further the assessment of the plant stress hypothesis (White, 1984). Finally, previous work has shown that variation in pinyon stress within a site results in quantifiable impacts on tree condition, as measured by water potentials, trunk growth, and per cent dead branches (Swaty *et al.*, 2004). These three data sets support the implication that water and drought stress drive the observed changes in arthropod community composition between mesic sandy-loam soils, and more xeric cinder soils.

Second, the ordination shown in Fig. 1 suggests there are different mechanisms driving the separations among sites within soils, and sites between soils. As previously mentioned, the separation of sites was based on field logistics and the need to find trees of the appropriate size, growing in apparently similar conditions, yet *post hoc* analyses of sites within soils (Fig. 1 and Table 2) show that each site had a distinct community composition. One explanatory variable that might be correlated (although not directly causative) to these differences is distance, such that sites within soils would be expected to be more similar to each other due to their proximity, rather than their shared low-stress plants. However, as the figure shows, sites within soils (heterogeneity driven by distance) separate along a top-to-bottom gradient, while sites between soils (heterogeneity driven by soil type) separate along a right-to-left gradient. The differences in directions of these gradients within the ordination suggest the factors that drive separation between sites, and separation between soils are orthogonal, although further work is needed to identify the mechanisms driving these patterns.

Contrasts with other communities

One of the assets of this study is the ability to compare the response of the arthropod community with that of other communities in the same system. Microbial communities at the same study sites, for example exhibit a pattern similar to what was found among the arthropods. Kuske *et al.* (2003) found that population densities of heterotrophic bacteria were 10 times higher in open spaces between trees of low-stress sites than the open areas at high-stress sites. This decrease in microbial activity was closely related to the reduction of organic material at high-stress sites.

In contrast to the arthropod and microbial communities however, Gehring *et al.* (1998) found an almost twofold increase in ectomycorrhizal colonisation on pinyon pines in high-stress sites. These findings support the hypothesis that stressed plants may invest more into their mycorrhizal mutualists to enhance water and mineral uptake when those resources are scarce. However, work by Swaty *et al.* (2004) has shown that when stress levels became very high, mycorrhizal communities decline, suggesting that the trees were no longer able to maintain these important mutualists, or that the mutualism had become parasitism. Thus, community responses to stress can be very different depending upon the ecological roles played by associated species, as well as the relative position of a system along a stress gradient.

Although these studies show that there may be variation in the direction of the response of a community to abiotic stress, each of these share two common threads. First, that changes in stress level within a system alters the community composition, and second, that the maximum overall diversity is provided by a mosaic of high- and low-stress conditions. Further work is needed to quantify the relationship between habitat heterogeneity and biodiversity both within this pinyon pine system and elsewhere.

The stress gradient as an analogue for climate change

As broad-scale changes in the global climate occur, the spatial distribution of the optimal conditions for plant species will shift. Betancourt *et al.* (1991) have shown that the distribution of pinyon pine (*Pinus* spp.) has shifted northward dramatically within the last 12 000 years, and Lyford *et al.* (2003) have shown that spatial shifts in Utah juniper populations (*Juniperus osteosperma*) have often been temporally punctuated and spatially disjunct. Although these studies assessed large-scale changes in the biogeographic distributions of a species (up to 135 km), these analyses focused on the expansion of a species into new suitable habitat. Within the context of anthropogenic climate change, it is expected that the spatial arrangement of climatic conditions will shift rapidly, at decadal rather than millennial timescales. The magnitude of these shifts has been suggested using a number of tools such as MAPSS (Mapped Atmosphere–Plant–Soil–System; Neilson, 1995; VEMAP, 1995; Bachelet, 2001), that suggest that climate change will result in large-scale changes in the spatial distribution of climate parameters associated with specific plant communities (Bachelet, 2001), and

major shifts in the distributions of dominant plants, including pinyon pine in the American West (Rehfeldt *et al.*, 2006). As the location of ideal climatic conditions moves, leaving the plant populations behind, the proportions of populations that are growing under unsuitable conditions should increase, particularly when those species are long-lived and have low vagility. Some of these changes have already been observed as large-scale tree mortality events in ponderosa and pinyon pine systems in the southwestern USA (Allen & Breshears, 1998; Ogle *et al.*, 2000; Breshears *et al.*, 2005; Mueller *et al.*, 2005). These changes on the landscape highlight the need for analogues for climate change such as this soil-stress gradient (Brown *et al.*, 2001). By taking advantage of such systems, the expected impact of climate change on entire communities can be more reasonably estimated.

