Forest Disturbance Effects on Insect and Bird Communities: Insectivorous Birds in Coast Live Oak Woodlands and Leaf Litter Arthropods in the Sierra Nevada

by

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PREFACE

Ecologists increasingly view disturbances as a natural part of the forest landscape. However, anthropogenic disturbances, brought about either by introduced species or forest management, may not mimic natural disturbances. Understanding the multi-trophic and multi-scale effects of anthropogenic disturbances is the first step in mitigating their negative effects. I studied forest disturbance in two different ecosystems in California: oak woodlands in the San Francisco Bay Area and mixed conifer forests in the Sierra Nevadas. The types of disturbance studied in each of these sytems are very different. In the Bay Area, I examine an invasive forest pathogen, while in the Sierras I study fire and forestry practices. However, that these studies can be viewed through a common lens of how habitat disturbance can have many multi-scale and multi-trophic level effects, despite the fact the the ecosystems and fauna studied are very different.

The first three chapters of this dissertation focus on insects and insectivorous birds in oak woodlands impacted by “sudden oak death”. Chapter 1 examines how foliar arthropods might respond in these woodlands. I compare the abundance of two guilds of arthropods on coast live oak versus bay trees, and also between symptomatic and asymptomatic oaks. I also look at abundances during two points in the spring that are roughly analogous to early and late nesting season of some songbirds in these woodlands. These findings have implications not only for the ultimate fate of arthropods in these woodlands, if oaks are replaced by bays, but also reveal how certain arthropod groups may be impacted by physiological changes in infected oaks.

In Chapter 2, I shift my focus to the predators of these foliar arthropods, two species of insectivorous birds. Through detailed foraging observations of chestnut-backed chickadees and oak titmice, I determine the tree species in oak woodlands from which these birds most prefer feeding, as well as the behaviors they use and the microhabitats from which they procure prey. By comparing foraging behavior in stands that reflect a gradient of SOD decline, I determine how these two species shift their foraging behavior in the face of the loss of a common foraging substrate, the coast live oak. I discuss how foraging behavior may impact the relative ability of these birds to compensate for the loss of oaks in ths ecosystem.

The ultimate fate of chickadee and titmice populations in affected oak woodlands depends on whether there are changes in their nesting success. In Chapter 3, I use nest boxes to examine relative use of artificial nest holes and nestling survival. I also use video cameras trained on the boxes to measure foraging effort, or the amount of time spent looking for food, and the composition of the diet delivered to nestlings by adult birds. The results from this chapter, combined with Chapters 1 and 2, reveal that oak decline from SOD may have complex direct and indirect effects on cavity-nesting, insectivorous birds related to changes in prey availability, behavioral responses to oak decline, natural cavity availability, and nestling diet.

In Chapters 4 and 5 I shift my focus to an entirely different ecosystem, the mixed-conifer forests of the Sierra Nevadas. The results from both of these chapters come from a portion of the Fire and Fire Surrogate (FFS) study. This study is a nationwide effort to examine the impacts of prescribed burning and fire risk reduction thinning techniques on the forest ecosystem. I studied leaf litter arthropods, with particular emphasis on the Coleoptera, and how they responded to burning, thinning, and combined treatments. Chapter 4 is largely a survey of the biodiversity at Blodgett Forest, where the study took place. It is one of only a very few studies of arthropod biodiversity in the Sierra Nevadas. In this chapter, I also use multiple regression to determine which habitat structural features are important in determining the abundances of various arthropod groups. This acts as a lead-in to Chapter 5, in which I specifically focus on the effects of the treatments on the abundance and diversity of leaf litter arthropod groups, and how changes in habitat features might influence beetle assemblage structure.

The two studies described above, the first on SOD in oak woodlands and the second on fire in the Sierras, share in common their focus on forest disturbance as well as on insect assemblages. Beyond this, the studies are quite independent and seek to answer different specific questions. I hope, however, that the results from this work may contribute to answering larger questions involving habitat disturbance, ecosystem resiliency, and multi-trophic level effects of habitat change.

ACKNOWLEDGEMENTS

First and foremost, I must extend my gratitude to my friend, mentor, and former advisor, the late Dr. Donald Dahlsten. This dissertation could not have been completed without Don's passion for this work and his support for me during my time at Berkeley. I will miss him greatly and remember him fondly.

A great thank you goes to Dr. Barbara Allen-Diaz for her encouragement, advice, and collaboration as I finished my Ph.D. Dr. Scott Stephens and Dr. Wayne Sousa were helpful during many facets of this project, and provided many helpful comments on the manuscript. David Rowney and Dr. Nadir Erbilgin were both very supportive in numerous ways during my time at Berkeley. They also provided excellent statistical advice. I also want to thank Letty Brown for her collaboration on the SOD project.

The insect work accompanying the fire and fire surrogate study required the help of dozens of scientists, technicians, and fire fighters. The staff at the Blodgett Forest Research Station, particularly Sheryl Rambeau, were helpful and accommodating during my time there. I want to thank Jason Moghaddas for his excellent and tireless logistical support with the FFS. Several scientists lent their time in helping me identify insects, including Dr. Kip Will, Dr. John Doyen, Dr. Phil Ward and Cheryl Barr.

I owe a great debt of gratitude to many colleagues who helped during long days in the field and with tedious insect sorting. Thanks especially to Diony Gamoso, Sarah Toas, Jenny Loda, Dr. Andrew Lawson, Marta Yamamoto, Alice Nguyen, Keith O'Brien, Deanna Simon, and many others.

Finally, I want to thank Allison Drew, for her constant support through this long process.

CHAPTER 1

Foliar arthropod abundance in coast live oak (*Quercus agrifolia*) woodlands: effects of tree species, seasonality, and "sudden oak death" infection

INTRODUCTION:

Oak woodlands are some of the most important and diverse terrestrial habitats in California (Griffin 1988). Coast Live Oak (*Quercus agrifolia*) is one of the most common oaks found in central California from the coast to the central valley, comprising over 320,000 ha (800,000 acres) within woodlands and mixed hardwood forests (Bolsinger 1988, Griffin 1988). Oak woodlands have been identified as critical habitats for many wildlife species (Block et al. 1990, Block and Morrison 1990, Tietje et al. 1997) and also support diverse arthropod assemblages (Southwood 1960). Several dozen species of Lepidoptera alone have been identified from coast live oak trees (Opler 1971, 1974, Brown 1980).

Sudden oak death (SOD) is an emerging threat to California's oak woodlands. This tree disease was first noticed in northern California's Marin county during the mid-1990's as large stands of coast live oak and tanoak (*Lithocarpus densiflorus*) began to die (McPherson et al. 2000). A pathogen of unknown origin was subsequently isolated from infected trees and described as *Phytophthora ramorum* (Werres et al. 2001, Rizzo et al. 2002*a*). Since then, over two dozen plant species have been shown to be hosts for the disease (USDA-APHIS 2005). At present, tens of thousands of oaks and tanoaks have died from *P. ramorum* in counties along the northern and central California coasts. Little is known about the transmission of the disease from tree to tree or changes in foliar chemistry of trees when they become infected. The potential for multi-trophic level effects of SOD is high, particularly because of the possibility of complete loss of oaks from woodlands. The loss of large areas of canopy cover has been shown to be a threat to arthropod populations due to a reduction in habitat size and the breakup of contiguous stretches of live canopy (Didham 1997, Watt et al. 1997). However, there may also be significant changes in foliar insect populations if infection by *P. ramorum* changes in the ways in which arthropods utilize oaks before they succumb to the disease, if herbivores respond differently to infected versus uninfected oaks.

SOD disease progression in coast live oak trees generally involves the development of one to several cankers on the main stem of the tree. The cankers begin in the phloem and may progress deeper into the xylem late in the infection progression (McPherson 2000, Rizzo et al. 2002*b*). These cankers may increase in size and partially or completely girdle the tree, eventually restricting water transport to the crown and causing the foliage to die. The disease's common name comes from the relatively rapid crown dieback that accompanies the latter stages of the disease as water transport up the main stem is restricted. While some trees have been shown to turn brown within months of their first visible symptoms, other trees remain green and standing for years after initial infection (Rizzo et al. 2002*a*). Swiecki and Bernhardt (2004) report that stem water potential of symptomatic coast live oaks remains as high or higher than asymptomatic oaks. This suggests that these trees are not experiencing water stress, at least until just before crown death, but little else is known about the condition of SOD-infected foliage in terms of leaf chemistry or nutrient availability, or how this pathogen might affect subsequent herbivory by foliar insects.

Pathogens and insects frequently share common host plants, but studies of the complex, three-way, host-pathogen-herbivore interaction are relatively rare (Hammerschmidt 1993, Hatcher 1995). Some negative responses of herbivores to pathogen attack on a host plant are the result of direct consumption of fungal tissue (Rostas et al. 2003 and citations within, Laine 2004). Indirect effects on herbivores to prior pathogenic attack are also possible. Attack from the pathogen may result in the plant acting as an "altered host" to herbivores (Hatcher 1995) by inducing a generalized defensive response in the host (Karban et al. 1987, Kreuss 2001). In this study we examine whether population abundances of foliar insects are different on oak trees exhibiting symptoms of SOD, versus apparently healthy trees. Many other complex, interacting factors, besides host condition, also govern the abundance and community composition of foliar arthropods. Thus, we also examine whether insect abundances differ on the two dominant tree species in these woodlands, coast live oak (*Quercus agrifolia*) and California bay-laurel (*Lithocarpus densiflorus*). This study is part of a larger study examining bird diet, foraging behavior, and nesting in Coast Live Oak woodlands. We therefore also look at whether insect abundances differ from early in the spring (March) to late in the spring (May), time periods roughly equivalent to early and late nesting season for many resident insectivorous birds.

METHODS:

We conducted this study at eight study sites in the greater San Francisco Bay area in California (Marin, Sonoma, and Contra Costa counties). We established one hectare plots at these eight sites to monitor long term vegetation change as a result of SOD. The sites were selected to reflect a range of infection and degree of tree dieback. The trees sampled in this study had been tagged and monitored for three years prior to sampling.

We used branch clipping to sample the foliar arthropods on our plots. Branch clipping has been shown to be an effective method of sampling the food supply of foliage feeding insectivores (Majer and Recher 1988, Johnson, 2000). A modified pole pruner with a collapsible net attached was used to collect samples, as per Johnson (2000). The pruner was able to reach 6-8 m into the canopy to collect samples. The net attachment was quickly put over a branch tip while attempting to minimally disrupt the branch. The net collar was cinched tightly around the branch with a string, preventing arthropods from flying away or falling from the branch tip. An approximately 30 cm clipping was then cut from the branch using the pruner, lowered, and the sample was carefully transferred to a plastic bag. Only trees with green foliage were selected. Samples were kept cold (4 °C) prior to sorting.

Samples were collected twice during the spring of 2004, once between March 19-22, and a second time between May 18-21. This study is part of a larger study of the effects of SOD on cavity-nesting insectivorous birds, and thus these time periods were chosen to roughly match early and late in the nesting season of chestnut-backed chickadees (*Parus inornatus*) and oak titmice (*Baeolophus inornatus*). Thirty trees (> 10 cm DBH) were randomly sampled at each of our eight plots: 10 bays, 10 oaks with symptoms of SOD, and 10 asymptomatic oaks. One 30 cm clipping was taken per tree, for a total of 240 samples per collection period. We were unable to find enough symptomatic trees at some of our sites, so the actual sample size was lower in some cases. The same trees were sampled in the May collection as were in the March collection. We attempted to select branch tip samples at mid-crown height when possible, or from as high in the crown of each tree as possible given the length of the pole pruner.

Symptomatic trees showed visible symptoms of SOD, including “bleeding” seeps on the trunk, the presence of fruiting bodies of the fungus *Hypoxylon* and bark beetle frass, and, in some cases, partial crown dieback (McPherson et al. 2000). Although these symptoms are not exclusive to *P. ramorum*, the causal agent of SOD, all of our sites are within the historic and current range of the pathogen, and it has been confirmed from nearby areas using PCR or direct culture (M. Garbelotto, pers. comm.). Other *Phytophthora* species, which exhibit similar symptoms, are present in these oak woodlands, but generally show lower incidence and lower mortality rates than *P. ramorum* (Hansen et al. 2003, Martin and Tooley et al. 2003, Murphy and Rizzo 2005, Wickland and Rizzo 2005). Thus it is not possible to entirely confirm that the symptomatic trees are infected with *P. ramorum*. All of the trees selected as “symptomatic” were declining with a suite of symptoms consistent with SOD, but we must be cautious in referring to these trees as being exclusively infected with *P. ramorum*.

Sorting:

Samples were sorted by emptying the collection bags into a bin and counting all arthropods that were both on the foliage and loose in the sample bags. Arthropods were identified to order and saved in vials of 95% ethanol. All leaves were removed from the branch samples and counted. The leaves were then dried in an oven for 48 h at 65 ºC and weighed with an electronic balance.

Analysis:

We standardized the numbers of each arthropod order to individuals per gram of dried leaf tissue to account for differing sizes of branch samples. General comparisons in terms of total numbers collected were made at the order level. For the analyses of the effects of tree species, collection time, and SOD on arthropod numbers, we divided the total catch into two broad functional groups: arthropods that feed directly on leaf tissue ("leaf feeders"), and those that use foliage more as a substrate rather than for feeding ("non-leaf feeders"). The first group includes caterpillars (Lepidoptera larvae), aphids (Homoptera), and tree-crickets (Gryllacrididae), and the second includes spiders (Araneae), ants (Formicidae), and other predators or scavengers.

The distribution of arthropods collected per sample was highly right-skewed, as is typical of aggregated count data of arthropods (Southwood 1978). Standard transformations failed to normalize the data due to the large number of zero counts. We therefore used non-parametric Wilcoxon rank-sum tests to test the effects of collection date (March versus May) on abundance of our two feeding guilds for both oaks and bays. We also tested for a tree species effect (oaks versus bays) in March and May for both guilds. Finally, we tested for an effect of SOD infection (symptomatic versus asymptomatic, oaks only), in March and May for both guilds.

Four commonly used indices were calculated to evaluate diversity and evenness of the arthropod captures. We used the Shannon diversity index (H), which is sensitive to rare species, and the Simpson's diversity index (D) which puts more weight on common species (Begon et al. 1990). We used non-metric multidimensional scaling (NMDS) to analyze patterns of arthropod assemblages at the ordinal level between tree species, collection times, and SOD-status. NMDS is an iterative ordination technique that is based on ranked distances that seeks to minimize the “stress” between the new reduced dimension ordination and the original multidimensional space. It is particularly appropriate for non-normal data, and several authors have considered it the most appropriate method for analyzing ecological community data (Kruskal and Wish 1978, Clarke 1993, McCune and Grace 2002). The data were grouped by collection (March or May), tree species (Oak or Bay), and disease status (for oaks only, SOD or no SOD) for the analysis, and each of the eight sites was used as a separate sampling unit, for a total of 48 points. We used the “slow and thorough” autopilot mode in PC-Ord (McCune and Mefford 1999) with a Sorenson distance matrix to seek the best NMS solution by sequentially stepping down in dimensionality. The stress at each dimensionality is compared against Monte Carlo results from 50 randomized runs to determine the lowest number of appropriate dimensions.

RESULTS:

A total 1343 individual arthropods in 17 orders were collected from the branch clip samples (Table 1). Arthropods from coast live oak trees represent the vast majority of the total collection (95%), versus those collected from bays. Over twice as many (931 vs. 412) arthropods were collected in March than in May on both tree species combined, and 67% of the total collection came from the March oak collection alone. Lepidoptera larvae constitute the majority (53%) of individual arthropods captured over the course of the study, followed by Homopotera (mainly Aphididae, 11%). Both the oak and the bay catch were dominated by Lepidoptera larvae (55% and 20%, respectively). The dominance of the foliar community by caterpillars is highest in the March collection, in which they represent 77% of the oak catch and 42% of the bay catch. The May catch is less dominated by a single order, and caterpillars comprise only 1.7% of this collection. We did not break down our catch by species, but the most abundant Lepidoptera species captured was the California oak moth, *Phryganidia californica*.

On oaks, leaf chewer (z= -10.57, P<0.0001) and non-leaf chewer (z= 3.44, P<0.001) abundance was significantly lower in May than in March. Abundance was the same for both feeding guilds on bay trees in March and May (leaf feeders: z= -1.84, P>0.05; non-leaf feeders: z= 0.94, P>0.05). Oaks consistently had more foliar arthropods than bays. This was true of both feeding guilds in March (leaf feeders: z= -10.21, P<0.0001; non-leaf feeders: z= -5.08, P<0.0001), and in May (leaf feeders: z= -5.63, P<0.0001; non-leaf feeders: z= -7.27, P<0.0001).

Considering only oak trees, there were significantly more leaf feeders on foliage from asymptomatic oak trees than symptomatic oak trees in the March collection (z= -2.61, P<0.01); there was no difference during the May collection (z= 0.22, P>0.05)(Fig. 2). There were no differences between symptomatic and asymptomatic oaks for non-leaf feeders in either month (March: z= -1.44, P>0.05; May: z= 0.37, P>0.05).

We calculated two diversity indices for the taxa captured on each tree species for each collection period (Table 2). These calculations were made based on total abundance of captured arthropods grouped at the order level. The results from both the Shannon and Simpson’s diversity indices follow the same overall pattern: diversity is higher on bay trees than on oaks and higher in May than in March. The highest Shannon diversity was recorded from the May oak collection, while the highest Simpson’s diversity was from the May bay collection. The March oak collection showed the lowest diversity from both indices. We also calculated diversity indices for symptomatic oaks versus asymptomatic oaks in March versus May (Table 3). Both indices were similar for diseased and non-diseased oaks for both collection periods.

NMDS ordination and subsequent Monte Carlo tests revealed that three axes were significant. Axis 1 and 2 described 61.3% of the total variability in the data (axis 1=25.4%, axis 2=35.9%). Plots, grouped by tree species, collection period, and disease status, were plotted on axes 1 and 2 (Fig. 3). The most apparent gradient is along axis 2, which separates the early from the late oak collection very well, and the bay collections less well. There is perhaps a very weak tendency for the symptomatic and asymptomatic oak groupings to separate in the March collection, but no apparent separation in the May collection. The bay points, from either collection, show little clustering, probably as a result of the few insects captured on bays overall. The diagrams also reflects the distinct communities on oaks versus bays, as the two tree species tend to cluster separately in both months.

DISCUSSION:

Arthropod herbivores respond at the population level to many interacting factors involving their host plant, the environment, and competitors. In this study we have shown that two of the dominant tree species within California oak woodlands support very different abundances of arthropod orders, and that the abundances of these taxa vary greatly over the course of the spring. We have also shown that oak trees that are symptomatic of sudden oak death support lower abundances of the “leaf feeding” arthropod guild than apparently healthy trees. Arthropod assemblages as a whole, as shown in the NMDS ordination, show a similar pattern: Bay and oak assemblages are well separated, as are oak assemblages from March versus May. Arthropod assemblages from symptomatic oaks do not separate particularly well from the asymptomatic oaks within a collection period, suggesting that while there are differences when considering single functional groups (i.e. leaf feeders), the difference is more difficult to detect at the community level. The dominance of the oak insect assemblage by Lepidoptera is reflected in the species diversity indices (Shannon and Simpson): diversity was lowest for the March oak catch which was heavily biased towards Lepidoptera. The May oak catch and both bay catches, while lower in overall numbers, are more diverse due to the more even representation of other taxa.