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References

- Allen, C.D. & Breshears, D.D. (1998) Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 14839–14842.
- Bachelet, D., Neilson, R.P., Lenihan, J.M. & Drapek, R.J. (2001) Climate change effects on vegetation distribution and carbon budget in the United States. *Ecosystems*, **4**, 164–185.
- Betancourt, J.L., Schuster, W.S., Mitton, J.B. & Anderson, R.S. (1991) Fossil and genetic history of a pinyon pine (*Pinus edulis*) isolate. *Ecology*, **72**, 1685–1697.
- Boege, K. & Marquis, R.J. (2005) Racing herbivory as you grow up: the ontogeny of resistance in plants. *Trends in Ecology and Evolution*, **20**, 441–448.
- Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G. *et al.* (2005) Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 15144–15148.
- Brown, J.H., Whitham, T.G., Ernest, S.K.M. & Gehring, C.A. (2001) Complex species interactions and the dynamics of ecological systems: long-term experiments. *Science*, **293**, 643–650.
- Christensen, K.M. & Whitham, T.G. (1993) Impacts of insect herbivores on competition between birds and mammals for pinyon pine seeds. *Ecology*, **74**, 2270–2278.
- Cobb, N.S., Mopper, S., Gehring, C.A., Caouette, M., Christensen, K.M. & Whitham, T.G. (1997) Increased moth herbivory associated with environmental stress of pinyon pine at local and regional levels. *Oecologia*, **109**, 389–397.
- Dungey, H.S., Potts, B.M., Whitham, T.G. & Li, H.F. (2000) Plant genetics affects arthropod community richness and composition: evidence from a synthetic eucalypt hybrid population. *Evolution*, **54**, 1939–1946.