The differences between the two tree species for both of the functional groups studied was clear: coast live oak trees harbor more foliar arthropods than California bay trees. This is consistent with other work finding few insects on bay trees (Fowells 1965). Chemical and morphological adaptations likely account for these differences. In addition to having very tough leaves, the foliage of bay trees contains numerous monoterpenoids and other allelochemicals that effectively deter feeding from all types of herbivores (Goralka and Langenheim 1995, 1996, Goralka et al. 1996). Oak trees rely more heavily on tannins and lignins, which contribute to overall leaf “toughness”, to deter herbivores (Casher 1996). The combination of allelochemicals and tough leaves likely make bay trees a much less desirable food source for arthropod herbivores. The drop in leaf feeding arthropods from March to May on oaks is due almost entirely to the decline in Lepidoptera larvae. Many Lepidoptera concentrate their feeding on branch tips early in the spring; new leaf growth contains fewer defensive compounds than mature leaves, making them more palatable to caterpillars (Feeny 1970). The flush of new leaf growth in March probably accounts for the high numbers of some Lepidoptera during this collection. However, tannin abundance has been shown to be a poor predictor of feeding in the most abundant Lepidoptera, *Phryganidia californica*, which feeds on young, mature, and old leaves equally (Mauffette and Oechel 1989). In California, the first of two generations of this species has matured by May, accounting for the decline in the numbers of larvae captured (Ohlendorf and Flint 2000). Mauffette and Oechel (1989) suggested that temperature requirements may explain the seasonality of this species, but increases in parasitoids and predators may also be a major factor.

Phytophthora infected oak trees were shown to harbor fewer leaf feeding arthropods. This significant difference was found in March, when the numbers of Lepidoptera were very high, and was not detected in the May collection, when leaf-feeders declined to a small fraction of their early spring abundance. This pattern was not significant for non-leaf feeding arthropods (such as Homoptera, Diptera, Araneae, and others), suggesting that the observed patterns are some consequence of unpalatablity of the foliage or some consequence of consumption or digestion of the leaf tissue. It is not known what changes, in terms of defensive compounds or nutritive quality, might occur in the foliage of oaks infected with a pathogen such as *P. ramorum*. We propose three, non-mutually exclusive, hypotheses that may explain the observed pattern of fewer leaf-feeders on symptomatic oaks. The three hypotheses involve water stress, induced defenses, and costs of pathogen resistance.

Evidence points to *P. ramorum* infected oaks as not being severely water stressed, at least until late in the disease progression (Sweicki and Bernhardt 2004). This work, however, was conducted only during the fall, so tree responses during the spring (the wet season) are hard to predict. One hypothesis is that there are water deficits in infected trees, perhaps brought about by canker development, that reduce leaf palatability to arthropods that feed directly on foliage. This change could be due to either changes in nutrients or defensive compounds. Increases in some plant secondary compounds have been shown in water stressed plants, but the pattern with phenolic compounds such as tannins is less clear (Gershenzon 1984, Mattson and Haack 1987). Larsson (1989) contended that leaf feeding arthropods should be negatively affected by water stress as secondary chemicals increase in the leaves of the stressed trees. Efficiency of herbivores and digestibility of leaf tissue has also been shown to be higher on leaves with higher water content (Mattson 1980). The relative amounts of defensive compounds and nutrients in water stressed oak foliage, as well as the digestibility of stressed leaves, needs further study to determine if this is a cause of the arthropod patterns seen in this study.

A second hypothesis is that infection by *P. ramorum* induces a generalized defensive response by the host tree. This hypothesis suggests that the reduced palatability of the oak foliage to the leaf feeding guild is a consequence of induced secondary compounds. Induced defenses to herbivores brought about by pathogen attack have been demonstrated in a number of systems (Hammond and Hardy 1988, Hatcher 1995). Karban et al. (1987) found that cotton seedlings infected with a pathogen were a poorer quality host for spider mites. Kreuss (2001) found that leaf beetles prefer healthy to diseased thistles as food and for oviposition. Examples from trees are less common, but tannins and other phenolic compounds have been shown to increase in oaks that have been wounded by herbivory (Schultz and Baldwin 1982). Foss and Rieske (2004) found that pin oak (*Quercus palustris*) stems with insect galls had fewer gypsy moth caterpillars on their foliage. Trees with galls also had higher foliar tannin concentrations than un-galled trees, but only early in the spring. It is not known whether a stem canker caused by a *Phytophthora* pathogen might elicit a similar response in coast live oaks, but, if so, increased tannins may be a mechanism that also helps protect symptomatic trees against herbivore attack.

One final hypothesis is that resistance to SOD exacts a cost on the host tree. It is known that there are trade-offs that plants make between resistance to herbivory or pathogenic attack and growth or reproduction (Purrington 2000). There is also evidence that, in some cases, the signaling pathways that are induced when a pant is attacked by a pathogen make them less able to defend against herbivores (Felton et al. 1999, Thaler et al. 1999, Bostock et al. 2001). Consequently, there is sometimes a trade-off between resistance to a pathogen and resistance to herbivores. This can be considered an alternative to the previous hypothesis, in which an induced defensive response to *P. ramorum* also protects from herbivory. In this case, the cost of SOD resistance is higher herbivory, and the asymptomatic trees harbor more leaf feeding arthropods. Examples with trees are scarce, but Rieske (2003) found that gypsy moths (*Lymantria dispar*) perform better on blight-resistant hybrids between American and Chinese chestnut trees than on blight-susceptible American chestnuts, indicating that blight resistance exacts a cost in terms of susceptibility to herbivory. The patchy distribution of SOD across the landscape suggests that a degree of genetic resistance to *P. ramorum* is possible in some oaks, and recent work has confirmed that there is genetically based variability in susceptibility of oaks to *P. ramorum* (Dodd et al. 2005). Thus, the trade-off between herbivore resistance and pathogen resistance could have an inherent genetic component.

Complex interacting factors clearly govern the distribution and abundance of foliar arthropods in coast live oak woodlands. These factors include host tree species, seasonality, and host tree condition. We have demonstrated that, during the spring, coast live oak trees harbor a much greater abundance of foliar arthropods than California bay trees, and that this difference is most pronounced during the early spring. Additionally, we have found that fewer arthropods utilize the foliage of oak trees with symptoms of SOD than the foliage of apparently healthy oaks. We have presented three hypotheses that may help to explain the pattern of fewer leaf feeding arthropods on symptomatic oaks. These hypotheses are not intended to be mutually exclusive; changes in water, nutrients, and defensive compounds may all play a role in causing this pattern. Future work should seek to confirm these patterns, and explore the relative foliar chemistry of infected versus uninfected oak leaves.

The loss of oaks from these woodlands may leave many foliar arthropods with few alternate hosts, especially as the other common tree species in these stands, the California bay-laurel, is much less preferred. However, there is potential for effects on leaf feeding arthropods even prior to oak death, as SOD appears to make oaks less palatable. Foliar arthropods are important members of the faunal community in oak woodlands as both defoliators and food for higher trophic levels, such as insectivorous birds. They deserve increased attention as the spatial and temporal distribution of these arthropods in the woodlands may play a vital role in determining aspects of the population ecology of their host plants and predators.

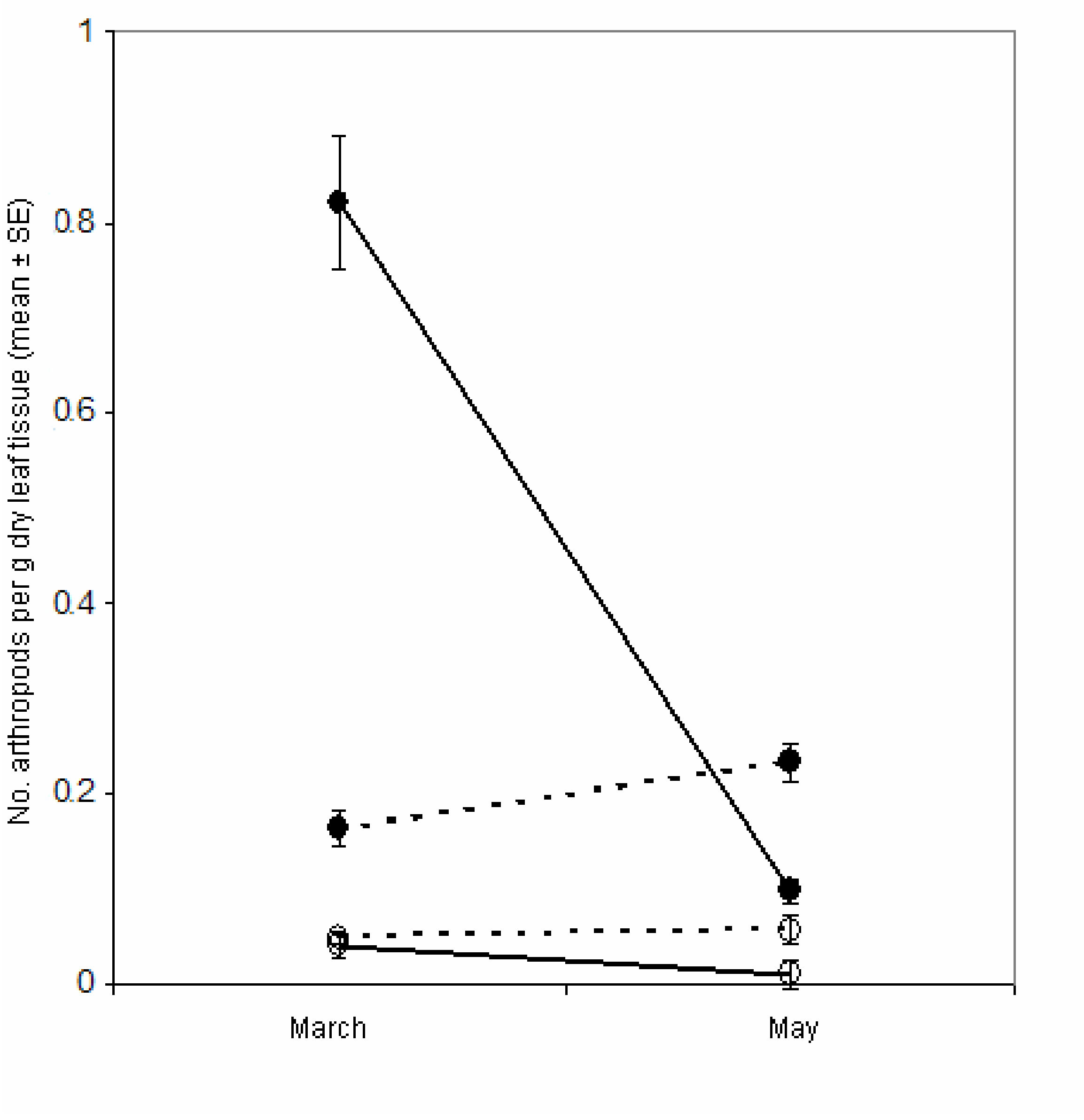

Figure 1. Abundance of leaf feeders and non-leaf feeders collected from *Q. agrifolia* and *U. californica* during the two collection periods (March and May). Points represent means per g of dry leaf tissue, per branch clip. Bars represent standard error. Solid circles are *Q. agrifolia*, open circles are *U. californica*. Solid lines are leaf feeders, dashed lines are non-leaf feeders.

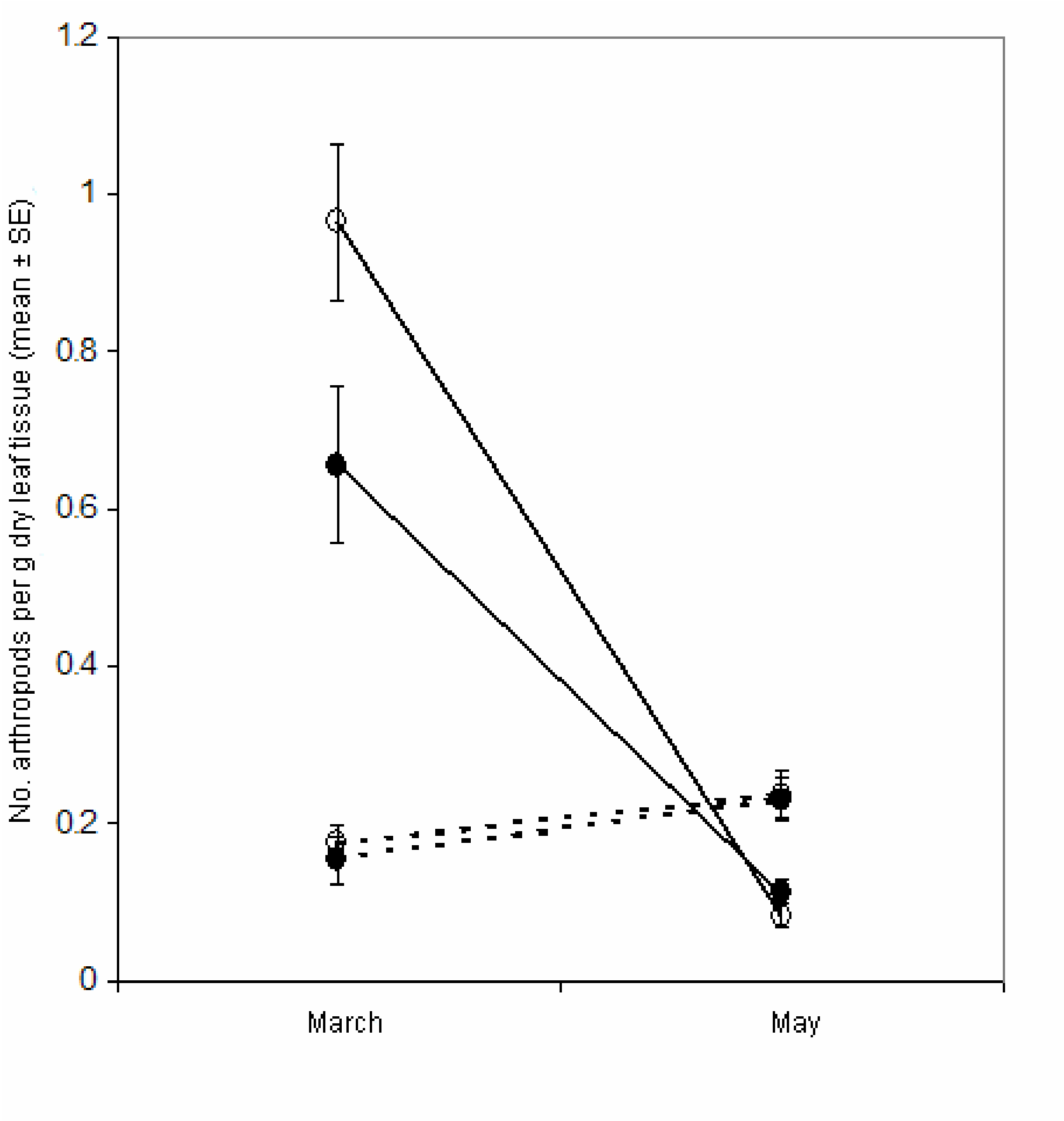

Figure 2. Abundance of leaf feeders and non-leaf feeders collected from symptomatic and asymptomatic *Q. agrifolia* during the two collection periods (March and May). Points represent means per g of dry leaf tissue, per branch clip. Bars represent standard error. Solid circles are symptomatic oaks, open circles are asymptomatic oaks. Solid lines are leaf feeders, dashed lines are non-leaf feeders.

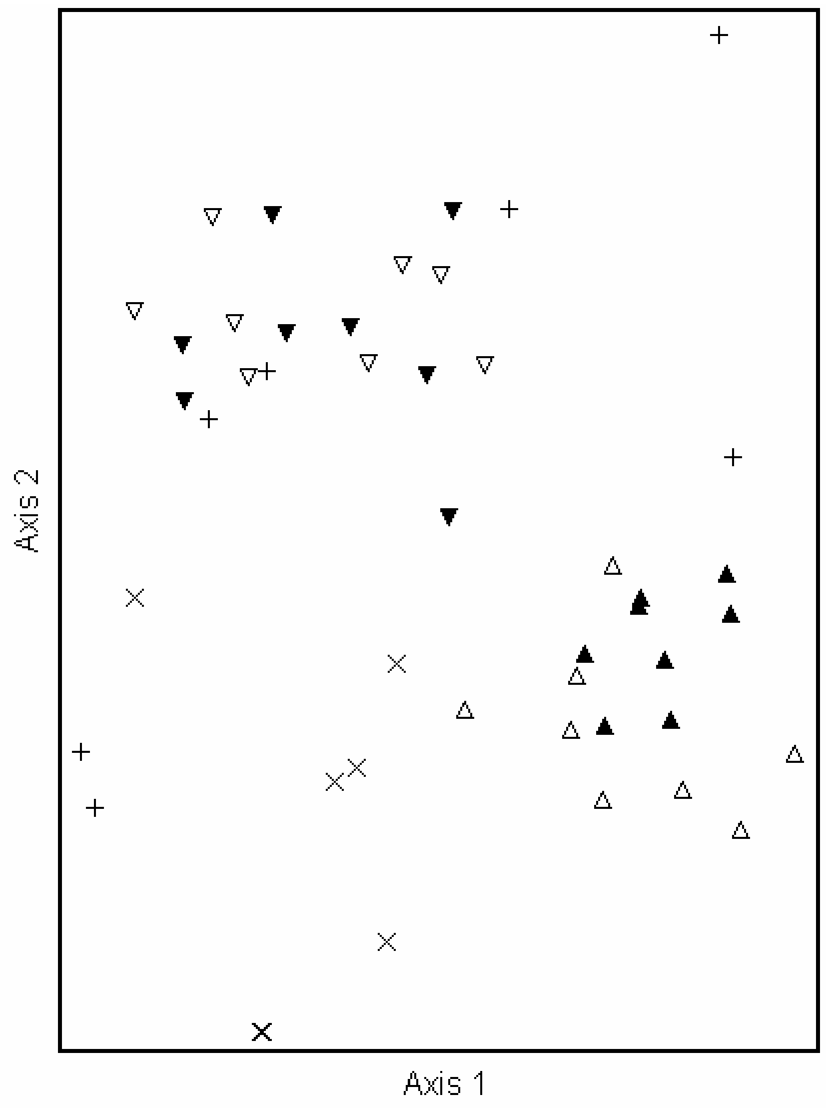

Figure 3. Non-metric multidimensional scaling ordination of arthropod assemblage data. Points are grouped by site, tree species, collection, and disease status (*Q. agrifolia* only). Points are as follows: March bay collection (X), May bay collection (+), symptomatic oaks (closed triangles), asymptomatic oaks (open triangles), March oak collection (up triangles), May oak collection (down triangles).

	Oak			Bay			Both sp.		
Order	March	May	total	March	May	total	March	May	both
Lepidoptera (larvae)	668	7	675	14	-	14	682	7	689
Homoptera	50	97	147	1	6	7	51	103	154
Araneae	37	85	122	7	4	11	44	89	133
Diptera	33	13	46	6	3	9	39	16	55
Coleoptera	26	19	45	1	2	3	27	21	48
Formicidae	22	22	44	1	2	3	23	24	47
Psocoptera	6	31	37	-	9	9	6	40	46
Hymenoptera	3	31	34	2	3	5	5	34	39
Lepidoptera (pupae)	-	31	31	-	2	2	-	33	33
Hemiptera	4	21	25	-	6	6	4	27	31
Gryllacrididae	15	-	15	-	1	1	15	1	16
Neuroptera (larvae)	1	5	6	1	-	1	2	5	7
Dermaptera	1	4	5	-	-	-	1	4	5
Lepidoptera (adult)	-	3	3	-	-	-	-	3	3
Opiliones	3	-	3	-	-	-	3	-	3
Raphidioptera	3	-	3	-	-	-	3	-	3
Neuroptera (adult)	1	2	3	-	-	-	1	2	3
Megaloptera	1	1	2	-	-	-	1	1	2
Phasmatodea (Timemidae)	-	2	2	-	-	-	-	2	2
Trichoptera	1	-	1	-	-	-	1	-	1
TOTAL	875	374	1249	33	38	71	908	412	1320

Table 1. Total numbers of each arthropod taxon collected from branch clippings.

	Oak			Bay			Both sp.		
Diversity Index	March	May	both	March	May	both	March	May	both
Shannon (*H*) (base *e*)	1.05	2.04	1.64	1.60	2.02	2.18	1.09	2.07	1.69
Simpson's (*D*)	1.69	5.74	2.94	3.77	6.61	7.82	1.74	6.04	3.12

Table 2. Shannon (base *e*) and Simpson's diversity indices calculated for each tree species for each month, as well as totals. Indices represent diversity at the order level.