- Gehring, C.A., Theimer, T.C., Whitham, T.G. & Keim, P. (1998) Ectomycorrhizal fungal community structure of pinyon pines growing in two environmental extremes. *Ecology*, **79**, 1562–1572.
- Gehring, C.A. & Whitham, T.G. (1994) Comparisons of ectomycorrhiza on pinyon pines (*Pinus edulis*; Pinaceae) across extremes of soil type and herbivory. *American Journal of Botany*, **81**, 1509–1516.
- Gitlin, A.R., Stihultz, C.M., Bowker, M.A., Stumpf, S., Paxton, K.L., Kennedy, K. *et al.* (2006) Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conservation Biology*, **20**, 1477–1486.
- Hanson, P.J. & Weltzin, J.F. (2000) Drought disturbance from climate change: response of United States forests. *Science of the Total Environment*, **262**, 205–220.
- Inbar, M., Doostdar, H. & Mayer, R.T. (2001) Suitability of stressed and vigorous plants to various insect herbivores. *Oikos*, **94**, 228–235.
- IPCC, Working Group 1 (2001) *Climate Change 2001: The Scientific Basis. United Nations Intergovernmental Panel on Climate Change* [WWW document]. URL <http://www.ipcc.ch/pub/reports.htm>. [Accessed March 2006].
- Kearsley, M.J.C. & Whitham, T.G. (1989) Developmental changes in resistance to herbivory: implications for individuals and populations. *Ecology*, **70**, 422–434.
- Koricheva, J., Larsson, S. & Haukioja, E. (1998) Insect performance on experimentally stressed woody plants: a meta-analysis. *Annual Review of Entomology*, **43**, 195–216.
- Krutch, J.W. (1974) *The Paradox of a Lava Flow*. Southwest Parks and Monuments Association, Phoenix, Arizona.
- Kuske, C.R., Busch, J.D., Ticknor, L.O., Gehring, C.A. & Whitham, T.G. (2003) The pinyon rhizosphere, plant stress, and herbivory affect the abundance of microbial decomposers in soils. *Microbial Ecology*, **45**, 340–352.
- Lyford, M.E., Jackson, S.T., Betancourt, J.L. & Gray, S. (2003) Influence of landscape structure and climate variability in a late Holocene natural invasion. *Ecological Monographs*, **73**, 567–583.
- Mueller, R.C., Scudder, C.M., Porter, M.E., Trotter, R.T., Gehring, C.A. & Whitham, T.G. (2005) Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *Journal of Ecology*, **93**, 1085–1093.
- Neilson, R.P. (1995) A model for predicting continental-scale vegetation distribution and water balance. *Ecological Applications*, **5**, 362–385.
- Ogle, K., Whitham, T.G. & Cobb, N.S. (2000) Tree-ring variation in pinyon predicts likelihood of death following severe drought. *Ecology*, **81**, 3237–3243.
- Oliver, I. & Beattie, A.J. (1996) Invertebrate morphospecies as a surrogate for species: a case study. *Conservation Biology*, **10**, 99–109.
- Parnesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.
- Price, P.W. (1991) The plant vigor hypothesis and herbivore attack. *Oikos*, **62**, 244–251.
- Rehfeldt, G.E., Crookston, N.L., Warwell, M.V. & Evans, J.S. (2006) Empirical analyses of plant–climate relationships for the western United States. *International Journal of Plant Science*, **167**, 1123–1150.
- Schowalter, T.D., Lightfoot, D.C. & Whitford, W.G. (1999) Diversity of arthropod responses to host-plant water stress in a desert ecosystem in southern New Mexico. *American Midland Naturalist*, **142**, 281–290.
- Scudder, C.M. (2005) *Negative impacts of drought on arthropods: community-level consequences of climate change*. MSc thesis, Thomas G. Whitham (chair), Northern Arizona University, Arizona.
- Siemann, E., Tilman, D., Haarstad, J. & Ritchie, M. (1998) Experimental test of the dependence of arthropod diversity on plant diversity. *American Naturalist*, **152**, 738–750.
- Swaty, R.L., Deckert, R.J., Whitham, T.G. & Gehring, C.A. (2004) Ectomycorrhizal abundance and community composition shifts with drought: predictions from tree rings. *Ecology*, **85**, 1072–1084.
- Swaty, R.L., Gehring, C.A., Van Ert, M., Theimer, T.C., Keim, P. & Whitham, T.G. (1998) Temporal variation in temperature and rainfall predicts ectomycorrhizal colonization and fungal community structure at two sites varying in soil nutrients and moisture. *New Phytologist*, **139**, 733–739.
- VEMAP (Vegetation/Ecosystem Modeling and Analysis Project) (1995) Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO₂ doubling. *Global Biogeochemical Cycles*, **9**, 407–437.
- Waring, G.L. & Cobb, N.S. (1992) The impact of plant stress on herbivore population dynamics. *Plant–Insect Interactions* (ed. by E. A. Bernays), Vol. 4, pp. 167–226. CRC Press, Boca Raton, Florida.
- Watt, A.D. (1994) The relevance of the stress hypothesis to insects feeding on tree foliage. *Individuals, Populations and Patterns in Ecology* (ed. by S. R. Leather, A. D. Watt, N. J. Mills and K. F. A. Walters), pp. 73–85. Intercept Limited, Andover, U.K.
- West, N. (1984) Successional patterns and productivity potentials of pinyon-juniper ecosystems. *Developing Strategies for Range Management: A report prepared by The Committee on Developing Strategies on Rangeland Management (National Research Council and The National Academy of Sciences)*, pp. 1301–1332. Westview, Boulder, Colorado.
- White, T.C.R. (1976) Weather, food, and plagues of locusts. *Oecologia*, **22**, 119–134.
- White, T.C.R. (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia*, **63**, 90–105.
- Whitham, T.G. & Mopper, S. (1985) Chronic herbivory: impacts on architecture and sex expression of pinyon pine. *Science*, **229**, 1089–1091.
- Wimp, G.M., Martinsen, G.D., Floate, K.D., Bangert, R.K. & Whitham, T.G. (2005) Plant genetic determinants of arthropod community structure and diversity. *Evolution*, **59**, 61–69.