	March		May	
Diversity Index	SOD -	SOD +	SOD -	SOD +
Shannon (*H*) (base *e*)	1.07	0.94	1.87	1.99
Simpson's (*D*)	0.58	0.62	0.19	0.18

Table 3. Shannon (base *e*) and Simpson’s diversity indices calculated for symptomatic and asymptomatic coast live oaks during each collection period, as well as totals. Indices represent diversity at the order level.

CHAPTER 2

Insectivorous birds change their foraging behavior in oak woodlands affected by *Phytophthora ramorum* (“sudden oak death”)

INTRODUCTION:

California’s oak woodlands serve as critical habitats for birds. Over 110 species have been shown to breed in oak woodlands (Verner 1980), and resources from oaks, such as acorns, nest cavities, and insects, are all important during different life history stages and seasons of the year. The tree disease known as “sudden oak death” (SOD) has caused significant dieback of oaks and other tree species in the coastal counties of northern and central California (McPherson et al. 2000). The disease affects dozens of plant species (USDA-APHIS 2005), but has particularly serious effects on a few tree species, including the coast live oak (*Quercus agrifolia*). *Phytophthora ramorum,* the causal agent of the disease, creates a canker in the phloem of these oaks, causes crown dieback, apparently serves as an entry point for secondary fungi and wood-boring insects, and often leads to the death of the tree (Werres et al. 2001, Rizzo et al. 2002). There is currently great concern over this disease, as there are still a large number of woodlands at risk throughout California (Meentemeyer et al. 2004), and the impacts of this disturbance on the ecology of California’s coast live oak woodlands are largely unknown.

It is now well established that disturbance plays a central role in structuring many ecological communities (Sousa 1984). Coping with a natural or anthropogenic habitat disturbance is one of several complex challenges that forest birds must navigate during the breeding season. Disturbances may impact a bird’s predation risk (Telleria et al.

2001, Raphael et al. 2002), ability to find mates or nesting sites (Hagan et al. 1996, Torres and Leberg 1996, Fort and Otter 2004*b*), or ability to procure food for themselves or nestlings (Nour 1998). Even vegetation communities undisturbed by anthropogenic impacts may present challenges to bird populations over the long-term due to successional processes (Holmes and Sherry 2001). Disturbance from forest pathogens such as *P. ramorum* present many unique challenges to bird populations: one or a few plant species may be selectively removed from the forest ecosystem (Rizzo et al. 2002), recovery of lost plant species may happen very slowly, if at all (Tindall et al. 2004), and, in the case of invasive introduced pathogens, the disturbance will not be one that has been experienced in the evolutionary history of the resident bird species.

Unfortunately, the responses of bird populations and communities to widespread forest pathogens are not well-known, partly because pre- and post-impact data are rare (Osborne 1985). This is especially true in well-known North American examples such as the loss of American chestnut (*Castanea dentata*) due to chestnut blight (*Cryphonectria parasitica*) and decline of elms (*Ulmus americana*) due to Dutch elm disease (*Ophiostoma ulmi*). Community responses of birds to other types of disturbance have been well studied. Studies on the effects of such disturbances as fire and logging have shown that community level changes in species composition are common, even if overall diversity remains similar (Dieni and Anderson 1999, Kotliar et al. 2002, Morissette et al. 2002). Despite the loss or addition of some species in disturbed habitats, a significant proportion of bird species are found in both disturbed and undisturbed habitats (Kotliar et al. 2002).

The behavioral responses of individual birds that remain in a habitat after a disturbance have not been studied as extensively as have overall community responses. While some studies have shown no impacts on behavior from disturbances such as logging (Lent and Capen 1995) and gypsy moth defoliation (Bell and Whitmore 2000), other types of disturbance have resulted in behavioral shifts. VanderWerf (1994) found that the elepaio (*Chasiempis sandwichensis*), a Hawaiian native bird, used more difficult foraging maneuvers in anthropogenically disturbed forests. Hurricane disturbance has been shown to cause the Antillean euphonia (Euphonia *musica*) to switch foraging maneuvers and substrates when the abundance of mistletoe, a preferred food, was decreased (Perez-Rivera 1991). Sugar maple (*Acer rubrum*) decline in northeastern North America has been shown to have subtle effects on the foraging and nesting behavior of forest birds (Darveau et al. 1992, DesGranges et al. 1987, Darveau and DesGranges 1992). Fort and Otter (2004*a*) found that not only did black-capped chickadees (*Poecile atricapillus*) in disturbed habitats have lower breeding success, they also exhibited reduced territorial behavior, allowing for increased intrusion into other pair's territories.

There is evidence that bird species that are able to compensate through behavioral plasticity stand a greater chance of persisting in disturbed habitats (Craig 2002). Black-capped chickadees have been shown to compensate for the negative effects of canopy dieback and reduced food quality by changing their foraging behavior (Mahony et al. 1997). The diverse foraging behavior of some bird species in the Dominican Republic has been linked to frequent hurricane disturbances (Latta and Wunderle 1998). We anticipate that the canopy dieback that is typical of *P. ramorum* affected forests could force resident bird species to similarly adopt new foraging strategies to survive in heavily infected or damaged oak woodlands. The objectives of this study are twofold: first, to determine the foraging behaviors and microhabitat use of two insectivorous, cavity-nesting birds (*Poecile rufescens* and *Baeolophus inornatus*) in California oak woodlands and, second, to determine whether sudden oak death affects the foraging behavior of these two species. This study is part of a larger study examining the impacts of oak decline on the prey, behavior, and nesting success of these bird species.

METHODS:

Study sites:

We selected eight oak woodland stands in Marin, Sonoma, and Contra Costa counties for this study (Fig. 1). The stands ranged in elevation from 50 to 450 m and slopes ranged from 20-50%. At each stand, we established a single, one ha square plot within and around which the various aspects of the study were conducted (the “core” plot). One corner of the plot was randomly selected, with the constraint that the rest of the plot must fit within the same or similar habitat type. We selected stands that were composed mainly (> 40% of basal area) of coast live oak (*Quercus agrifolia*). California bay-laurel (*Umbellularia californica*) was a co-dominant at most of our sites. Several other tree species were present in lower abundances on the sites, including madrone (*Arbutus menziesii*), toyon (*Heteromeles arbutifolia*), California black oak (*Quercus kelloggii*), Oregon white oak (*Quercus garryana*), and Douglas-fir (*Pseudotsuga menziesii*). The eight sites represented a range of SOD incidence (many infected trees to few infected trees), time since initial *P. ramorum* infection (very recent to as long as 10+

years), and degree of tree damage related to *P. ramorum* (few to many killed and damaged trees). Damaged trees were those for which the trunk had snapped and fallen, or those which had lost one or several main stems. Damaged trees also included those in which the crown had died and was beginning to turn brown.

Vegetation monitoring:

We monitored trees on the plot within five, .08 ha circular sub-plots randomly established within the 1 ha main plot. All trees (> 10 cm DBH) on the sub-plot were tagged and monitored over the course of the study from 2002 to 2004. Tree height and symptoms of *P. ramorum* infection were recorded. Light measurements were made using an LAI-2000 plant canopy analyzer (Li-Cor, Inc., Lincoln, NE), which measures percent diffusion of light through the canopy. Volume of coarse woody debris (m^3 per ha) was recorded on each sub-plot using the Brown (1974) protocol. For details of the vegetation monitoring protocols see Brown and Allen-Diaz (2005). A summary of the vegetation data used in our bird foraging analysis (see below) is provided (Table 1).

Study species:

Chestnut-backed chickadees (*Poecile rufescens*) and oak titmice (*Baeolophus inornatus*) are both common cavity-nesting bird species in California’s oak woodlands. Both of these species are permanent residents who feed primarily on arthropods during the breeding season, but supplement their diet with seeds and other plant material (Cicero 2000, Dahlsten et al. 2002). Oak titmice in particular feed upon acorns during the winter months (Cicero 2000). These species initiate nest-building in late February to early March, have laid their first clutch in late March, and nestlings have generally fledged by mid-June. Both of these species are considered secondary cavity nesters or weak excavators, and thus tend to nest in preexisting holes rather than excavating their own cavities.

Foraging methods:

We recorded the foraging behavior of individual chestnut-backed chickadees and oak titmice at each of our eight study sites during the springs of 2002, 2003 and 2004. Three of the eight sites were set up only after the 2002 season, and were thus only visited for two years. All observations took place between 0600 – 1300 h. Our observations were scheduled to encompass most of the breeding season of these two species in the San Francisco Bay Area: mid-March to mid-June. Each site was visited once per week. Two observers collected data in 2002 and 2003, and a single observer collected data in 2004. All observers were trained prior to data collection to ensure standardization of our sampling methods.

Foraging observations took place in the core 1 ha plot and within 50 m of the plot, giving a total observational area of 4 ha per site. Within a given day, observers walked the entire 4 ha observational area, attempting to divide effort equally across the plot. At least one, but not more than three, hours were spent on a plot during any given visit. The protocol used for recording foraging behavior was an adapted version of several methods used in other studies (Holmes et al. 1979, Robinson and Holmes 1984, Remsen and Robinson 1990). Once a bird was sighted, we waited 10 seconds before collecting data to ensure that we did not bias our observations towards highly visible foraging events. A foraging event was considered a strike or attempt at a food item, regardless of whether the foraging event was successful at procuring prey. We were careful not to include such behaviors as bill-wiping, procuring nest material, or short flights as foraging events. We only recorded the first foraging event observed and then moved to another bird. We used initial observations only, rather than strings of sequential observations, as sequential observations on the same bird have been shown to not be independent of one another (Hejl et al. 1990). We also attempted to only collect data from an individual bird once during any given trip to a site. We minimized the chance of this by marking locations of foraging observations on maps of each site and not collecting another observation from the same species within 50 m of a previous observation earlier in the same day.

Foraging behaviors were classified into several categories: “perch glean”, which included all maneuvers in which prey was taken from a surface while the bird was upright; “hang glean”, when a bird hung all or mostly upside-down to procure food; “hover glean”, when prey was taken from a surface while the bird was hovering in mid-air; “tear”, when part of a substrate was pulled back to reveal prey; “peck”, when the bird hammered like a woodpecker to find prey; “probe”, when all or part of the bird’s bill was inserted into a small space to obtain prey; and “hawk”, when the bird flew from a perch to obtain flying prey. Some maneuvers did not fit cleanly into any category and were described as hybrids of other maneuvers. The substrate from which prey was taken was also recorded as “foliage”, “small twigs”, “bark”, “lichen”, “dead foliage”, and “leaf litter”. The height above ground level of the bird when it foraged was also recorded. Height estimations were made using clinometers when possible, and estimated by eye in some cases. Characteristics of the tree in which the bird was foraging were also recorded. This included the tree species, DBH, height, whether the tree was live or dead, and if the tree showed visible symptoms of SOD, including bleeding, *Hypoxylon* fungus, or bark beetle (Coleoptera:Scolytidae) attack.

Statistical analysis:

The combined the results from the three years of the study were used for analysis. This was done because there were insufficient data for several of the study sites to analyze each year separately and visual examination of plots of the data showed similar patterns across the three years.

For our summary statistics, each plant species, maneuver, and substrate used was considered separately. However, for our other analyses, we grouped observations within these categories because there were very few observations on certain substrates or tree species, or of certain maneuvers by the birds. Plant species were grouped into the categories “coast live oak”, “bay”, and “other”, which encompasses all other plant and tree species. Substrates were grouped as “foliage”, “bark”, “small twigs”, and “other” which included lichen, dead foliage, cones or flowers, leaf litter, or ends of broken branches. Maneuvers were grouped as “perch glean”, “hang glean”, or “other”, which encompassed hovers, probes, pecks, and maneuvers that were more difficult to categorize. The Shannon diversity index “H” (base *e*) was used to determine diversity of foraging sites, maneuvers, and substrates. Differences in foraging diversity between species were measured using paired t-tests.

Contingency table analysis was used to determine the interdependence of tree species used, maneuver used, and substrate used for each bird species (Zar 1999). Chi square tests were first used to test for overall independence of the three factors for each bird species. If significant differences were found, we used pair-wise tests for partial independence to determine which factors were dependent on one another.

Preference of each bird species for the various tree species was determined using chi-square tests. Again, we did not have enough observations on some tree species to analyze all species separately, and therefore used the “coast live oak”, “bay”, and “other” groupings for these data. The number of foraging observations on each tree species was used to determine observed frequencies of tree use, and the basal area of each tree species relative to total basal area was used to determine expected counts of use of each tree species. Basal area was used because it is proportional to canopy volume for many tree species (Waring et al. 1982), and thus it is a better predictor than stem count of the leaf area available to the birds for foraging. The eight sites were considered units of replication. Linear regression was used to compare bird use of a given tree species with prevalence of that tree species on the plots. Percent use of a given tree species was set as the independent variable and the percent of total basal area comprised by the given tree species was the dependent variable.

We used principal components analysis (PCA) to develop an index of sudden oak death impact for our eight sites. We then used this index to determine the effect of SOD on the foraging behavior of our two study species. We used five environmental variables as important indicators of sudden oak death infection on our sites: the percent of total basal area in dead coast live oak trees, the percent of total basal area in live coast live oak trees, the amount of light penetrating the canopy, the volume of coarse woody debris on the forest floor, and the percent of all coast live oaks that are symptomatic of SOD. These variables were selected because they represent the range of impacts that sudden oak death may have on a stand, as opposed to using a single metric. A PCA was conducted using a matrix of these five variables for each of our eight study sites using

PC-ORD (McCune and Mefford 1999). Results from the PCA indicated that the first axis extracted 74% of the variance. The eigenvalue of 3.724 was much greater than all other axes (all of which were less than 1), indicating that axis 1 was the only significant axis for interpretation (McCune and Grace 2002). This axis represents a strong gradient from high SOD impact (low proportion of live oaks, high proportion of dead oaks, high light penetration, high woody debris volume, and high incidence of SOD) to low impact of SOD. We adjusted this axis by taking the inverse of the PCA values, so that the index ran from least affected to most affected sites. We then made all values of PC1 positive, setting the least affected site as 1. The most affected site received a score of 6.18. These adjustments did not change the scale of the original PCA axis and were done simply to ease interpretation and analysis. We then employed a form of principal components regression (PCR), in which the SOD index was used as an independent variable for linear regressions against percent use of our three tree species categories (oak, bay, or other) to determine how tree use patterns relate to the amount of SOD impact on a site. PCR is a well-known means of reducing the dimensionality of a data set down to one or a few important gradients, and has been used in a variety of ecological studies to classify habitat (Howard and Larson 1985, Maurer 1986, Graham 2003). The resulting axes are frequently used in a multiple regression analysis; as only a single axis was significant in this study, the use of linear regression was acceptable.

RESULTS:

We collected a total of 596 foraging observations over the three-year course of this study (Table 2). We collected more chestnut-backed chickadee observations than oak titmouse observations (320 to 276, respectively). We were able to record at least 30 observations for both species from most sites, but in some cases we recorded fewer than 20 observations, and only 8 chickadee observations were recorded from one site. This was a result of the few nesting pairs of chickadees in the vicinity of this plot, rather than a lack of observer effort at this site.

Coast live oak was the tree used for the most raw numbers of foraging events for both chickadees (53% of observations) and titmice (65%, Table 3). California bay-laurel was the next most used tree by both bird species, and a total of 12 other tree, shrub, and plant species were used. Prey caught directly out of the air accounted for the remaining small fraction of foraging behavior. Chickadees used a significantly greater diversity of plant species for foraging than titmice, as measured by the Shannon index (chickadees: 1.21 ± 0.33, titmice: 0.62 ± 0.34; $P < 0.001$, t-test). The majority of foraging maneuvers by both species were directed towards foliage (Table 4). Bark, small twigs, and lichen were also used to a much lesser degree, and a handful of other substrates were used as well. Diversity of substrate use was not significantly different between chickadees and titmice (chickadees: 1.06 ± 0.24, titmice: 1.18 ± 0.13; $P = 0.36$, t-test). Chickadees perched and hung in approximately equal proportions to capture prey (~42% each), while perch gleans were the most common maneuver for titmice (60%, Table 5). Maneuver diversity was not significantly different between the species (chickadees: 1.18 ± 0.13, titmice: 1.22 ± 0.12; $P = 0.63$, t-test).

We compared bird use of SOD-symptomatic oaks to asymptomatic oaks and tested the null hypothesis that symptomatic or asymptomatic oaks were used in the same proportion by the birds as they are present in the environment. We accepted the null hypothesis, as we found no significant difference in use of symptomatic or asymptomatic oaks for both chickadees (X^2 = 3.41, df=7, P=0.84) and titmice (X^2 = 6.63, df=7, P=0.47). We also tested the null hypothesis that both bird species did not discriminate based on tree size. We rejected the null hypothesis, as both bird species used larger trees (measured by DBH) than expected, based on the trees present at the sites (chickadees: t=3.827, df=7, P<0.001, titmice: t=3.948, df=7, P<0.001). When comparing chickadees to titmice, there was no significant difference in the size of trees used between the two species (t=0.401, df=7, P=0.5).

Contingency table analysis was used to test for independence of tree species use, maneuver, and substrate use. Initial tests indicated overall independence for these variables for both species, so subsequent pairwise tests were used to test for partial independence (Zar 1999). We constructed stacked bar plots to display the pairwise associations for both bird species (Fig. 2 a-f). Maneuver used by chickadees was dependent on tree species (Fig. 2a: $\bullet^2$ = 11.55, df=4, P=0.02), and substrate used was dependent on maneuver (Fig. 2e: $\bullet^2$ = 15.8, df=6, P<0.0001). However, substrate was found to be independent of tree species (Fig. 2c: $\bullet^2$ = 7.67, df=4, P=0.26). For titmice, substrate used was dependent on both tree species (Fig. 2d: $\bullet^2$ = 18.28, df=4, P<0.01) and maneuver (Fig. 2f: $\bullet^2$ = 17.69, df=6, P<0.01), but maneuver was independent of tree species (Fig. 2b: $\bullet^2$ = 3.02, df=4, P=0.55).

Both chickadees ($r^2 =$ 0.84, P<0.01) and titmice ($r^2 =$ 0.69, P<0.01) showed increased use of living coast live oak on sites with more coast live oak present (Fig. 3a). However, only titmice showed disproportionately greater use of live coast live oak than expected ($\bullet^2$ = 68.9, df=7, P<0.0001); chickadees used oaks in approximately the same proportion as present on the sites ($\bullet^{2}$ = 6.82, df=7, P=0.45). Titmice used "other" tree species more on sites where this tree category was more abundant (r^{2}= 0.5, P<0.05; Fig. 3b); this trend was only marginally significant for chickadees (r^{2}= 0.39, P<0.10). Chickadees overall used "other" tree species more than expected ($\bullet^{2}$ = 70.8, df=7, P<0.0001), while titmice did not use "other" tree species more than expected ($\bullet^{2}$ = 10.54, df=7, P=0.16). Use of bay trees was not significantly correlated with the amount of bay present on our sites for either chickadees (r^{2}= 0.22, P=0.24) or titmice (r^{2}= 0.13, P=0.37; Fig. 3c). Bay was used significantly less than expected (avoided) for both species (chickadees: $\bullet^{2}$ = 14.55, df=7, P=0.04; titmice: $\bullet^{2}$ = 38.13, df=7, P<0.0001). Dead coast live oak trees were used very little by both species (7 total observations for chickadees, 6 for titmice).

Use of coast live oak by titmice declined significantly with increasing sudden oak death (r^{2}= 0.79, P<0.01, Fig. 4a). Use of other tree species (and non-tree plants) was greater on the heavily affected sites (r^{2}= 0.74, P<0.01). There was a trend towards greater use of bay by titmice on the more heavily affected sites (r^{2}= 0.39, P<0.10). The relationship between SOD and chickadee tree use was not linear across the range of SOD impact on our sites: a reciprocal (1/x) transformation of the x-axis produced the best fit for use of the three tree categories. Use of coast live oaks by chickadees was significantly negatively correlated with increasing SOD, but use appears to level off at about 30-40% on our most impacted sites (r^{2}= 0.75, P<0.01, Fig. 4b). Conversely, use of other tree species increases initially, but levels off at about 40-50% on the most impacted sites (r^{2}= 0.67, P<0.01). Use of bay does not change, regardless of SOD impact (r^{2}= 0.11, P=0.43).

DISCUSSION:

Birds are known to have strong preferences for certain tree species (Holmes and Robinson 1981), and these preferences have been linked to associated differences in prey availability (Robinson and Holmes 1982) and vegetation structure (Whelan 2001). The results from this study confirm the results of past work that emphasized the importance of oaks to chestnut-backed chickadees and oak titmice (Wagner 1981, Dahlsten et al. 2002). Oaks are preferred by titmice, while more diverse stands of tree species are preferred by chickadees. Both species avoided California bay trees for foraging. Both of our study species spent the majority of their time perch gleaning from tree foliage. There are, however, important differences in the patterns of tree species and foraging maneuvers used by the two birds. Chickadees are more diverse foragers than oak titmice: they use a greater variety of tree species for foraging while titmice concentrate on coast live oaks. This is in line with the results of Wagner (1981) who found that these species exploit different foraging niches. Both species use different maneuvers on different substrates, suggesting that the procurement of prey items from various parts of trees requires flexible foraging behavior. However, we have shown that chickadees foraging on different trees tend to use the same microhabitats while using a variety of maneuvers, while titmice use the same maneuvers in a variety of microhabitats. This suggests that chickadees diversify the way they procure prey items by shifting their behavior, while titmice broaden their search areas to find prey that can be easily exploited within a narrower set of behaviors.

The foraging preferences of these species most likely reflect the distribution of prey in the environment. Several studies have shown that birds shift their foraging behavior based on temporal changes in food availability (Keane and Morrison 1999, Naef-Daenzer et al. 2000) or in relation to vegetation structure (Holmes and Schultz 1988). Previous studies (Chapter 1) have shown that Lepidoptera abundance is significantly lower on bay trees than coast live oak trees. Lepidoptera larvae have been shown to be the most heavily represented group in the diets of related bird species (Grundel and Dahlsten 1991, Banbura et al. 1999). It is quite likely that Lepidoptera larvae are high quality food resource and a critical for these birds to feed to their young during the nesting period. Therefore, the very low abundance of any kind of arthropod prey on bay trees likely explains the avoidance of this tree as a foraging site. Prey distribution also likely explains why neither bird switched to bay trees on the sites heavily affected by SOD.

Bird species that do not respond to a disturbance by leaving a disturbed area are faced with a variety of challenges, including potential changes in stand structure and the availability of preferred foraging substrates. In this study, the loss of coast live oaks on heavily SOD-affected sites clearly represents the loss of a preferred foraging tree for titmice, and chickadees are at least faced with the loss of a common site for foraging, even if coast live oaks are used only opportunistically. The future ability of these bird species to persist in SOD-disturbed habitat may be a function of their ability to modify their behavior to exploit other tree species. This has been demonstrated for fairly dramatic disturbances, such as hurricanes or human disturbance (Perez-Rivera 1991, VanderWerf 1994), but disturbances that result in more subtle changes, such as losses of prey due to pesticides, can lead to behavioral compensation by birds (Hunter and Witham 1985, Sample et al. 1993, Howe et al. 2000). Forest pathogens such as *P. ramorum* may disturb an ecosystem in unique ways: for example, in contrast to the widespread disturbance caused by a fire, logging, or natural disaster, sudden oak death in California has selectively removed a forest dominant from some oak woodlands. Some prior work has shown that elm dieback caused by Dutch elm disease can impact bird community composition (Canterbury and Blockstein 1997), and may have minor impacts on the nesting behavior of some species (Osborne 1983, 1985). The ability of resident bird species to adjust to and survive in these altered woodlands may rest to a large degree on their ability to utilize the new forest structure. This is one of few studies that have demonstrated that dieback from a forest pathogen can lead to changes in the tree species used by birds.

Our results indicate that both chestnut-backed chickadees and oak titmice adopt different foraging strategies in stands that are heavily affected by SOD versus lightly affected stands. Rather than continuing to maintain the same tree use profile regardless of oak dieback, both species shift their foraging away from oaks in the heavily impacted stands. Both chickadees and titmice increase their use of “other” tree species; titmice also slightly increase use of bay trees, but not significantly so. Over the range of SOD infection represented by our eight sites, titmice seem to reduce their use of oaks slightly less than do chickadees. Chickadees, in fact, show a pattern in which use of oaks declines sharply over the first part of the SOD gradient, and then levels off. The “other” tree species that chickadees use may not provide prey of high enough quality to rely on these non-oaks exclusively. Alternatively, oaks may provide a critical resource that cannot be obtained on other plants, and thus chickadees must continue to use oaks a certain fraction of the time regardless of their abundance on the plots.

A lack of high quality food resources has been implicated in poor breeding success in a number of habitats (Holmes 1990, Riddington and Gosler 1995, Howe et al. 1996, Eeva et al. 1997), and the removal of a dominant woodland tree species such as cost live oaks will likely affect the prey available to these bird species. The ability of these two species to continue to nest in heavily affected woodlands may be a function of their ability to compensate for the loss of coast live oaks. Both of these bird species show some degree of compensation for the loss of coast live oaks by switching to a diversity of other tree species. However, oak titmice are being forced to switch away from their most preferred foraging site (oaks) and onto trees that are less preferred, while chickadees appear to be increasing their use of a diversity of “other” tree species, a preferred group of tree species. Titmice may be switching onto trees in which they are less efficient foragers or provide them with lower quality food resources. Conversely, chickadees show greater foraging flexibility and may be better equipped to deal with oak decline than are titmice. We do not yet know, however, if there are impacts of sudden oak death on the nesting success of these two bird species. Ultimately the true measure of whether either of these species compensate for the loss of oaks will be if they continue to meet the dietary demands of their broods and maintain the same or similar population levels in affected woodlands, or whether they simply leave the affected stands.

There has been an increased recognition in recent years of the importance of integrating an understanding animal behavior into conservation biology (Sutherland 1998, Caro 1999). Behavior has been shown to be an underutilized tool in terms of predicting landscape-level responses (Lima and Zollner 1996) and threats of extinction (Reed 1999). This study demonstrates that behavioral responses of two resident bird species may be important factors in their ability to persist after a disturbance. Both chestnut-backed chickadees and oak titmice are able to compensate, to some degree, for the loss of a dominant forest tree due to a pathogen. It is a diverse range of tree species that provide the necessary foraging substrates for both of these species on heavily SOD-affected sites. This is consistent with other studies that have shown that high forest diversity results in higher quality bird habitat (Hobson and Bayne 2000, Gabbe 2002, Girard et al. 2004), and that both vegetation structure and diversity are important at different scales (Bersier and Meyer 1994). As sudden oak death continues to spread in California, it may be necessary to implement a variety of forest management plans to either attempt to slow the spread of the disease or deal with impacted areas. Planners should consider not only the community and population level responses of resident bird species, but also how individual species respond behaviorally to fully understand the impact of disturbances. The responses of these two common, resident bird species in affected woodlands demonstrate the importance of oaks in our landscape, while at the same time reinforcing the importance of managing for resilient, diverse forest ecosystems.

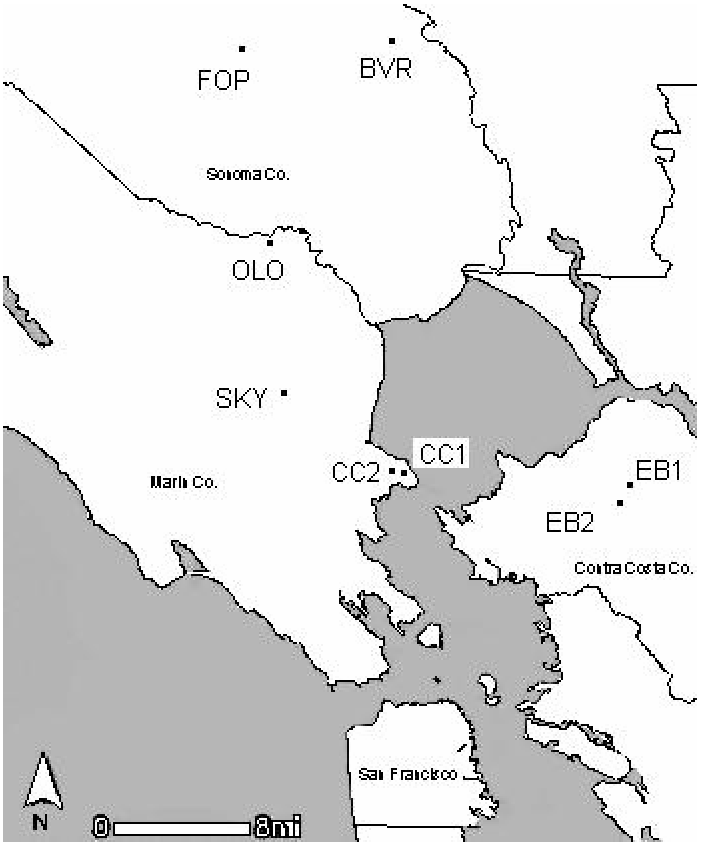

Figure 1. Map of the study sites selected for this study. Codes for the study sites are as follows: BVR = Bouverie preserve, CC1 = China Camp State Park (Miwok Meadows), CC2 = China Camp State Park (Back Ranch Meadows), EB1 = Briones Regional Park (Alhambra Valley), EB2 = Briones Regional Park (Bear Creek), FOP = Fairfield-Osborn Preserve, OLO = Olompali State Historic Park, SKY = Skywalker Ranch.

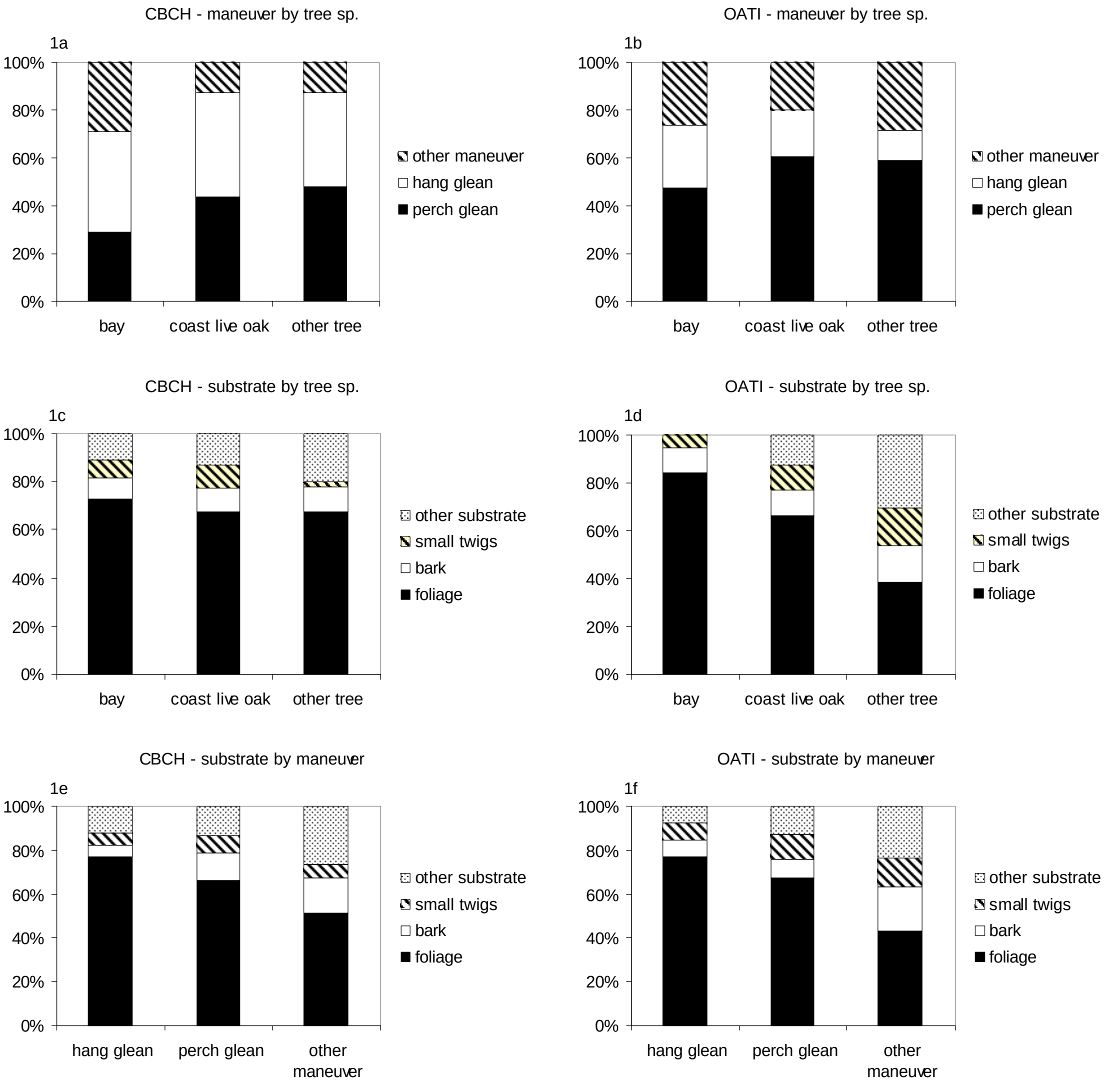

Figure 2 a-f. Stacked bar plots of pairwise comparisons of tree species used, maneuver used, and substrate used by chestnut-backed chickadees (CBCH) and oak titmice (OATI). Contingency table analyses with chi-square tests were used to test for independence (see text).

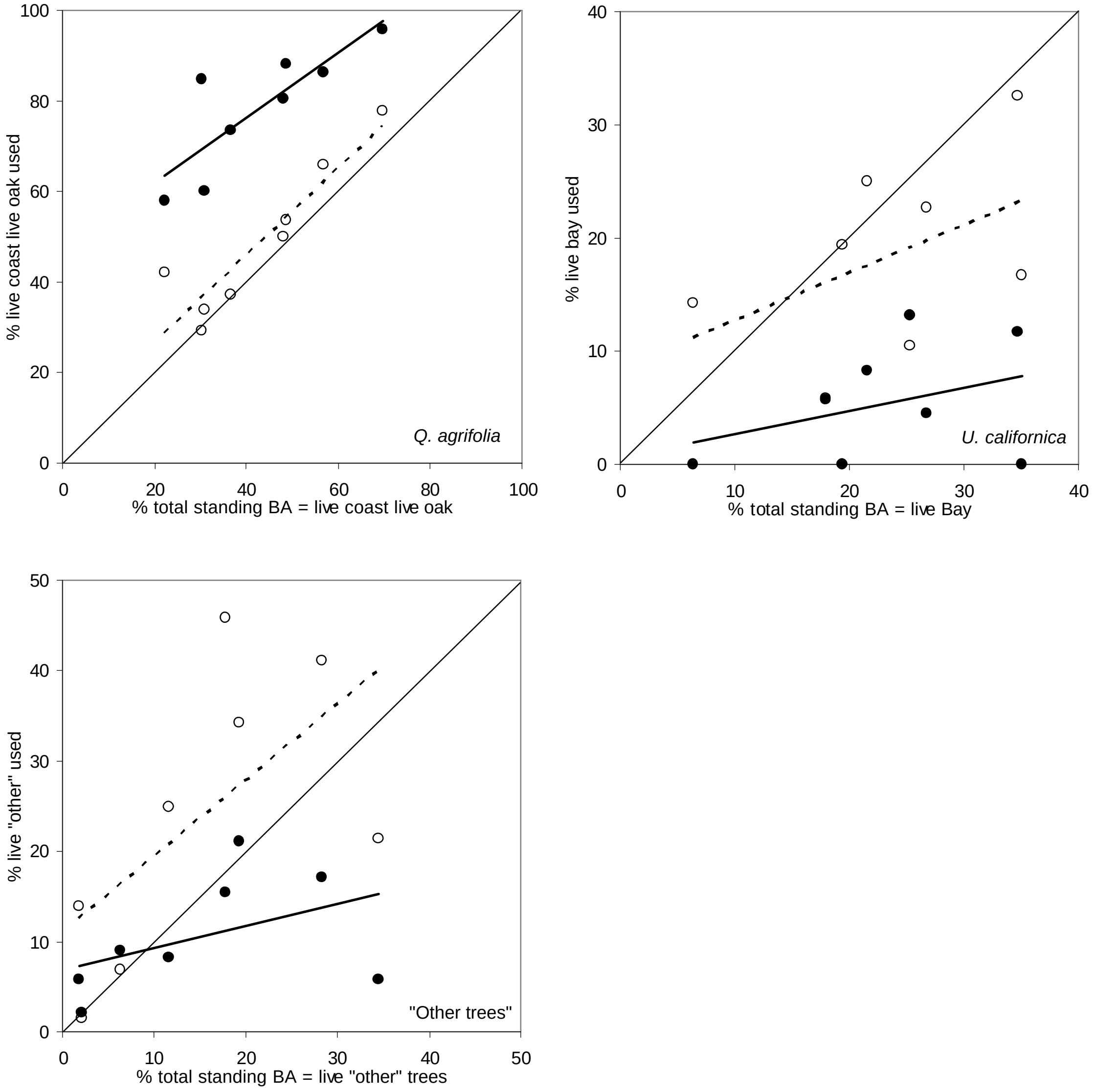

Figure 3 a-c. Preference figures for the three tree species categories for the two study species: chestnut-backed chickadees (open circles, dashed line) and oak titmice (closed circles, bold solid line). The diagonal line on each plot indicates “no preference”, i.e. equal proportion of a tree species used and present in the environment. Species lines that lie approximately along the diagonal indicate no preference, above the line indicate a preference, and below the line indicate avoidance. These were tested using chi-square tests (see methods).

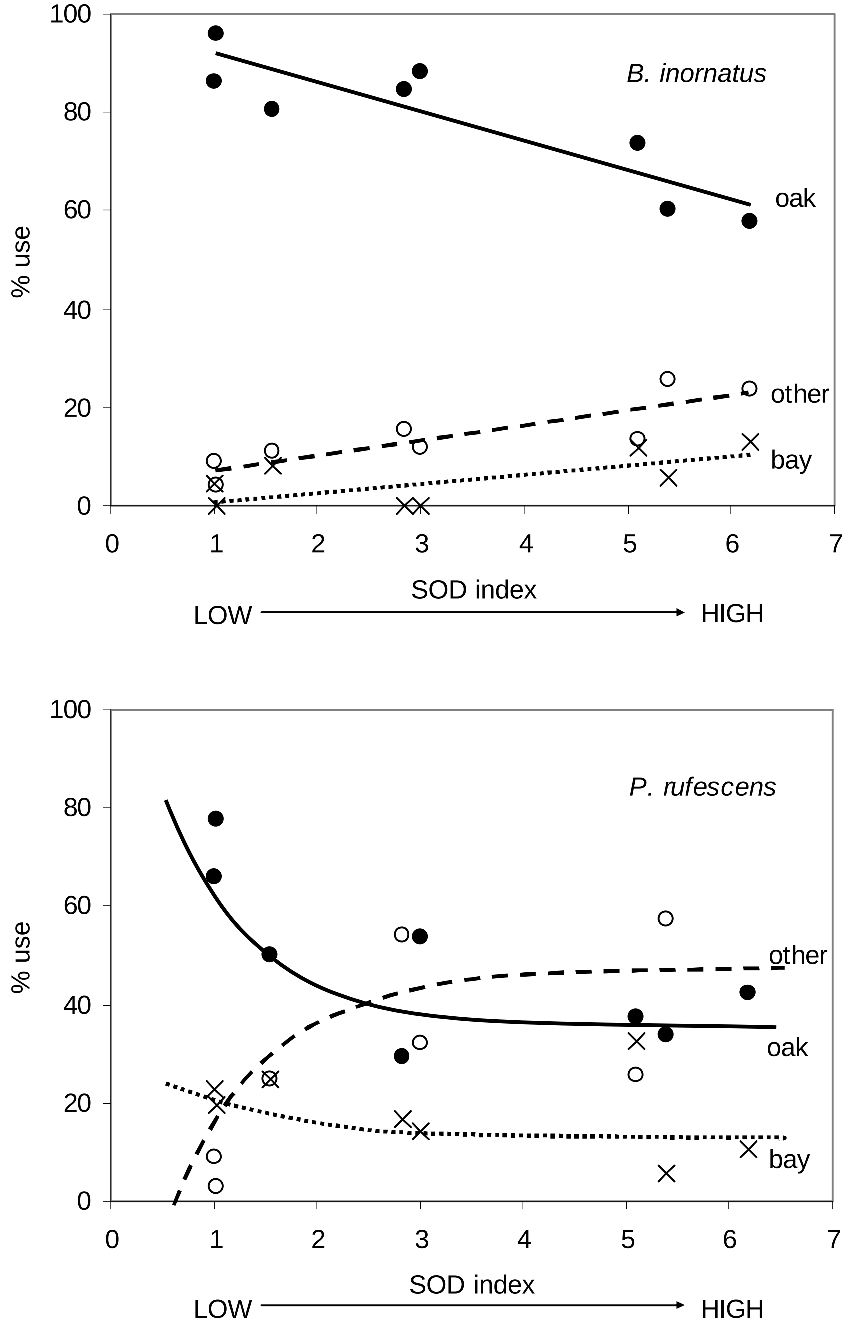

Figure 4 a-b. Percent use of three tree species categories relative to SOD dieback for *B. inornatus* (a) and *P. rufescens* (b). Coast live oak = closed circles and solid line, bay = "x" and dotted line, "other" trees = open circles and dashed line. SOD index runs from low to high along the x-axis. See methods for details of the SOD index.