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Appendix 1. Species list.

Order	Family	Species
Acari	Oribatulidae	<i>Eporibatula</i> sp. 1
Acari	Oribatulidae	<i>Eporibatula</i> sp. 2
Acari	Oribatulidae	<i>Eporibatula</i> sp. 3
Acari		Parasitic sp. 1
Opiliones		Opilionid sp. 1
Araneida	Salticidae	<i>Eris</i> sp. 1
Araneida	Salticidae	<i>Eris</i> sp. 2
Araneida	Salticidae	<i>Sassacus</i> sp. 1
Araneida	Salticidae	<i>Pellenes</i> sp. 1
Araneida	Salticidae	<i>Agassa</i> sp. 1
Araneida	Salticidae	<i>Sarinda</i> sp. 1
Araneida	Salticidae	<i>Metacyrba?</i> sp. 1
Araneida	Salticidae	<i>Peckhamia</i> sp. 1
Araneida	Theridiidae	<i>Enoplagnatha</i> sp. 1
Araneida	Theridiidae	<i>Achaeranea</i> sp. 1
Araneida	Theridiidae	<i>Euryopsis</i> sp. 1
Araneida	Theridiidae	<i>Theridion</i> sp. 2
Araneida	Theridiidae	Theridiid sp. 1
Araneida	Theridiidae	Theridiid sp. 2
Araneida	Philodromidae	<i>Philodromus</i> sp.
Araneida	Philodromidae	<i>Tmarus</i> sp. 1
Araneida	Thomisidae	<i>Misumena vatia</i>
Araneida	Thomisidae	<i>Misumenops</i> sp.
Araneida	Thomisidae	<i>Xysticus</i> sp.
Araneida	Dictynidae	<i>Mallos</i> spp.
Araneida	Clubionidae	Clubionid sp.
Araneida	Oxyopidae	<i>Oxyopes</i> sp. 1
Araneida	Anyphaenidae	Anyphaenid sp. 1
Araneida	Araneidae	<i>Araneus</i> sp. 1
Araneida	Araneidae	Spider sp. 1
Collembola	Sminthuridae	Sminthurid sp.
Thysanoptera	Thripidae	Thripid sp.
Thysanoptera	Phlaeothripidae	Phlaeothripid sp.
Orthoptera	Tettigoniidae	<i>Eremopedes</i> sp. 1
Pscoptera		<i>Pscoptera</i> sp. 1
Homoptera	Aphidae	<i>Essigella</i> sp. 1
Homoptera	Aphidae	<i>Cinara</i> spp.
Homoptera	Cicadellidae	Spotted small
Homoptera	Cicadellidae	Spotted large
Homoptera	Cicadellidae	Juniper leafhopper
Homoptera	Cicadellidae	<i>Cuerna obtusa</i>
Homoptera	Cicadellidae	Green leafhopper
Homoptera	Cicadellidae	Sharpshooter
Homoptera	Cicadellidae	Cicadellid spp.
Homoptera	Membradidae	Juniper membracid
Homoptera	Achilidae	Achilid sp. 1
Homoptera	Cixiidae	Cixiid sp. 1
Homoptera	Issidae	<i>Picumma</i> sp. 1
Homoptera	Delphacidae	Delphacid sp. 1
Homoptera	Delphacidae	R & W psyllid
Homoptera	Delphacidae	B & W psyllid
Homoptera	Delphacidae	Juniper Psyllidae
Hemiptera	Miridae	<i>Deraeocoris</i> sp. 1
Hemiptera	Miridae	<i>Atractotomus</i> sp. 1
Hemiptera	Miridae	<i>Pilophorus</i> sp. 1
Hemiptera	Miridae	Juniper mirid sp. 1
Hemiptera	Miridae	Juniper mirid sp. 2
Hemiptera	Miridae	<i>Ceratocapsus</i> sp. 1
Hemiptera	Miridae	<i>Psallus</i> nymphs
Hemiptera	Miridae	<i>Psallus</i> sp. 1

Appendix 1. Continued.