	% live	% dead	light (mean ± SE)	CWD	% symptomatic	SOD index
BVR	55.06	13.31	0.06 ± 0.01	4.72	2.02	1.56
CC1	22.72	25.88	0.31 ± 0.02	46.86	11.00	6.18
CC2	34.12	23.44	0.13 ± 0	42.95	24.60	5.39
EB1	72.37	6.37	0.08 ± 0	2.51	7.21	1.02
EB2	61.63	6.01	0.08 ± 0	1.20	1.98	1.00
FOP	36.11	8.86	0.1 ± 0.02	9.14	12.15	2.84
OLO	46.85	5.66	0.19 ± 0.02	22.28	8.07	3.00
SKY	39.26	31.88	0.19 ± 0.01	26.74	18.85	5.10

Table 1. Summary of the vegetation data used in the principal components analysis to develop an index of SOD decline. % live and % dead refer the percent of live or dead coast live oak out of the total basal area of trees measured. Light is average % difn, or diffuse light through the canopy, from the five subplots. CWD is the total volume of coarse woody debris in m^3 per ha per site. Percent symptomatic is the percent of standing, live and dead, *Q. agrifolia* showing bleeding from stem cankers of all measured trees. Higher index values indicate greater impact from SOD. SOD index values were obtained from a principal components analysis (PCA) of the five habitat variables. A single axis was found to be significant. The PCA values were adjusted by making all values positive, and setting the lowest value equal to one. These adjustments were made for ease of interpretation and analysis, and did not change the relationships among the values for the sites.

	P. rufescens	*B. inornatus*	TOTAL
EB2	44	22	66
EB1	67	47	114
BVR	8	36	44
FOP	24	13	37
OLO	28	17	45
SKY	43	68	111
CC2	68	35	103
CC1	38	38	76
TOTAL	320	276	596

Table 2. Total foraging observations of chestnut-backed chickadees (*Poecile rufescens*) and oak titmice (*Baeolophus inornatus*) on the eight study sites. The study sites are in order from least to most impacted by SOD.

	P. rufescens	%	*B. inornatus*	%	total count	%
Quercus agrifolia	169	52.81	218	78.99	387	65.37
Umbellularia californica	55	17.19	19	6.88	74	12.50
Arbutus menziesii	28	8.75	8	2.90	36	6.08
Quercus kelloggii	30	9.38	8	2.90	38	6.42
Quercus douglasii	9	2.81	5	1.81	14	2.36
Lonicera hispidula	9	2.81	-	-	9	1.52
Heteromeles arbutifolia	7	2.19	4	1.45	11	1.86
Manzanita sp.	2	0.63	2	0.72	4	0.68
Pseudostuga menziesii	2	0.63	-	-	2	0.34
Quercus lobata	-	-	2	0.72	2	0.34
Toxicodendron diversilobum	2	0.63	-	-	2	0.34
Aesculus californica	-	-	1	0.36	1	0.17
grass	-	-	1	0.36	1	0.17
Corylus cornuta ssp. *californica*	1	0.31	-	-	1	0.17
no plant	6	1.88	8	2.90	14	2.36
TOTAL	320	100	276	100	592	100

Table 3. The plant species used and counts of foraging observations on each plant species by chestnut-backed chickadees (*Poecile rufescens*) and oak titmice (*Baeolophus inornatus*). “No plant” indicates foraging observations in which prey was taken directly from the air.

	P. rufescens	%	*B. inornatus*	%	total count	%
foliage	221	69.06	178	64.49	399	66.95
bark	30	9.38	29	10.51	59	9.90
small twigs	18	5.63	25	9.06	43	7.21
lichen	15	4.69	16	5.80	31	5.20
dead foliage	11	3.44	10	3.62	21	3.52
cones/fruit/flowers	13	4.06	3	1.09	16	2.68
small twigs/lichen	4	1.25	6	2.17	10	1.68
n/a	4	1.25	2	0.72	6	1.01
leaf litter	2	0.63	4	1.45	6	1.01
broken branch	2	0.63	2	0.72	4	0.67
downed wood	-	-	1	0.36	1	0.17
TOTAL	320	100	276	100	596	100

Table 4. The substrates used and counts of foraging observations on each substrate by chestnut-backed chickadees (*Poecile rufescens*) and oak titmice (*Baeolophus inornatus*). “N/a” indicates no substrate.

	P. rufescens	%	*B. inornatus*	%	total count	%
perch glean	137	42.81	165	59.78	302	50.67
hang glean	135	42.19	49	17.75	184	30.87
hover glean	27	8.44	19	6.88	46	7.72
tear	11	3.44	23	8.33	34	5.70
peck	4	1.25	8	2.90	12	2.01
probe	3	0.94	5	1.81	8	1.34
hang tear	1	0.31	3	1.09	4	0.67
perch glean/tear	1	0.31	3	1.09	4	0.67
lunge glean	-	-	1	0.36	1	0.17
peck glean	1	0.31	-	-	1	0.17
TOTAL	320	100	276	100	596	100

Table 5. The foraging maneuvers used and counts of foraging observations for each maneuver by chestnut-backed chickadees (*Poecile rufescens*) and oak titmice (*Baeolophus inornatus*).

CHAPTER 3

Cavity nesting birds in coast live oak (*Quercus agrifolia*) woodlands impacted by *Phytophthora ramorum*: use of artificial nest boxes and arthropod delivery to nestlings.

INTRODUCTION:

The invasive, non-native, forest pathogen *Phytophthora ramorum* has emerged as a significant threat to oak woodlands in California. *P. ramorum* has been implicated as the causal factor in the widespread mortality of coast live oaks (*Quercus agrifolia*), termed “sudden oak death” (SOD), along the northern and central California coast (Rizzo et al. 2002). Dozens of plant species have been demonstrated to be hosts for this pathogen, but coast live oaks are one of only a few species that show dramatic, stand-level dieback once infected. Thousands of oaks have died across 14 counties in California, and the wide host range of *P. ramorum* suggests that oak habitats across the state, and potentially around the country, are at risk (Meentemeyer et al. 2004). Continued oak dieback from SOD could have severe consequences for the bird communities that use oak habitats.

Oak woodlands are structurally and floristically diverse and harbor an equally diverse community of over 110 breeding bird species (Verner 1980). Insectivorous, cavity-nesting birds constitute an important guild of about a dozen species of breeding birds within these woodlands. A number of habitat variables that are important to these birds could be impacted by SOD, including stand density, tree species composition, canopy density, and cavity availability, as well as abiotic factors, such as moisture and temperature, which may change with the disappearance of the forest canopy.

The nesting success of birds in affected oak woodlands may be affected directly in a number of ways by these changes: more open stands may result in thermal stress for nestlings, populations of nest predators could potentially increase as stands become more open, or the loss of cavity bearing trees may make nest sites scarce. Alternatively, cavity-nesting birds could be impacted indirectly by changes to lower trophic levels. Our previous work (Chapters 1 and 2) has shown that populations of foliar arthropods could be changed or reduced in stands affected by SOD. Changes to this important prey group may ultimately impact the nesting success of cavity-nesting birds if prey quality is reduced, or if adult birds are unable to adequately provision their nestlings. Cavity-nesting birds have been shown to be sensitive to habitat structural change and key members of diverse forest communities (Bednarz 2004) and thus it is important to understand the impacts that an invasive forest pathogen such as *P. ramorum* might have on this group of birds

The purpose of this study was to determine whether SOD indirectly affects the nesting behavior of cavity-nesting birds in coast live oak woodlands. We examined the species of birds using nest boxes and the types of prey delivered by adult birds to nestlings in eight sites across the San Francisco Bay area that represent a gradient from high to low SOD impact. We determined if SOD, through its effect on dominant canopy tree mortality, impacts several key aspects of insectivorous, cavity-nesting bird nesting behavior including nest box occupancy, survivorship of nestlings, foraging effort, and prey delivery. Other studies have shown that bird communities can change drastically along gradients of disturbance (Blair 1996), and also that changes in lower trophic levels can have consequences for birds at the population level (Holmes 1990, Canaday 1997).

We predict that increasing impact from SOD will lead to increased use of artificial nest boxes, changes in the diet provided by adult birds to their nestlings, increased foraging effort by adult birds, and reduced nestling survivorship along our gradient of SOD impact.

METHODS:

Study sites:

We selected eight oak woodland stands in Marin, Sonoma, and Contra Costa counties for this study (Fig. 1). The stands ranged in elevation from 50 to 450 m and slopes ranged from 20-50%. At each stand, we established a single, one ha square plot within and around which the various aspects of the study were conducted (the "core" plot). One corner of the plot was randomly selected, with the constraint that the rest of the plot must fit within the same or similar habitat type. We selected stands that were composed mainly (> 40% of basal area) of coast live oak (*Quercus agrifolia*). California bay-laurel (*Umbellularia californica*) was a co-dominant at most of our sites. Several other tree species were present in lower abundances on the sites, including madrone (*Arbutus menziesii*), toyon (*Heteromeles arbutifolia*), California black oak (*Quercus kelloggii*), Oregon white oak (*Quercus garryana*), and Douglas-fir (*Pseudotsuga menziesii*). The eight sites represented a range of SOD incidence (many infected trees to few infected trees), time since initial *P. ramorum* infection (very recent to as long as 10+ years), and degree of tree damage related to *P. ramorum* (few to many killed and damaged trees). Damaged trees were those for which the trunk had snapped and fallen, or those which had lost one or several main stems. Damaged trees also included those in which the crown had died and was beginning to turn brown.

Vegetation monitoring:

We monitored trees on the plots within five, .08 ha circular sub-plots randomly established within the 1 ha main plot. All trees (> 10 cm DBH) on the sub-plot were tagged and monitored over the course of the study from 2002 to 2004. Tree height and symptoms of *P. ramorum* infection were recorded. Light measurements were made using an LAI-2000 plant canopy analyzer (Li-Cor, Inc., Lincoln, NE), which measures percent diffusion of light through the canopy. Volume of coarse woody debris (m^3 per ha) was recorded on each sub-plot using the Brown (1974) protocol. For details of the vegetation monitoring protocols see Brown and Allen-Diaz (2005). A summary of the vegetation data used in our bird foraging analysis (see below) is provided (Table 1).

Sudden oak death decline index:

We developed an index of oak woodland decline (“SOD index”) against which we can compare our nesting data. The index is based upon habitat structural features of oak woodlands that may be impacted by *P. ramorum* infection. The habitat variables and scores for the SOD index are shown in Table 1. Details of the decline index were provided in Chapter two.

Study species:

Chestnut-backed chickadees (*Poecile rufescens*) and oak titmice (*Baeolophus inornatus*) are both common cavity-nesting bird species in California’s oak woodlands. Both of these species are permanent residents who feed primarily on arthropods during the breeding season, but supplement their diet with seeds and other plant material (Cicero

2000, Dahlsten et al 2002). Oak titmice in particular feed upon acorns during the winter months (Cicero 2000). These species initiate nest-building in late February to early March, lay their first clutch in late March, and nestlings have generally fledged by mid-June. Both of these species are considered secondary cavity nesters or weak excavators, and thus tend to nest in preexisting holes rather than excavate their own cavities.

Nest methods:

Nine artificial nest boxes (Schwegler "woodcrete" nest boxes, Schwegler Vogel- & Naturschutzprodukte, Schorndorf, Germany) with 32 mm entrance holes were established on fence posts on each of our 1 ha plots. These boxes have been used successfully in other studies of chickadees and titmice in nearby locales (Klientjes and Dahlsten 1992, 1994). Three transects of three boxes each were set up at 50 m spacing. The entrance hole to the box was approximately 2m above the ground. On three plots the boxes were set up in the fall of 2001, and the other five plots were set up in the fall of 2002. These boxes were checked at least once a week from late February to late June during 2002, 2003, and 2004. We recorded presence of nesting material, eggs, nestlings, and if appropriate, reason for abandonment (predation, etc.). A nest was considered active if at least 1 egg had been laid. Adults were captured at the nest and banded with aluminum and plastic color bands. Nestlings were also banded with aluminum bands at between 12-15 days old. For each of the eight plots, we calculated the percent of eggs that eventually fledged the nest for each species. Linear regression was used to determine the relationship between SOD decline (vis a vis the decline index) as the independent variable and survivorship and percent occupancy as dependent variables (Zar 1999). Distributions of the dependent variables were checked and determined to approximate normal distributions without transformations. We used percent of laid eggs that eventually hatched and fledged the nest as our measure of nesting success. We considered the following groups for analysis: all four species that used the nest boxes together, chickadees and titmice combined as an arboreal insectivore guild, and titmice alone. We used $\bullet < 0.05$ as the cutoff for significance, but considered $\bullet < 0.10$ to represent a trend.

Territories:

We mapped observations of individual oak titmice and chestnut-backed chickadees to help determine the number of territories present on or within 50 m of our 1 ha study plots, giving a total area of 4 ha for this portion of the study. While observing the foraging behavior of these two species for another study (see Chapter 2), we marked the locations of any birds seen on a map. If possible, we marked several locations to which the bird traveled and foraged or sang. On the same maps, we also marked the location of any natural nest cavities that we found were occupied by either of these species. We then used these maps to reconstruct rough territories of titmice and chickadees and determine the number of chickadee and titmice pairs in the 4 ha area.

Videos:

Digital video cameras were used to record visits of adult chestnut-backed chickadees and oak titmice birds to nest boxes. The cameras used were Panasonic PV DV-51, 18x optical zoom cameras with 120 minute digital video tapes. The cameras were set up facing the side of the box on tripods approximately 2 m from the nest. The video cameras were focused such that, when a bird landed on the outside of the box at the nest opening, the upper 2/3rds of the bird was visible. This allowed a clear view of any prey items held in the beak of the bird. Videos were taken at occupied nests between 0600 and 1000. Each nest was filmed at least once and as many as twice during the breeding season: once when nestlings were between 1-4 days old and a second time when the nestlings were between 12-15 days old.

These videos were used to determine the length of each foraging trip away from the nest (“foraging effort”) and the type of prey delivered to nestlings. In most cases, adult birds resumed what appeared to be normal foraging behavior within 10 minutes of the start of recording. We did not use videos in cases where the adult birds seemed disturbed for longer periods. We measured the length of a foraging trip from the time when a bird left the box until it first landed back on the box. If the birds had been color banded we could distinguish the individual adults from one another, otherwise we assumed the birds alternated when taking trips for the purposes of determining trip length. We calculated foraging effort directly as the mean number of seconds per trip, and also on a “per nestling” basis to account for effects of different brood sizes.

We identified the types of prey that the birds delivered to nestlings by viewing the videos frame by frame. Resolution of the videos was good and in many cases identification to order was possible. However, for very small prey, or when the bird entered the box very quickly, we could not determine the type of prey, or even whether the bird had any prey at all. Each prey item was recorded as a single observation, even if the bird had several prey items in its beak at once. The total number of observations is therefore the total number of prey items identified, plus any unidentifiable trips. For prey summary results we used the results from both recordings per box.

We used t-tests to compare foraging effort and nestling diet (% Lepidoptera and order richness) between chickadee and titmice nestlings (Zar 1999). These analyses used each nest box as an independent sampling unit, and we pooled data if more than one video was recorded from a box. Linear regression was use to determine if there was a relationship between foraging effort (seconds per foraging trip away from the nest) and SOD decline, based on our SOD index. We also regressed two measures of dietary diversity against SOD decline: prey richness (the number or orders represented by prey) and percent Lepidoptera in nestling diet. For these regression analyses, we only used pooled data from multiple recordings per box and used each site as an independent sampling unit, and thus data from individual nests within a site were grouped for analysis. We analyzed the data on a per species basis (chickadees and titmice separately), and also with the species grouped together as a guild of insectivorous cavity-nesters.

RESULTS:

Over the course of this 3 year study there were a total of 171 boxes available for nesting (27 in 2002 and 72 in 2003 and 2004). Of these boxes, only 27 (15.79%) contained active nests at any point (Table 2), although other boxes did show signs of roosting or initial nest building. Oak titmice were the most common nesting species in the boxes (10 nests), followed by Chestnut-backed chickadees and Bewick's wrens (8 nests each). A single pair of Violet-green swallows nested in one box. Due to the low number of total nests in this study, many of the data on nestling survivorship, prey, and foraging effort are based upon only one or two nests per species per plot. It is important, therefore, to view these results with some caution.

The active nests were not distributed equally across the sites (Table 3). Total box occupancy ranged from zero nests (site OLO) to nearly 30% occupancy (SKY). We found a marginally significant trend (• = 0.10) for increased use of nest boxes as SOD impact increased ($r^2 = 0.41$, $P = 0.09$). However, the differences in occupancy by site may be a result of the fact that boxes were established at three heavily impacted sites (CC1, CC2, and SKY) a year earlier than the other sites.

Very few nests of any bird species failed over the course of the study (2 out of 27), defined as nests that had eggs but fledged no young (Table 4). Chestnut-backed chickadees had the largest clutches, the most nestlings, and fledged the most young of any species, although none of the between species differences were significant (ANOVA, $P>0.05$). A greater percentage of chickadee eggs eventually hatched and fledged the nest than other species (91%). In contrast, Bewick's wrens fledged 78% of eggs, while titmice fledged 81%.

The total number of chestnut-backed chickadee territories over two years on our sites ranged from 2 at BVR to 7 at EB2 (Table 5). Chickadees appear to be most abundant on our EB1 and EB2 sites. Titmouse territory numbers ranged from a low of 2 (CC2) to a high of 9 (SKY).

A total of 11 prey categories were identified in the bills of chickadees and titmice as they were delivering prey to their nestlings (Table 6). We observed 335 chickadee trips and 293 titmouse trips. For many foraging trips, it was not possible to identify prey items either because the bird flew into the nest box too quickly, or because the prey item was obscured in some way. Overall, we were able to identify prey items on 37% of chickadee trips and 58% of titmouse trips. Titmice delivered prey from all 11 of the prey categories to their nestlings, while chickadees only delivered 7 of the more common prey types. Lepidoptera larvae comprised 41% of the identified diet of chickadees, and nearly 59% of the identified titmouse diet. Spiders, Homoptera, and Orthoptera (mainly Gryllacrididae) were other common groups for both species.

Nestling survivorship (% of eggs that fledged) was not significantly related to our SOD decline index for any of the groups we considered: all species (r^2 = 0.21, P = 0.30), chickadees and titmice together (r^2 = 0.17, P = 0.36), and titmice only (r^2 = 0.19, P = 0.46). The lack of fit for the "all species" grouping and the "arboreal insectivore" grouping was largely due to low survivorship at our BVR site. This low survivorship was the result of a single chickadee nest that failed entirely. If we remove this site from the analysis the fits improve dramatically, showing a significant decline in nest success with increasing SOD for all species (r^2 = 0.96, $P < 0.001$), and the arboreal insectivore guild (r^2 = 0.68, $P < 0.05$).

Foraging trip length per nestling, measured as seconds away from the nest per foraging trip, was significantly greater ($P<0.05$) for titmice than chickadees (Table 7). The difference was also significant at the • = 0.10 level for trip length when considered per nest rather than per nestling. There were no significant differences between species for either of our two dietary measures: mean % Lepidoptera or mean number of orders ($P > 0.10$).

Foraging trip length increased significantly ($P<0.05$) with SOD impact when chickadees and titmice were pooled as an arboreal insectivore guild (Table 8). Trip length was only significant at the • = 0.10 level when considered on a per nestling basis. There were no significant relationships between SOD decline and foraging trip length for chickadees and titmice analyzed separately.

We found no significant relationship between SOD decline and either the percent Lepidoptera in the nestling diet or the order richness of nestling diet ($P >> 0.10$).

DISCUSSION:

One of the most striking results of this study is the very low occupancy rates of the nest boxes in this study. Fewer than 16% of the total boxes available to the birds were used over the course of three breeding seasons. Thus, conclusions about many aspects of this study, which are contingent on larger sample sizes of nests, must be interpreted with caution. The number of natural nest cavities is a limitation on cavity-nesting bird populations in many habitats, so providing nest boxes is a useful management tool for increasing populations of cavity-nesters (Newton 1994). However, our low box occupancy results are more in line with the work of Waters et al. (1990) in oak-pine woodlands in California. They found that cavity-nesting bird populations did not change as a result of artificially reducing the number of natural nest cavities. Our results support the same result: natural cavities are probably not a major limiting factor for these cavity-nesters in coast live oak woodlands. Our territory data support this conclusion as well; there were an average of almost five chickadee and titmouse territories within each of the eight, four ha study areas within which we monitored territories. There are few studies of density of these species in the same or similar habitat in California for comparison, although Hertz et al. (1976) found that chestnut-backed chickadee territories occupied about 1.3 ha each, and titmice about 0.5 - 0.6 ha each in mixed blue oak (*Quercus douglasii*) - coast live oak habitat. Although we did not measure territory size, but rather number of territories per plot, these results are roughly in line with our findings. Thus, it appears that our plots still support healthy population levels of these species despite low box occupancy. Considering that the numbers of territories that we recorded did not include territories of Bewick's wrens or other species that might use the boxes, we would have expected higher box occupancy on our sites.

Because of the significant habitat changes that have resulted from *P. ramorum* infection on our sites, we expected that cavity availability would be negatively affected. We did not measure cavity availability directly, but it is likely that natural cavity abundance would decline on sites heavily impacted by SOD as coast live oak trees die and fall to the ground. Coast live oaks that have been infected with *P. ramorum* have lower survival than asymptomatic trees (McPherson and Standiford 2005), have extensive trunk cankers, and are frequently attacked by beetles (McPherson et al. 2000). If these trees tend to fall quickly after death as a result of SOD infection, they may not have time to develop cavities or be used as cavity trees. The end result would be a decline in the number of natural cavities on a heavily impacted site due to the loss of oaks. Showalter and Whitmore (2002) found a similar pattern in eastern forests affected by gypsy moth defoliation, in that the increase in snag numbers was only a temporary benefit to cavity-nesters. The trend in box use that we witnessed supports this hypothesis: box use tended to be greater on the heavily impacted sites. However, this result may be confounded by the fact that boxes on our three most heavily impacted sites were set up six months earlier than on some of the less impacted sites. There was an increase in box usage from 2002 to 2004, and thus the apparent SOD effect may actually reflect the local bird community adjusting to the use of artificial boxes.

There were no differences in egg, nestling, or fledgling production between the three species (oak titmice, chestnut-backed chickadees, and Bewick's wrens) that commonly occupied the boxes in this study. The clutch size and fledgling results from this study are in line with other studies of the Oak titmouse (Dixon 1954, Cicero 2000). Mean clutch size of Bewick's Wrens was slightly higher, but within one standard deviation, of that reported elsewhere in the literature for California (6.38 versus 5.5 eggs per nest, Kennedy and White 1997). Chestnut-backed chickadees on our oak woodland study sites appear to have greater nesting success than in other habitats in California. Numbers of eggs, nestlings, and fledglings are greater in this study than in reported values from Monterey pine forests and riparian zones in nearby counties, and from the mid-elevation Sierra Nevada (Dahlsten et al. 2002). Results from these three species suggest that the habitat quality of coast live oak woodland is as great or greater than other studied habitats in California.

We used percent of eggs that eventually fledged the nest as a measure of survivorship in this study. Our hypothesis was that survivorship would decline with increasing SOD, as adult birds would have more difficulty provisioning their nests in the disturbed habitats. Several other studies have demonstrated that disturbances such as fire (Haugaasen 2003), pollution (Eeva et al 1997), insecticide application (Howe et al 1996), and gypsy moth defoliation (Pelech and Hannon 1995) can impact nestling growth and survivorship. Very few studies, however, have examined how a forest pathogen might impact nestlings (Canterbury and Blockstein 1997, Darveau et al 1997). The lack of active nests in our nest boxes clearly made it difficult to make firm conclusions about how SOD impacts nest success. In several cases we had only a single nest per site, and one of our sites had no nests, so our results for a given site may be highly skewed by a single clutch or brood. A trend of decreasing survivorship (for all species pooled) with increasing SOD was found only when one of our sites with a single failed nest was removed from analysis. This result suggests future studies should follow more nests in more study plots over a longer period of time to determine if this is a true trend or a spurious result.

Our diet results are based on prey items delivered to nestlings, rather than on stomach samples from adult birds. While adult and nestling diets are sometimes substantially different, (Markman et al. 2002), they are frequently very similar, or at least show a great deal of overlap (Ydenberg 1994). Caterpillars dominated the nestling diet of both of our focal study species, comprising over 41% of chickadee diet and almost 59% of titmouse diet. Spiders were also important in the diets of both species. Our chickadee results are similar to other results from chickadees in nearby Monterey pine habitats (Kleintjes and Dahlsten 1994). Our nestling diet results of oak titmice are also similar to those of Klientjes and Dahlsten (1992), although they found Orthopterans to be more prominent in titmouse nestling diet than did we. We witnessed no plant material being delivered to nestlings of either species, which contrasts with published values for adult oak titmice. Other studies have found plant material constituting from 27%-57% during the spring, and higher in the winter months (Cicero 2000 and references therein).

We measured the impact of SOD on the diets of chickadees and titmice by comparing their nestling dietary diversity (“order richness”) and dominance of the nestling diet by caterpillars ("% Lepidoptera"). Caterpillars have been shown to be important in the diets of related bird species, and nestlings have been shown to exhibit reduced growth (Goodbred and Holmes 1996) and feeding efficiency (Banbura et al 1999) when caterpillar prey are scarce. Increased caterpillar biomass has been shown to initiate a dietary switch away from spiders in British tits (Naef-Daenzer et al 2000). Other songbirds have been found to switch prey items when arthropod abundance is reduced through insecticide applications (Sample et al 1993). We found no differences in either of our measures of nestling diet as SOD increases, suggesting a high degree of dietary stability across our sites, despite a wide variation in SOD impact. This result suggests two possibilities: either that the prey base of these birds is relatively constant at the plot level across our study sites, or that adult birds are continuing to procure the same prey items despite changes to their habitat. In Chapter 1, we found that both tree species and infection status affects the capture of potential prey items at the scale of the individual tree. We do not have plot-wide data on prey item availability, but we can assume that as proportions of trees in our plots change, the proportions of the insects on those trees will change at the scale of the plot as well. Therefore, the plots where many oaks have died are therefore likely to have different arthropod assemblages than the intact plots. We therefore believe that the adult birds are procuring food for their young from different communities of arthropods from the plots along our SOD gradient.

This evidence suggests the adult birds are continuing to procure similar food items across our SOD gradient, despite differences in the arthropod community. In Chapter 2, we described the foraging behavior of chestnut-backed chickadees and oak titmice on these same study sites. We found that both of these species change the proportions of different tree species used for foraging as SOD increases. The observation of high dietary stability across our sites in this study suggests that as these birds modify the proportions of trees upon which they feed, they manage to continue to procure a high quality diet for their young.

Impact from SOD may also manifest itself as a change in the amount of time spent away from the nest by adult birds. We measured "foraging effort" as the amount of time spent away from the nest by adult birds on foraging trips. We expected that on the heavily impacted sites, adult birds would need to spend longer on a given foraging trip to procure food, due to the disturbance in the oak woodlands from SOD. We hypothesized that the changes in foraging behavior exhibited by the birds on heavily affected sites (Chapter 2) may entail a cost in terms of the amount of time spent to find high quality prey items. For each species separately, we were unable to detect an affect of SOD on foraging effort. However, when we considered the species together as an "arboreal insectivore" guild, we found that adult birds did spend longer on each foraging trip as SOD impact increased. The relationship was not as strong when we considered foraging trip on a per nestling basis, but there was still a trend. Our results are similar to other studies that have shown some minimal effects of prey reduction or habitat disturbance on feeding. Some studies found a decrease in feeding rate (Howe et al 2000) or increased searching behavior (Naef-Daenzer 1999) in areas of reduced arthropod prey, while others showed increased feeding rate in sub-optimal (fragmented) habitats (Nagy and Smith 1997, Nour 1998). These results are more consistent with the former two studies, perhaps suggesting that the adults are compensating by taking longer trips to search for high quality prey items that may be scarce on high SOD sites, rather than making more trips for low quality prey.

The results from this study build upon other work on arthropod populations (Chapter 1) and insectivorous bird foraging (Chapter 2) in oak woodlands impacted by SOD. We expected that changes to the arthropod populations in affected woodlands and shifts in foraging behavior would affect aspects of the nesting behavior of our study species. Our hypotheses that box occupancy would increase, nestling diet would change, that foraging effort would increase, and that nestling survivorship would decrease in heavily affected woodlands, were not supported or only partially supported. Our box occupancy rate data may have been confounded by the length of time that boxes had been established on the various sites. Nestling diet remained remarkably stable across our study sites, despite evidence of shifts in foraging behavior (Chapter 2). Foraging effort did appear to increase on the most heavily affected sites, but we could only detect this change at the guild level, rather than for individual species. Finally, our weak evidence for decreased nestling survivorship on heavily affected sites must be viewed with caution due to low sample sizes. A lack of active nests in our nest boxes was the most significant setback that we encountered in this study. However, this in itself is an interesting finding as it supports past work that has shown nest cavities to not be a limiting factor in other oak woodlands.

The effects of sudden oak death that we have shown are small and relatively subtle. However, continued spread of the disease and increasing impact from SOD may exacerbate the impacts that we have demonstrated. While a large area of coast live oak woodland has been affected by SOD already, It is small relative to the total susceptible habitat. The ultimate fate of these woodlands are unknown, but an increase in the relative abundance of California bay trees, the other common tree in these woodlands, is likely (Brown and Allen-Diaz 2005). This may mean a sharp decline in the abundance and type of preferred prey, specifically caterpillars, that are available to birds, as bays are known to harbor fewer foliar arthropods (Chapter 1). Additionally, chickadees and titmice choose not to switch to bay trees for foraging as oaks decline (Chapter 2). The ability of these cavity-nesting birds to compensate for the loss of coast live oaks may decline both as the scale of the disease increases across California, and also as currently infected trees die, causing further decline within already impacted woodlands.

We believe that future studies should continue to focus on the effects of this important disease on many aspects of avian natural history. Continuing nest box studies on a larger scale and over a longer period of time will help researchers understand details of nesting behavior, such as nestling survivorship and prey delivery. There are no studies that have examined the utility of bays as cavity trees. Supplementing nest box studies with more studies on natural nests, cavity availability, and territory size will help ecologists predict the ultimate effects of SOD on bird populations as these woodlands change. This will also help managers decide on appropriate actions to mitigate effects the effects of SOD, while promoting cavity nesting bird diversity and abundance.

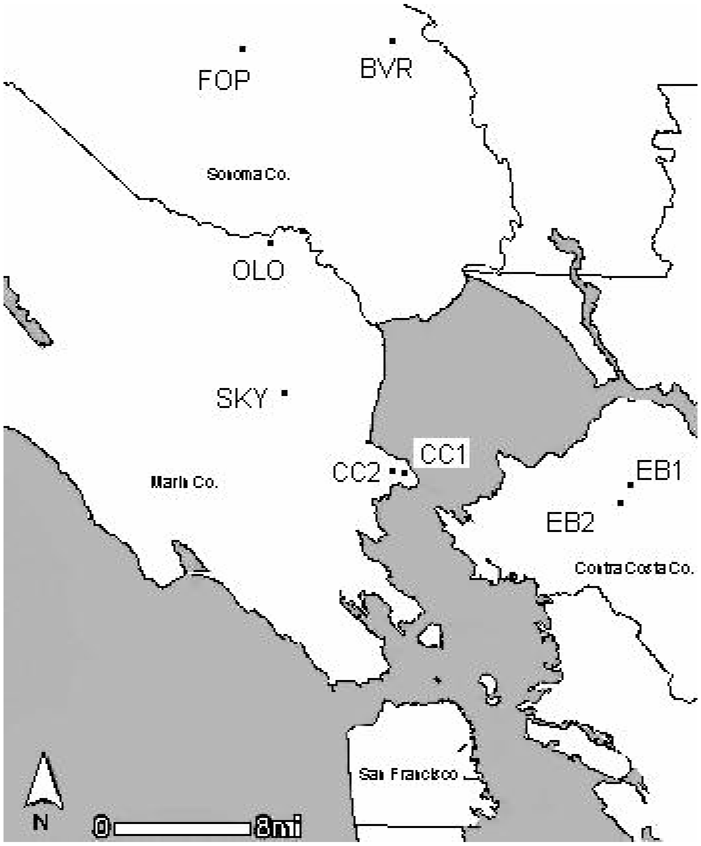

Figure 1. Map of the study sites selected for this study. Codes for the study sites are as follows: BVR = Bouverie preserve, CC1 = China Camp State Park (Miwok Meadows), CC2 = China Camp State Park (Back Ranch Meadows), EB1 = Briones Regional Park (Alhambra Valley), EB2 = Briones Regional Park (Bear Creek), FOP = Fairfield-Osborn Preserve, OLO = Olompali State Historic Park, SKY = Skywalker Ranch.

	% live	% dead	light (mean ± SE)	CWD	% symptomatic	SOD index
BVR	55.06	13.31	0.06 ± 0.01	4.72	2.02	1.56
CC1	22.72	25.88	0.31 ± 0.02	46.86	11.00	6.18
CC2	34.12	23.44	0.13 ± 0	42.95	24.60	5.39
EB1	72.37	6.37	0.08 ± 0	2.51	7.21	1.02
EB2	61.63	6.01	0.08 ± 0	1.20	1.98	1.00
FOP	36.11	8.86	0.1 ± 0.02	9.14	12.15	2.84
OLO	46.85	5.66	0.19 ± 0.02	22.28	8.07	3.00
SKY	39.26	31.88	0.19 ± 0.01	26.74	18.85	5.10

Table 1. Summary of the vegetation data used in the principal components analysis to develop an index of SOD decline. % live and % dead refer the percent of live or dead coast live oak out of the total basal area of trees measured. Light is average % difn, or diffuse light through the canopy, from the five subplots. CWD is the total volume of coarse woody debris in m^3 per ha per site. Percent symptomatic is the percent of standing, live and dead, *Q. agrifolia* showing bleeding from stem cankers of all measured trees. Higher index values indicate greater impact from SOD. SOD index values were obtained from a principal components analysis (PCA) of the five habitat variables. A single axis was found to be significant. The PCA values were adjusted by making all values positive, and setting the lowest value equal to one. These adjustments were made for ease of interpretation and analysis, and did not change the relationships among the values for the sites.

	Year (total nests available)			
	2002 (27)	2003 (72)	2004 (72)	TOTAL (171)
B inornatus	1 (3.70%)	3 (4.17%)	6 (8.33%)	10 (5.40%)
P. rufescens	-	2 (2.78%)	6 (8.33%)	8 (3.70%)
Thryomanes bewickii	-	5 (6.94%)	3 (4.17%)	8 (3.70%)
Tachycineta thalassina	-	1 (1.39%)	-	1 (0.46%)
TOTAL	1 (3.70%)	11 (15.28%)	15 (20.83%)	27 (15.79%)

Table 2. Total numbers of nests and percent occupancy for each species for each of the three years nest boxes were established. Numbers in parentheses next to years are the total number of boxes available across our study sites.

	# nests	total avail.	% occupancy
BVR	3	18	16.67
CC1	7	27	25.93
CC2	4	27	14.81
EB1	1	18	5.56
EB2	2	18	11.11
FOP	2	18	11.11
OLO	0	18	0.00
SKY	8	27	29.63
TOTAL	27	171	15.79

Table 3. Total number of active nests and percent occupancy of nest boxes on our eight study sites.

	# nests	nests failed	% failed	eggs/nest	nstl/nest	fledg/nest	% eggs hatched	% nestlings fledged	% eggs fledged
B inornatus	10	0	0.00	6.40 ± 1.07	5.70 ± 1.34	5.00 ± 1.83	89.06	87.72	78.13
P. rufescens	8	1	12.50	7.00 ± 1.20	6.88 ± 1.46	6.38 ± 2.72	98.21	92.73	91.07
Thryomanes bewickii	8	1	13	6.38 ± 1.06	5.50 ± 2.45	5.50 ± 2.45	81.48	100.00	81.48
Tachycineta thalassina	1	0	0	4.00 ± 0.00	4.00 ± 0.00	3.00 ± 0.00	100.00	75.00	75.00
TOTAL	27	2	7.4	6.48 ± 1.08	5.93 ± 1.89	5.48 ± 2.43	91.43	92.50	84.57

Table 4. Nesting data from the four species of birds that used nest boxes in our study. Failed nests are those in which the female laid eggs but no fledglings left the nest. Egg, nest, and fledgling data are all mean ± standard deviation.

	P. rufescens		*B. inornatus*	
	total	mean per year	total	mean per year
BVR	2	1	5	2.5
CC1	4	2	7	3.5
CC2	4	2	2	1
EB1	6	3	6	3
EB2	7	3.5	3	1.5
FOP	4	2	3	1.5
OLO	4	2	3	1.5
SKY	5	2.5	9	4.5
mean per site	4.5	2.3	4.8	2.4
TOTAL	36	18	38	19

Table 5. Total number of territories of chickadees (*P. rufescens*) and titmice (*B. inornatus*) from 2003 and 2004 on our eight study sites and the per year average.

	P. rufescens			*B. inornatus*		
	total obs.	% of identified	% of total	total obs.	% of identified	% of total
Lepidoptera	51	41.13	15.22	99	58.58	33.79
Araneae	24	19.35	7.16	14	8.28	4.78
unidentified Arthropod	17	13.71	5.07	6	3.55	2.05
Homoptera	7	5.65	2.09	15	8.88	5.12
Orthoptera	16	12.90	4.78	4	2.37	1.37
Diptera	1	0.81	0.30	9	5.33	3.07
Phasmidae: Timemidae	0	0.00	0.00	7	4.14	2.39
Coleoptera	2	1.61	0.60	3	1.78	1.02
gall	0	0.00	0.00	3	1.78	1.02
Hymenoptera: Formicidae	0	0.00	0.00	2	1.18	0.68
Dermaptera	0	0.00	0.00	1	0.59	0.34
nothing (empty bill)	6	4.84	1.79	6	3.55	2.05
no identification	211	-	62.99	124	-	42.32
identified	124	-	37.01	169	-	57.68
total observations	335	-	-	293	-	-

Table 6. Total number of prey, percent of total identified prey, and percent of total trips of each prey category identified from nest box videos.