Order	Family	Species
Hemiptera	Miridae	<i>Psallus</i> sp. 2
Hemiptera	Miridae	<i>Chlamydatius</i> sp. 1
Hemiptera	Miridae	<i>Phytocoris</i> spp.
Hemiptera	Miridae	<i>Lygus</i> sp. 1
Hemiptera	Miridae	<i>Lygus</i> sp. 2
Hemiptera	Miridae	<i>Lopidea</i> sp. 1
Hemiptera	Miridae	<i>Stenodema</i> sp. 1
Hemiptera	Miridae	<i>Prepops</i> sp. 1
Hemiptera	Nabidae	<i>Nabis</i> sp. 1
Hemiptera	Anthocoridae	<i>Orius</i> sp. 1
Hemiptera	Lygaeidae	<i>Cymodema</i> sp. 1
Hemiptera	Lygaeidae	<i>Melanopleurus</i> sp. 1
Hemiptera	Lygaeidae	<i>Nysius</i> sp. 1
Hemiptera	Lygaeidae	<i>Nysius</i> sp. 2
Hemiptera	Rhopalidae	<i>Arhyssus</i> sp. 1
Hemiptera	Rhopalidae	<i>Harmostes</i> sp. 1
Hemiptera	Rhopalidae	<i>Stictopleurus</i> sp. 1
Hemiptera	Rhopalidae	<i>Leptocoris</i> sp. 1
Hemiptera	Pentatomidae	<i>Thyanta</i> sp. 1
Hemiptera	Pentatomidae	<i>Dendrocoris</i> sp. 1
Hemiptera	Pentatomidae	<i>Rhytidilomyia</i> sp. 1
Hemiptera	Pentatomidae	<i>Mormidea?</i> sp. 1
Hemiptera	Berytidae	<i>Neides</i> sp. 1
Hemiptera	Alydidae	<i>Alydus</i> sp. 1
Hemiptera	Coreidae	<i>Leptoglossus</i> sp. 1
Hemiptera	Reduviidae	<i>Zelus socias</i>
Hemiptera	Tingidae	Tingid sp. 1
Neuroptera	Chrysopidae	Chrysopid larva
Neuroptera	Chrysopidae	<i>Chrysopa</i> sp. 1
Neuroptera	Chrysopidae	<i>Eremochrysa</i> sp. 1
Neuroptera	Hemerobiidae	Hemerobiid larva
Neuroptera	Hemerobiidae	<i>Hemerobius</i> sp. 1
Neuroptera	Hemerobiidae	<i>Micromus</i> sp. 1
Neuroptera	Hemerobiidae	<i>Symphorobius</i> sp. 1
Neuroptera	Hemerobiidae	<i>Symphorobius</i> sp. 2
Neuroptera	Raphidiidae	Raphidiid sp. 1
Neuroptera	Coniopterygidae	Coniopterygid sp. 1
Coleoptera	Coccinellidae	<i>Scymnus</i> adults sp. 1
Coleoptera	Coccinellidae	<i>Scymnus</i> sp. 2
Coleoptera	Coccinellidae	<i>Hyperaspis</i> sp. 1
Coleoptera	Coccinellidae	<i>Hippodamia</i> L&A
Coleoptera	Coccinellidae	<i>Mulsantina picta</i>
Coleoptera	Coccinellidae	<i>Myzia interrupta</i>
Coleoptera	Melyridae	<i>Amecocerus</i> sp. 1
Coleoptera	Melyridae	<i>Attalus</i> sp. 1
Coleoptera	Chrysomelidae	<i>Alticina</i> sp. 1
Coleoptera	Chrysomelidae	<i>Chaetocnema</i> sp. 1
Coleoptera	Chrysomelidae	<i>Alticina</i> sp. 3
Coleoptera	Chrysomelidae	<i>Pachybrachus</i> sp. 1
Coleoptera	Chrysomelidae	<i>Pachybrachus</i> sp. 2
Coleoptera	Chrysomelidae	<i>Paria</i> sp. 1
Coleoptera	Chrysomelidae	<i>Saxinus</i> sp. 1
Coleoptera	Cleridae	<i>Enoclerus moestus</i>
Coleoptera	Cleridae	<i>Phyllobaenus</i> sp. 1
Coleoptera	Phalacridae	Phalacrid sp. 1
Coleoptera	Phalacridae	Phalacrid sp. 2
Coleoptera	Curculionidae	<i>Lixus?</i> sp. 1
Coleoptera	Curculionidae	<i>Brachyrhininae?</i> sp. 1
Coleoptera	Curculionidae	<i>Pissodes</i> sp. 1
Coleoptera	Curculionidae	Curculionid sp. 1