	P. rufescens	*B. inornatus*	df	t	P	
mean trip length	284.62 ± 75.08	490 ± 254.95	8.36	2.17	0.06	•
mean trip length per nestling	40 ± 12.44	80.86 ± 40.86	8.45	2.69	0.03	*
mean % leps	0.43 ± 0.28	0.61 ± 0.19	9.94	1.46	0.17	ns
mean no. orders	2.64 ± 1.14	3.44 ± 1.93	13.26	0.32	0.32	ns

• $P < 0.1$
* $P < 0.05$

Table 7. Summary of foraging effort (trip length) and dietary (% Lepidoptera in diet and "order richness") data for our two focal study species. Means are per nest box ± standard deviation. If more than one video was taken per box the data were pooled. F- and P-values are from one way ANOVAs comparing *P. rufescens, B. inornatus,* and *Thyromanes bewickii*. *Tachycineta thalassina* was omitted as there was only a single nest.

	P. rufescens			*B. inornatus*			species pooled		
	df	r^2	P	df	r^2	P	df	r^2	P
mean trip length	4	0.28	0.36 ns	4	0.42	0.24 ns	6	0.58	0.05 *
mean trip length per nestling	4	0.29	0.35 ns	4	0.45	0.22 ns	6	0.48	0.09 •
mean % Lepidoptera in diet	4	0.29	0.35 ns	4	0.32	0.32 ns	6	0	0.90 ns
mean # orders in diet	4	0	0.96 ns	4	0.29	0.35 ns	6	0.01	0.87 ns

• $P < 0.1$
* $P < 0.05$

Table 8. Results of linear regressions between foraging effort (trip length) and dietary (% Lepidoptera in diet and "order richness") data as dependent variables and our SOD index (see methods) as the independent variable. If more than one video was taken per box the data were pooled.

CHAPTER 4

Biodiversity of Coleoptera and other leaf litter arthropods and the importance of habitat structural features in a Sierra Nevada mixed-conifer forest.

INTRODUCTION:

The maintenance of high biodiversity is a goal shared by many conservationists and managers, either due to the increased productivity and ecosystem processes that may be associated with areas of high biodiversity (Tilman 1996, McCann 2000), or because it is a admirable goal in its own right (Simberloff 1999). There is increased recognition among ecologists that temperate forests deserve increased attention in studies of biodiversity, and that baseline conditions need to be established for long-term studies on the effects of management to be successful (Noss 1990, Ehrlich 1996, Simberloff 1999, Perry 1998). Arthropods have repeatedly been shown to be valuable ecological indicators (Kremen et al. 1993), and can be substantially impacted by intensive management (Niemela 1997). Despite this, the arthropod assemblages in one of the most important forest ecosystems in California, Sierran mixed-conifer forests, are almost entirely unknown (Kimsey 1996).

The large geographic area and the range of management practices used in the mixed-conifer forests of the Sierra Nevada mountains of California make this ecosystem particularly worthy of increased study. Over two-thirds of the 6000 km^2 of mixed-conifer forest in the Sierras is available for timber harvesting, while only 8% is formally designated for conservation (Davis and Stoms 1996). This habitat is important for birds and other wildlife (Verner and Larson 1989, Block and Morrison 1990), and management in these forests has been shown to have important impacts on plant diversity (Battles et al. 2001). The diversity of arthropod groups in California as a whole is high (Kimsey 1996), but, aside from some studies examining high altitude endemic populations (Papp 1978), the species diversity of Sierran arthropods is unknown. Knowledge of litter-dwelling groups such as Coleoptera is particularly rare (Kimsey 1996). This group, as well as other litter arthropods such as ants (Hymenoptera: Formicidae) and spiders (Araneae), are particularly important to study due to their roles as predators, decomposers, and herbivores (Petersen and Luxton 1982).

Our primary objective in this study was to determine the richness and diversity of leaf litter arthropods, with special attention to the Coleoptera, in a representative Sierran mixed-conifer forest. Various structural features of the forest ecosystem play important roles in maintaining diversity and abundance of leaf litter arthropods at many scales (Noss 1990), and understanding the value of these habitat features is critical in managed forests (Nilsson 2001). Therefore, we also determined the habitat characteristics of particular importance to the most common species and groups of species on our study sites. These results will provide a baseline for future comparisons of leaf litter fauna in Sierra Nevada ecosystems and help determine the potential effects of future forest management.

The results in this paper are pre-treatment data from a larger study examining the effects of prescribed burning and harvesting treatments on many aspects of the mixed-conifer ecosystem, such as vegetation, soils, and wildlife (Stephens and Moghaddas

2005*a*, *b*). For the larger study, treatments were implemented in the summer and fall of 2002 after this pre-treatment work, and initial post-treatment data were collected in 2003. For the purposes of this analysis, we use data primarily from 2001, prior to implementation of the treatments. However, we do use data from all years of the study for overall richness estimates (species lists). A subsequent paper and analysis (Chapter 5) will focus exclusively on the effects of treatments on the leaf litter fauna at Blodgett Forest.

METHODS:

Study site:

We conducted this study at Blodgett Forest, an experimental forest owned by the University of California (Fig. 1). Blodgett is located in the mid-slope of the Sierra Nevadas, between approximately 1200 – 1500 m, near the Georgetown Divide (38º 52'N, 120º 40' W). Olsen and Helms (1996) provide a detailed description of the forest, its history, and current management regimes. In short, the site is typical of a highly productive, Sierran mixed-conifer forest (Allen 1988). Large scale logging was undertaken between 1900 and 1913, and most of the property was harvested with the seed-tree method at that time. Large fires in the early part of the century also burned much of the forest, and were a common feature of the landscape prior to European settlement (Stephens and Collins 2004). Fire has been largely excluded from the property at a large scale since the middle of the 20th century. The University of California has managed Blodgett since the mid-1930's and has undertaken a range of harvesting practices on the property, including a variety of even- and uneven-aged management regimes, single tree selection, and retention of old growth reserve stands. The site is dominated by five major overstory conifer species, Douglas-fir (*Pseudostuga menziesii*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), and incense cedar (*Calocedrus decurrens*), and one major hardwood, black oak (*Quercus kellogii*). The understory is dominated by a variety of shrub and herb species.

Blodgett Forest covers approximately 1200 ha and is divided into 90 compartments with a mean area of 13 ha each. Twelve compartments were selected at random for this study and 25 0.04 ha circular plots were established in each. The plots were spaced 60 m apart on a grid system within each compartment. Tree species, DBH, total height, height to live crown base, and crown position were recorded for all trees larger than 10 cm DBH. Fuel loads, litter, and duff measurements were made along two random azimuth transects from the center of each vegetation plot. Refer to Stephens and Moghaddas (2005*a*, *b*) for a full description of plot setup and the vegetation and CWD characteristics measured.

Arthropod collection:

We used pitfall traps to collect leaf litter arthropods on our plots during the summers of 2001, 2002, and 2003. The drawbacks of pitfall trapping have been well explored (Spence and Niemela 1994), but they remain one of the simplest and most efficient means of sampling ground dwelling arthropods. Pitfall traps do not sample abundance of a species directly, but rather a function of a species abundance and activity, which can be affected by habitat. We refer to species abundance in this paper with an understanding that our catches reflect “activity-density”. Nonetheless, sufficient sampling over the length of the active period has been found to provide reasonable abundance estimates for groups such as carabid beetles (Baars 1979, Niemela et al. 1990). Each year we randomly selected 5 plots from each of the twelve compartments for trapping. Five traps were placed at each plot along a random azimuth from the plot center. The trap design was similar to that used by Lemieux and Lindgren (1999), which minimizes incidental catches of reptiles and small mammals, with propylene glycol used as a killing agent and preservative. We made collections at four monthly intervals during the summer, the first soon after snowmelt in late May and at subsequent four week intervals. Traps were kept open for five days at a time. This compromise between trapping over several months for short periods of time allowed us to sample the active period for most leaf litter invertebrates at Blodgett with a low risk of depleting the local fauna. Traps were kept closed in the field between trapping periods to avoid the “digging in” effect (Digweed et al. 1995). Arthropod samples were collected in vials of 95% ethanol for storage and sorting.

Sorting and identification:

Arthropod samples were sorted in the lab by K. Apigian and trained technicians. All arthropods were initially sorted into “morphospecies”, and a reference collection was made. Identifications of beetles and ants were made by comparisons with museum reference collections, identification keys, and experts. Any groups from the reference collection that were split after identification were rechecked for accuracy. If we were unable to identify all beetles to species, we assigned them a morphospecies label (i.e. *Actium* sp. 1, or unknown Staphylinid sp. 1). It was not feasible to identify some difficult ant genera (e.g. *Formica*) to species given the volume of ants collected. Thus, for our quantitative comparisons, we grouped ants by genera, although a complete species list was made. Spiders were identified as Lycosidae or "other", as Lycosids were by far the most abundant family captured. In several traps we collected hundreds of small, immature Lycosids that likely fell into the trap with an adult, which were later excluded from analyses.

Data from all three summers of trapping were used to formulate complete species lists of Coleoptera (beetles) and Formicidae (ants) and report total captures of each species or genus. We also calculated total species richness for all years of the study. All other analyses utilize only data from the collections during the summer of 2001, prior to harvesting and fire treatments being implemented on the site. In several cases, one or several traps within a plot were disturbed or destroyed by wildlife, we therefore consolidated our catches by plot and divided by the number of traps to standardize abundances of our taxa. We also summed our four monthly samples together per plot. Some compartments were inaccessible late in the summer of 2001 due to active logging operations, so we also divided by the number of months sampled to give us 60 plots for analysis in 2001 that represent abundances of our taxa "on a per trap, per month" basis.

We calculated a total species area curve for all years of trapping, and for 2001 alone, using PC-Ord (McCune and Mefford 1999) to determine how adequately we sampled the beetle community at Blodgett. We calculated alpha, beta, and gamma diversity for the beetle community. Alpha diversity was calculated at two scales: based on the mean plot species richness (sample size=60) and the mean compartment species richness (sample size=12). Gamma diversity was calculated as the total diversity across all of our samples, and was determined separately for 2001 and all years combined. We also calculated beta diversity, a measure of heterogeneity of the beetle community across sample units, at the plot and compartment scale using Whittaker's (1972) equation: • = (•/•)-1.

As even very intensive sampling fails to account for all species in most insect communities, we calculated several non-parametric estimators of species richness. Raw species richness totals form a lower bound of the estimate of total species richness. The non-parametric Chao 1, Chao 2, first-order jackknife, and second-order jackknife estimators predict total species richness based on some combination of the abundance and incidence of singletons and doubletons in the sample (see Colwell and Coddington 1994 for equations). The bootstrap method (Smith and van Belle 1984) uses a resampling procedure to estimate richness. The relative bias, precision, and accuracy of these procedures has been reviewed at length with little overall consensus on the best procedure (Smith and VanBelle 1984, Palmer 1990, Colwell and Coddington 1994, Hellman and Fowler 1999). The least biased predictor has been found to be a function of sample size, or proportion of the total community sampled. For smaller sample sizes, the Jackknife and Chao estimators have been found to be least biased (Palmer 1990, Hellman and Fowler 1999), but at larger sample sizes they all show positive bias, particularly in a community with many rare species (Palmer 1995). The bootstrap procedure has been found to be less likely to overestimate with large sample sizes (Smith and van Belle 1984, Poulin 1998). We calculated the Chao 1, Chao 2, first-order jackknife ($Jack_1$), second-order jackknife ($Jack_2$), and bootstrap (Boot) estimators for our beetle community for all years of sampling, 2001 only, and took means at the plot and compartment scales. We compared these estimates of alpha, beta, and gamma diversity with our raw species richness totals.

We used rank-abundance diagrams ("Whittaker plots") to depict the diversity and evenness of the beetle community at our study site. Log_{10} abundance of each species was plotted against species rank. The shape of these plots is useful in interpreting the structure of the community (Whittaker 1965, Krebs 1989). We also plotted our species abundance data using geometric (x2) classes on the x-axis and abundance on the y-axis to observe how closely our data conform to a lognormal distribution (Preston 1948).

We tested the influence of a variety of structural habitat variables on abundance of select leaf litter taxa using multiple regression. Fifteen taxa, or groups of taxa, with high representation in our catches were chosen for analysis: total Coleoptera, Carabidae, Tenebrionidae, Staphylinidae, four beetle species with greater than 10% representation in 2001 (*Eleodes cordata*, *Pactopus horni, Metrius contractus,* and Aleocharine sp. 2), total ants, four ant genera with greater than 10% representation (*Camponotus, Formica*, *Leptothorax*, and *Liometopum*), total spiders, and Lycosidae. We also analyzed the effects of the habitat variables on our 5 species richness extrapolations ($Chao_1$, $Chao_2$, $Jack_1$, $Jack_2$, and Boot). Losses of some traps made it impossible to use raw species richness per plot as a variable in our multiple regressions, as the number of species captured is dependent on sampling effort. We therefore used rarefaction (Hurlbert 1971) to standardize plot richness to the smallest sample (n = 24 individuals). The habitat variables used were: mean percent canopy cover, mean percent slope, mean percent bare mineral soil, presence of logging (skid) trails on the plot (Y or N), mean duff depth (cm) , mean litter depth (cm) , mean fuel depth (cm), total CWD vol/ha (m^3), total conifer basal area (m^2), total hardwood basal area (m^2), and sapling density per hectare. These analyses were conducted at the plot level, for a total sample size of 60. The plots were not entirely randomly located across the forest, but rather, nested within compartments. They were, however, located far enough apart (min 60 m) to be considered independent. Additionally, several compartments were adjacent and plots were often located closer to plots in adjacent compartments rather than to those in their own compartment.

Mean abundances of the various taxa taken “per trap, per month” were used and multiplied by 100 to give more reasonable means and parameter estimates. When necessary, we transformed our variables with either a log(x+1) or a • (x + 0.5) function (Zar 1999) to improve normality and homogeneity of variance. We removed outlier plots with a mean of greater than 2 standard deviations away from the species mean. We then used a mixed, stepwise multiple regression function in JMP (SAS institute, 2003) to select terms to be included in the final models. This procedure alternates between adding and removing terms from the model in a stepwise fashion depending on a set criterion (prob to enter model < 0.25, prob to leave > 0.25)

We ran a canonical correspondence analysis (CCA) of a matrix of our beetle species against an environmental matrix with the same habitat variables listed above in

PC-Ord. CCA was used because we were interested specifically in how the beetle community was structured relative to these habitat variables which might be impacted by various forest management treatments (McCune and Grace 2002). We removed beetle species that appeared in fewer than 20% of our plots, and removed outlier plots with an average of greater than 2 standard deviations away from the overall mean, measured by Sorenson distance. We conducted a Monte Carlo randomization test (99 randomizations) to test the null hypothesis that there is no relationship between the species and environmental matrices and to determine if the eigenvalues and species-environment correlations were significant. Vectors which reflect the strength of the habitat variables with our plots and species were displayed on biplots of the first two ordination axes.

RESULTS:

For all three summers of this study combined we captured 15,683 beetles in 51 families and 278 species (App. 1). Fifty-nine percent of the catch was represented by three families: the Carabidae, Tenebrionidae, and Staphylinidae. We were able to identify 90% of the beetles to genus, and 43% to species. Approximately a third of the unidentified species were Staphylinids. Over 46,000 ants were captured, and 24 species in 12 genera were represented (App. 2). Of the over 6800 spiders captured in the traps, one third of the overall individuals were wolf spiders (Lycosidae). Many other arthropods were captured in the traps as well: Archaeognatha and Collembola were captured in great abundance, and numerous mites and Opiliones were caught as well.

We calculated a species accumulation curve to determine if we had successfully sampled most of the beetle assemblage at Blodgett Forest (Fig. 2). An asymptotic curve indicates a community has been well sampled and most of the species have been counted; the curve for all years of sampling shows continued accumulation of species even with three summers of intensive sampling. The curve for 2001 has clearly not reached an asymptote, and overall species accumulation (richness) appears to be at least 2 standard deviations less than the curve for all years, suggesting lower overall richness in 2001 relative to the other years.

The non-parametric estimators of species richness also all estimated greater overall gamma richness than the raw species richness total (Table 1). The bootstrap estimator predicted an additional 25 species in the total community, while the second-order jackknife estimator predicted that we had not sampled over 147 beetle species. Estimates based on the 2001 data alone showed a similar pattern of predictions by the various estimators. Notably, all of the estimators applied to the 2001 failed to predict the total species richness achieved in three years of sampling; all of the estimators were at least 26 species short. Estimates of alpha diversity also varied greatly at the plot and compartment scale: The Chao 2 estimator and second-order Jackknife both estimated that we had undersampled the beetle richness by half at both the compartment and plot scales. The bootstrap estimate was more conservative, predicting a richness increase of fewer than 20% at both scales. The beta diversity of 6.6 at the plot level was high, suggesting a great deal of heterogeneity in the beetle community between plots; heterogeneity was less when considered at the compartment scale. As each of the non-parametric estimators predicted a relatively greater increase in alpha than gamma diversity, beta diversity estimates were concordantly lower than with the raw species totals.

Rank-abundance (r-a) diagrams display more information about community evenness and dominance than simple diversity indices (Krebs 1989). The r-a diagram for the beetle assemblage at Blodgett Forest shows a pattern of few species dominating the total capture (Fig. 3). Fifty percent of the total capture is, in fact, dominated by only 6 species (*E. cordata*, *P. horni*, *M. contractus*, Aleocharinae sp. 2, *D. californica*, and unknown Ptiliid sp. 1). The long right tail on the diagram is indicative of an assemblage with many very rare species: over 25% of the species were represented by only a single individual, and over 42% of species by 3 or fewer individuals. The plot of species versus abundance (Fig. 4) again reveals that a large proportion of the species in our total sample are relatively rare, as is typical of a logarithmic or lognormal distribution (Preston 1948, May 1975).

Multiple regression of our habitat variables (Table 2) on our taxa and richness measures revealed important habitat features for some groups (Table 3). Exceptions were for the common carabid beetle *M. contractus*, for which only 2 variables with low explanatory power were retained, and total Coleoptera abundance, for which the null model was the best fit to the data. There was considerable variation in which other variables were important for the other taxa; each of the variables was important for at least one group, although percent canopy cover and total hardwood basal area were important for many groups. For beetle species and families, canopy cover and both hardwood and conifer basal area were important in many cases. No single variable was of primary importance to all ant genera, although percent bare mineral soil, duff depth, and sapling density appear to be only marginally important. Wolf spiders (Lycosidae) were negatively associated with steep slopes, skid trails, and high hardwood basal area. The pattern for total spider abundance was likely driven by this common group, but duff depth was also important.

There were several common variables that were important across all of our beetle species richness measures. Conifer basal area, percent bare mineral soil, and canopy cover were of primary importance, while fuel depth was of lesser importance.

Only the first axis of the CCA of the beetle-plot data was found to be significant by a Monte Carlo randomization test (Table 4). This axis explained relatively little of the structure in the data (8.6%). The species-environment correlation was significant along this axis ($P<0.05$). The relationship between the habitat variables and the most common species confirms the results of the multiple regressions of the common beetle species: *P. horni* is strongly positively related to high bare mineral soil, Aleocharinae sp. 2 is associated with plots with high conifer basal area, *E. cordata* is found on plots with high hardwood basal area, and *M. contractus* is not strongly associated with any of the habitat vectors. The CCA results also suggest that E. cordata is associated with relatively high fuel depth, a result not obtained from the multiple regressions. Several other less common species are displayed as well; several show close association with high conifer basal area, and percent bare mineral soil, and fewer with fuel depth and hardwood basal area. The plots were not grouped into distinct clusters in ordination space indicating an absence of well-defined assemblages among the plots (Fig. 4B).