Appendix 1. Continued.

Order	Family	Species
Coleoptera	Curculionidae	Curculionid sp. 2
Coleoptera	Alleculidae	<i>Hymenorus?</i> sp. 1
Coleoptera	Scolytidae	Scolytid sp. 1
Coleoptera	Histeridae	Histerid sp. 1
Coleoptera	Staphylinidae	Staphylinid sp. 1
Coleoptera	Anthicidae	<i>Notoxus</i> sp. 1
Coleoptera	Meloidae	<i>Epicauta</i> sp. 1
Coleoptera	Buprestidae	Buprestid sp. 1
Coleoptera	Buprestidae	Buprestid sp. 2
Coleoptera	Mordellidae	Mordellid sp. 1
Coleoptera		Coleoptera sp. 1
Coleoptera		Yellow-brown adult
Diptera	Tephritidae	Tephritid sp. 1
Diptera		Flies
Diptera	Syrphidae	Syrphid larva
Lepidoptera	Gelechiidae	Gelechiid sp. 1
Lepidoptera	Gelechiidae	Gelechiid sp. 2
Lepidoptera	Noctuidae	Noctuid sp. 1
Lepidoptera	Noctuidae	Noctuid sp. 2
Lepidoptera	Geometridae	Geometrid sp. 1
Lepidoptera		Lep sp. 1
Lepidoptera		Lep sp. 2
Lepidoptera		Lep sp. 3
Lepidoptera		Lep sp. 4
Lepidoptera		Lep sp. 5
Lepidoptera		Lep sp. 6
Lepidoptera		Lep sp. 7
Lepidoptera		Lep sp. 8
Lepidoptera		Microlep adults
Hymenoptera	Diprionidae	<i>Neodiprion edulicolis</i>
Hymenoptera	Pamphiliidae	Pamphiliid sp. 1
Hymenoptera	Tenthredinidae	Tenthredinid sp. 1
Hymenoptera	Formicidae	<i>Liometopum luctuosum</i>
Hymenoptera	Formicidae	<i>Dorymyrmex paiute</i>
Hymenoptera	Formicidae	<i>Formica neorufibarbis</i>
Hymenoptera	Formicidae	<i>Myrmecocystus mendax</i>
Hymenoptera	Formicidae	<i>Crematogaster navajoa</i>
Hymenoptera	Formicidae	<i>Crematogaster emeryana</i>
Hymenoptera	Formicidae	<i>Monomorium cyaneum</i>
Hymenoptera	Formicidae	<i>Camponotus vicinus</i>
Hymenoptera	Braconidae	Braconid spp.
Hymenoptera	Braconidae	Braconid sp. 1
Hymenoptera	Braconidae	Braconid sp. 2 aphid
Hymenoptera	Braconidae	Braconid sp. 4
Hymenoptera	Braconidae	Braconid sp. 5
Hymenoptera	Braconidae	Braconid sp. 6
Hymenoptera	Braconidae	Braconid sp. 7
Hymenoptera	Braconidae	Braconid sp. 8
Hymenoptera	Braconidae	Braconid sp. 10
Hymenoptera	Braconidae	Braconid sp. 11
Hymenoptera	Braconidae	Braconid sp. 12
Hymenoptera	Braconidae	Braconid sp. 13
Hymenoptera	Braconidae	Braconid sp. 14
Hymenoptera	Braconidae	Braconid sp. 15
Hymenoptera	Braconidae	Braconid sp. 17
Hymenoptera	Braconidae	Braconid sp. 19
Hymenoptera	Braconidae	Braconid sp. 20
Hymenoptera	Braconidae	Braconid sp. 21
Hymenoptera	Braconidae	Braconid sp. 22
Hymenoptera	Braconidae	Diapriid sp. 2 aphidiid

Appendix 1. Continued.

Order	Family	Species
Hymenoptera	Braconidae	Dryinid sp. 1 braconid
Hymenoptera	Braconidae	Dryinid sp. 3 braconid
Hymenoptera	Ichneumonidae	Ichneumonid sp. 1
Hymenoptera	Ichneumonidae	Ichneumonid sp. 2
Hymenoptera	Ichneumonidae	Ichneumonid sp. 3
Hymenoptera	Ichneumonidae	Ichneumonid sp. 4
Hymenoptera	Ichneumonidae	Braconid sp. 3 – ichneumonid
Hymenoptera	Torymidae	Torymid sp. 1
Hymenoptera	Torymidae	Torymid sp. 2
Hymenoptera	Torymidae	Torymid sp. 3
Hymenoptera	Torymidae	Torymid sp. 4
Hymenoptera	Torymidae	Torymid sp. 5
Hymenoptera	Torymidae	Torymid sp. 6
Hymenoptera	Torymidae	Torymid sp. 7
Hymenoptera	Pteromalidae	Pteromalid sp. 1
Hymenoptera	Pteromalidae	Pteromalid sp. 2
Hymenoptera	Pteromalidae	Pteromalid sp. 3
Hymenoptera	Pteromalidae	Pteromalid sp. 4
Hymenoptera	Pteromalidae	Pteromalid sp. 5
Hymenoptera	Pteromalidae	Pteromalid sp. 6
Hymenoptera	Pteromalidae	Pteromalid sp. 7
Hymenoptera	Pteromalidae	Pteromalid sp. 8
Hymenoptera	Pteromalidae	Pteromalid sp. 9
Hymenoptera	Pteromalidae	Pteromalid sp. 10
Hymenoptera	Pteromalidae	Pteromalid sp. 11
Hymenoptera	Pteromalidae	Pteromalid sp. 12
Hymenoptera	Pteromalidae	Pteromalid sp. 13
Hymenoptera	Pteromalidae	Pteromalid sp. 14
Hymenoptera	Pteromalidae	Pteromalid sp. 15
Hymenoptera	Pteromalidae	Pteromalid sp. 16
Hymenoptera	Pteromalidae	Pteromalid sp. 17
Hymenoptera	Pteromalidae	Pteromalid sp. 18
Hymenoptera	Pteromalidae	Pteromalid sp. 19
Hymenoptera	Pteromalidae	Pteromalid sp. 20
Hymenoptera	Chalcididae	Chalcidid sp. 1
Hymenoptera	Eurytomidae	Eurytomid sp. 1
Hymenoptera	Eurytomidae	Eupelmid sp. 1
Hymenoptera	Eurytomidae	Eupelmid sp. 2
Hymenoptera	Eurytomidae	Eupelmid sp. 3
Hymenoptera	Eurytomidae	Eupelmid sp. 4
Hymenoptera	Encyrtidae	Encyrtid sp. 1
Hymenoptera	Encyrtidae	Encyrtid sp. 2
Hymenoptera	Encyrtidae	Encyrtid sp. 3
Hymenoptera	Encyrtidae	Encyrtid sp. 4
Hymenoptera	Encyrtidae	Encyrtid sp. 5
Hymenoptera	Encyrtidae	Encyrtid sp. 6
Hymenoptera	Encyrtidae	Encyrtid sp. 7
Hymenoptera	Encyrtidae	Encyrtid sp. 8
Hymenoptera	Encyrtidae	Encyrtid sp. 9
Hymenoptera	Encyrtidae	Encyrtid sp. 10
Hymenoptera	Encyrtidae	Encyrtid sp. 11
Hymenoptera	Encyrtidae	Encyrtid sp. 12
Hymenoptera	Encyrtidae	Encyrtid sp. 13
Hymenoptera	Encyrtidae	Encyrtid sp. 14
Hymenoptera	Encyrtidae	Encyrtid sp. 15
Hymenoptera	Encyrtidae	Encyrtid sp. 16
Hymenoptera	Encyrtidae	Encyrtid sp. 17
Hymenoptera	Encyrtidae	Encyrtid sp. 18
Hymenoptera	Encyrtidae	Encyrtid sp. 19
Hymenoptera	Eulophidae	Eulophid sp. 1

Appendix 1. Continued.

Order	Family	Species
Hymenoptera	Eulophidae	Eulophid sp. 2
Hymenoptera	Eulophidae	Eulophid sp. 3
Hymenoptera	Eulophidae	Eulophid sp. 4
Hymenoptera	Eulophidae	Eulophid sp. 5
Hymenoptera	Eulophidae	Eulophid sp. 6
Hymenoptera	Eulophidae	Eulophid sp. 7
Hymenoptera	Eulophidae	Eulophid sp. 8
Hymenoptera	Eulophidae	Eulophid sp. 9
Hymenoptera	Eulophidae	Eulophid sp. 10
Hymenoptera	Eulophidae	Eulophid sp. 11
Hymenoptera	Eulophidae	Eulophid sp. 12
Hymenoptera	Eulophidae	Eulophid sp. 13
Hymenoptera	Eulophidae	Eulophid sp. 14
Hymenoptera	Eulophidae	Eulophid sp. 15
Hymenoptera	Eulophidae	Eulophid sp. 16
Hymenoptera	Eulophidae	Eulophid sp. 17
Hymenoptera	Eulophidae	Eulophid sp. 18
Hymenoptera	Eulophidae	Eulophid sp. 19
Hymenoptera	Eulophidae	Eulophid sp. 20
Hymenoptera	Mymaridae	Mymarid sp. 1
Hymenoptera	Mymaridae	Mymarid sp. 2
Hymenoptera	Figitidae	Figitid sp. 1
Hymenoptera	Figitidae	Braconid sp. 9 figitid
Hymenoptera	Cynipidae	Charipid sp. 1

Appendix 1. Continued.

Order	Family	Species
Hymenoptera	Diapriidae	Diapriid sp. 1
Hymenoptera	Diapriidae	Diapriid sp. 3
Hymenoptera	Scelionidae	Scelionid sp. 1
Hymenoptera	Scelionidae	Scelionid sp. 2
Hymenoptera	Scelionidae	Scelionid sp. 3
Hymenoptera	Scelionidae	Scelionid sp. 4
Hymenoptera	Scelionidae	Scelionid sp. 5
Hymenoptera	Scelionidae	Scelionid sp. 6
Hymenoptera	Scelionidae	Scelionid sp. 7
Hymenoptera	Scelionidae	Scelionid sp. 8
Hymenoptera	Platygasteridae	Platygasterid sp. 1
Hymenoptera	Platygasteridae	Platygasterid sp. 2
Hymenoptera	Platygasteridae	Platygasterid sp. 3
Hymenoptera	Platygasteridae	Platygasterid sp. 4
Hymenoptera	Platygasteridae	Platygasterid sp. 5
Hymenoptera	Platygasteridae	Platygasterid sp. 6
Hymenoptera	Platygasteridae	Platygasterid sp. 7
Hymenoptera	Platygasteridae	Platygasterid sp. 2
Hymenoptera	Bethylidae	Bethylid sp. 1
Hymenoptera	Bethylidae	Bethylid sp. 2
Hymenoptera	Dryinidae	Dryinid sp. 2
Hymenoptera	Dryinidae	Dryinid sp. 4
Hymenoptera	Dryinidae	Dryinid sp. 1