DISCUSSION:

There is a critical lack of information about even the most basic aspects of biodiversity in our temperate forests, including, specifically, the number of species present (Ehrlich 1996). Information on mammal and bird diversity in western forests of the United States is generally available for many habitat types, but information on the most speciose groups, specifically beetles and other soil arthropods, is sorely lacking. This is the first study to document leaf litter biodiversity in the Sierra Nevadas of California, and one of only a few studies in the western US to report richness of beetles and other leaf litter groups.

Despite the high beetle richness we found from our samples, it is clear that we have only sampled a portion of the full diversity of beetles and ants at Blodgett Forest. Pitfall trapping inherently limits our collection to active, ground-dwelling species, although there is an incidental by-catch of families more generally associated with other microhabitats (e.g. Scolytidae, Cerambycidae). The shape of our species accumulation curve indicates that sampling at 60 plots for three summers (in fact, with 4 collections of 5 traps at each of those plots) was not sufficient to result in an asymptote. The question of how many leaf litter beetle species there are in this habitat is still open. The non-parametric estimators of species richness that we used to estimate total richness were not in agreement: estimates ranged from a low of 312 species (the bootstrap estimate), to a high of 435 species (the Jackknife 2 estimator). It is quite likely that the higher estimates are positively biased as a result of the high number of rare species in our sample (Palmer, 1995). The shape of the species-accumulation curve also suggests that the higher estimates are not conservative enough. The bootstrap estimate is likely closer to the actual number of litter beetle species, given the volume of sampling and the number of individuals captured in this study (Smith and van Belle 1984). As we only collected a relatively small number of genera, we did not generate a species accumulation curve for our ant collection, but the 12 genera and 24 species are probably much closer to the true number of litter dwelling species at Blodgett than our beetle catch estimates.

Our measurements of alpha, beta, and gamma diversity reveal an interesting pattern. Raw species richness from 2001 alone was much lower than for all years of the study, as would be expected due to lower sampling. But each of the richness estimators underestimated the total, three-year richness based upon this one year of sampling. This is an indication that there is considerable between year variation in species presence (or, at least, catchability) and that multi-year sampling is necessary to approach a true diversity estimate. The higher three year total than the estimate based on 2001 may also be due to the fact that fire and harvesting treatments had been implemented on some of the study plots in 2002, and thus may have attracted specialized species that are adapted to those habitats. This would also explain the pattern of the 2001 species accumulation curve appearing to be significantly shallower than the total curve.

We used beta diversity in this study as a measure of heterogeneity of beetle assemblages across our study site, independent of any environmental gradient (Whittaker 1972). Our results indicate that there is a great deal of heterogeneity of beetle assemblages at the plot level, and much less so at the compartment level. This simply indicates that there are more species shared between two compartments than between two plots, as would be expected given that compartment samples are pooled plot samples. The high beta diversity at the plot level, however, is a good indication that the high species richness on our study site is partitioned very unequally on fairly small spatial scales. This is consistent with Niemela et al.'s (1996) work on carabid beetles, who found that this group can display heterogeneity in assemblage membership over scales as small as 10-15m. Indeed, Blodgett Forest is fairly homogenous at the scale of the compartments that we sampled, possibly due to the long history of management, including logging and fire exclusion for much of the past century. This is partially an artifact of the design of this study, as compartments were randomly selected among stands with similar histories to provide similar initial conditions for testing effects of fire and logging treatments. Nonetheless, there is still a great deal of small scale heterogeneity within the compartments, brought about by natural forest processes, and management activites such as group selection harvests.

Our rank abundance diagrams indicate that the beetle community at Blodgett follows a common lognormal or logarithmic distribution. Distinguishing between these two distributions is difficult with communities that have been inadequately sampled. Continued sampling would theoretically push the distribution of Figure 4 to the right and reveal more of the distribution if the community fit a lognormal pattern. The fact that we do not see a mode, or "peak" in our species abundance distribution suggest inadequate sampling, or that the community fits a classic logarithmic distribution as predicted by Fisher et al. (1943). The most notable features of these diagrams is the long "right tail", indicating the presence of many rare species in the forest, and the dominance of the community by only a few species. A lognormal species abundance pattern is typical in communities that are structured by multiple independent, interacting factors (May 1986), as is likely the case with our beetle collection.

Understanding the habitat structural features that are important for insect taxa allow us to make better predictions about the effects of management (Niemela 1996) and may help to determine the structural features that are critical in determining desirable stand structures, such as in old-growth stands (Willett 2001). Among the elements that have been shown to impact leaf litter arthropod diversity and abundance are volume and connectivity of coarse woody debris (Schiegg 2000, Kehler 2004), dead trees (Kaila 1997), soil conditions (Sanderson et al. 1995), microclimate (Judas et al. 2002), and leaf litter type (Koivula et al. 1999). Our habitat analyses, using multiple regression and CCA, indicate that a variety of structural features are important in determining the diversity and abundance of our focal taxa. For most of our groups, however, there is clearly a great deal of variation that is not explained by the habitat elements that we selected. The fact that the null model was the best fit to our total Coleoptera abundance, and also that our ordination results explained relatively little of the total variation in beetle species abundance, indicates that there are likely a number of important factors that structure the beetle community at Blodgett forest. Many of these are known to be important but were simply not measured or included in our analyses, such as soil pH (Sanderson 1995), moisture (Antvogel and Bonn 2001), bulk density (Rushton et al. 1991), plant species richness (Jeanneret et al. 2003), and other factors. This result is consistent with others who have found that abundance of groups as diverse as beetles are not consistently explained by only a few habitat features (Humphrey et al. 1999, Johnson and Jonsell 1999, Rieske and Buss 2001, Jeanneret et al. 2003).

On a species by species (or family by family) basis, there were, however notable patterns that may have application to management in the future. Overall, canopy cover, basal area of both hardwoods and conifers, and percent bare mineral soil appear to be the most consistently important factors. Fuel depth was also important in terms of structuring the CCA ordination. Surprisingly, volume of coarse wood debris was found to be a relatively unimportant factor for most of the groups we analyzed. This is not consistent with many other studies that have linked CWD to high leaf litter arthropod abundance (Harmon et al. 1986, Kehler 2004, Schiegg 2000). It is possible that there was simply not enough variability in this metric across our study plots to be important. Changes to these important factors can be expected when burning and harvesting treatments are implemented on our study sites. Basal area and canopy cover are expected to decrease with the harvesting treatments and prescribed burns will undoubtedly increase the percentage of bare mineral soil. Fuel and coarse woody debris will be consumed to some degree as well.

In conclusion, Blodgett Forest has a high diversity leaf litter arthropod fauna, particularly of beetles and ants. The community is heterogeneous in its composition at the scale of the plots used in this study, and a variety of habitat features contribute to this heterogeneity. Continued management at this and other sites in the Sierra mixed-conifer ecosystem should seek to preserve the varied habitat structures that contribute to this high diversity.

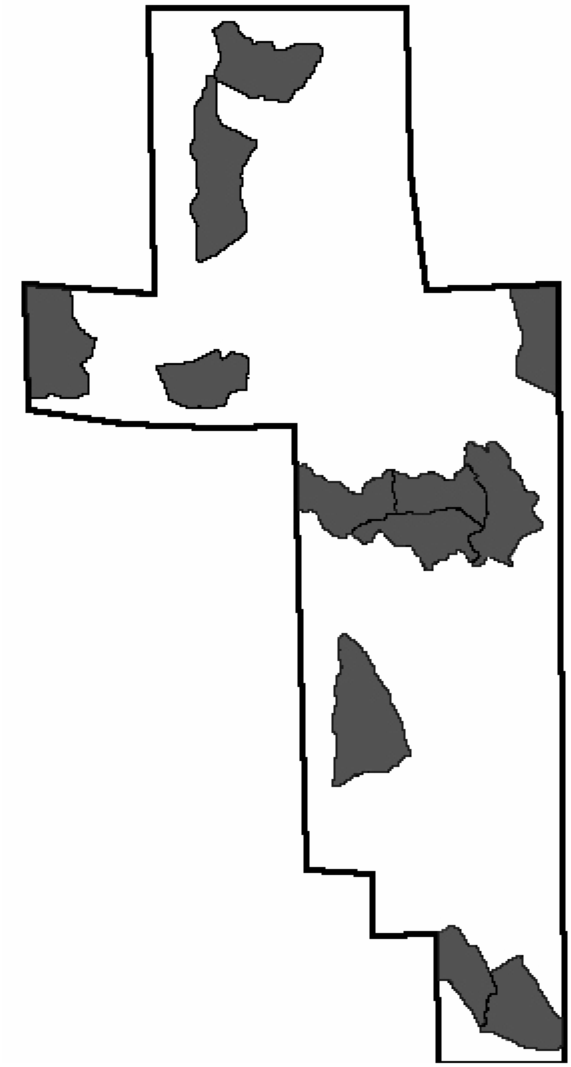

Figure 1. Map of the study site showing location of Blodgett Forest within California. Compartments are delineated within the forest. Shaded compartments were selected for this study. Plot locations are not shown.

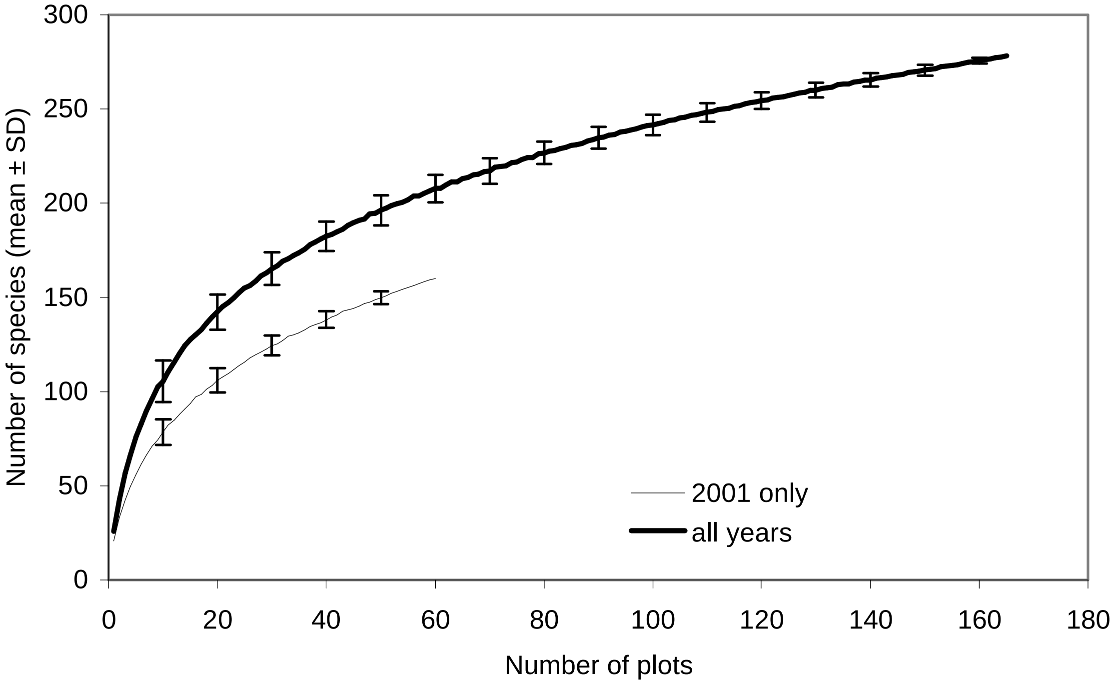

Figure 2. Species area curves of the number of species captured by plot sampled in 2001 (thin line) and all years (bold line). Error bars represent 1 SD.

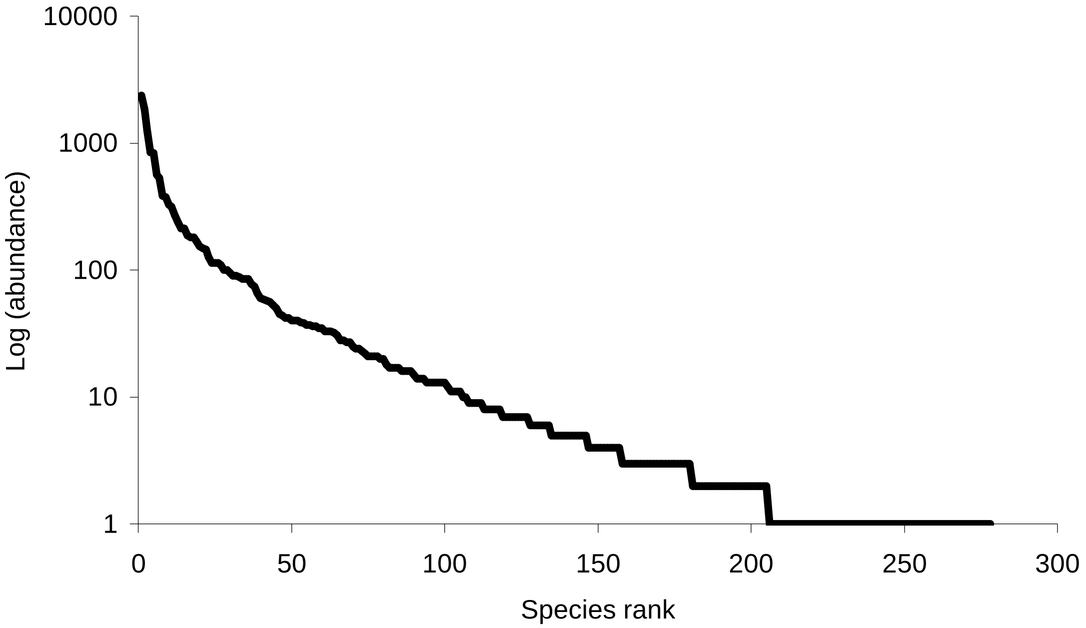

Figure 3. Rank-abundance plot of beetle species at Blodgett Forest. All 278 species from three summers of trapping are represented.

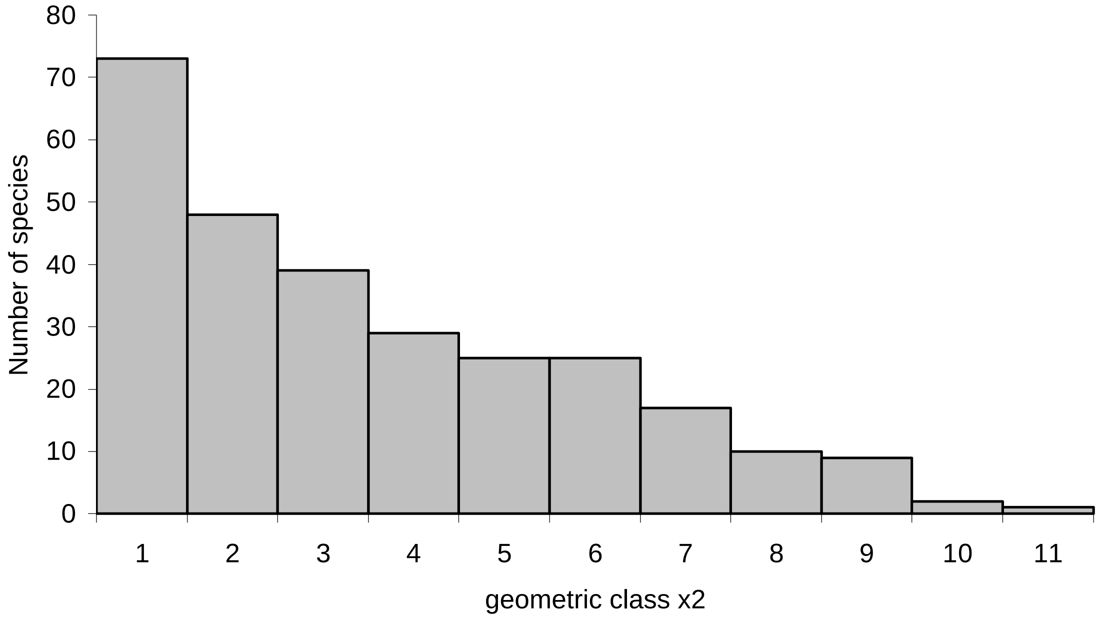

Figure 4. Number of beetle species plotted against abundance on a geometric ($\log_2$) scale. Note the lack of a mode, or "peak", in the distribution. All 278 species from three summers of trapping are represented.

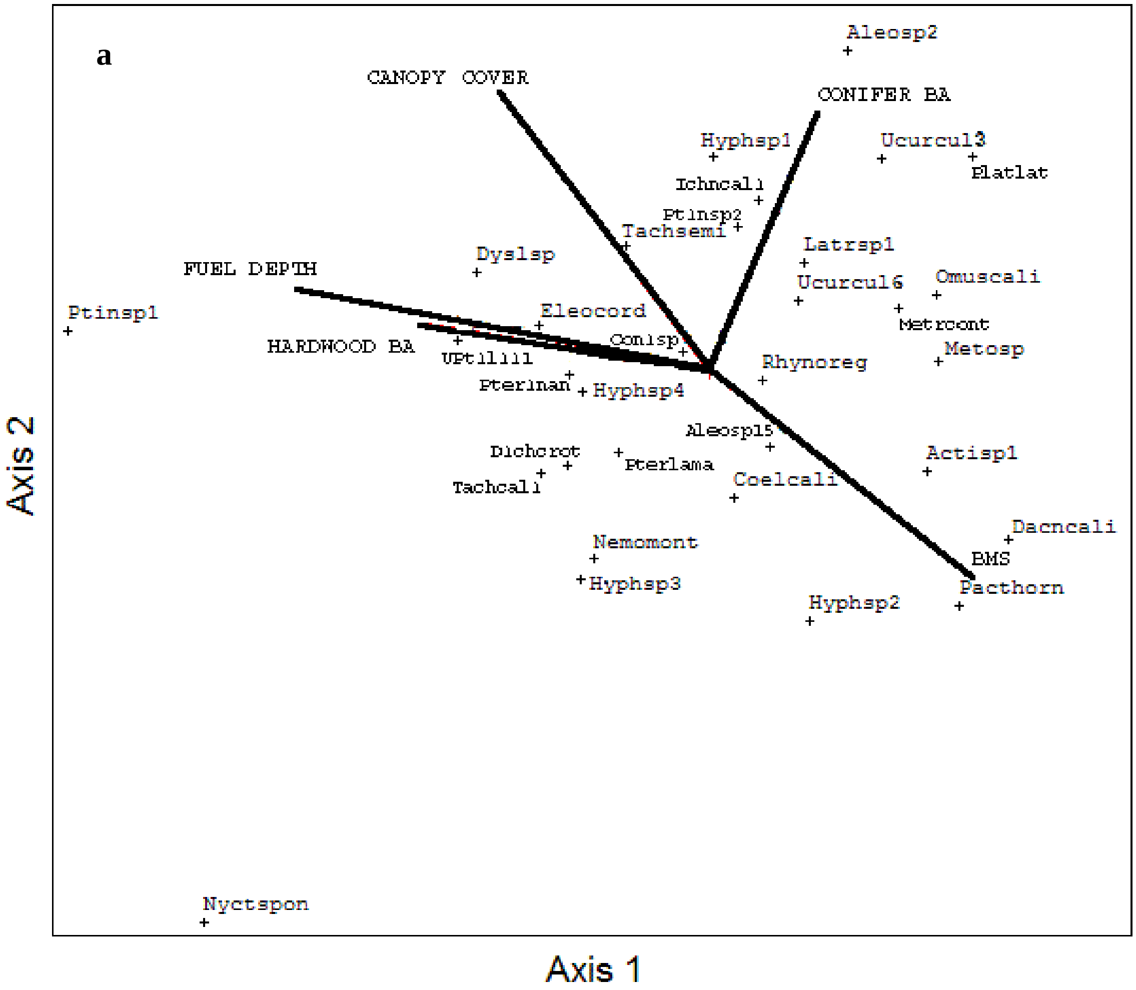

Figure 5. Canonical correspondence analysis (CCA) of 33 beetle species and 58 plots at Blodgett Forest. This analysis includes only the most common of the total 161 species from 2001. Habitat variables with Pearson correlation greater than 0.200 were plotted as vectors. Note that the species biplot (*a*) and the plot biplot (*b*) are on different scales. The vectors are to scale on both plots.

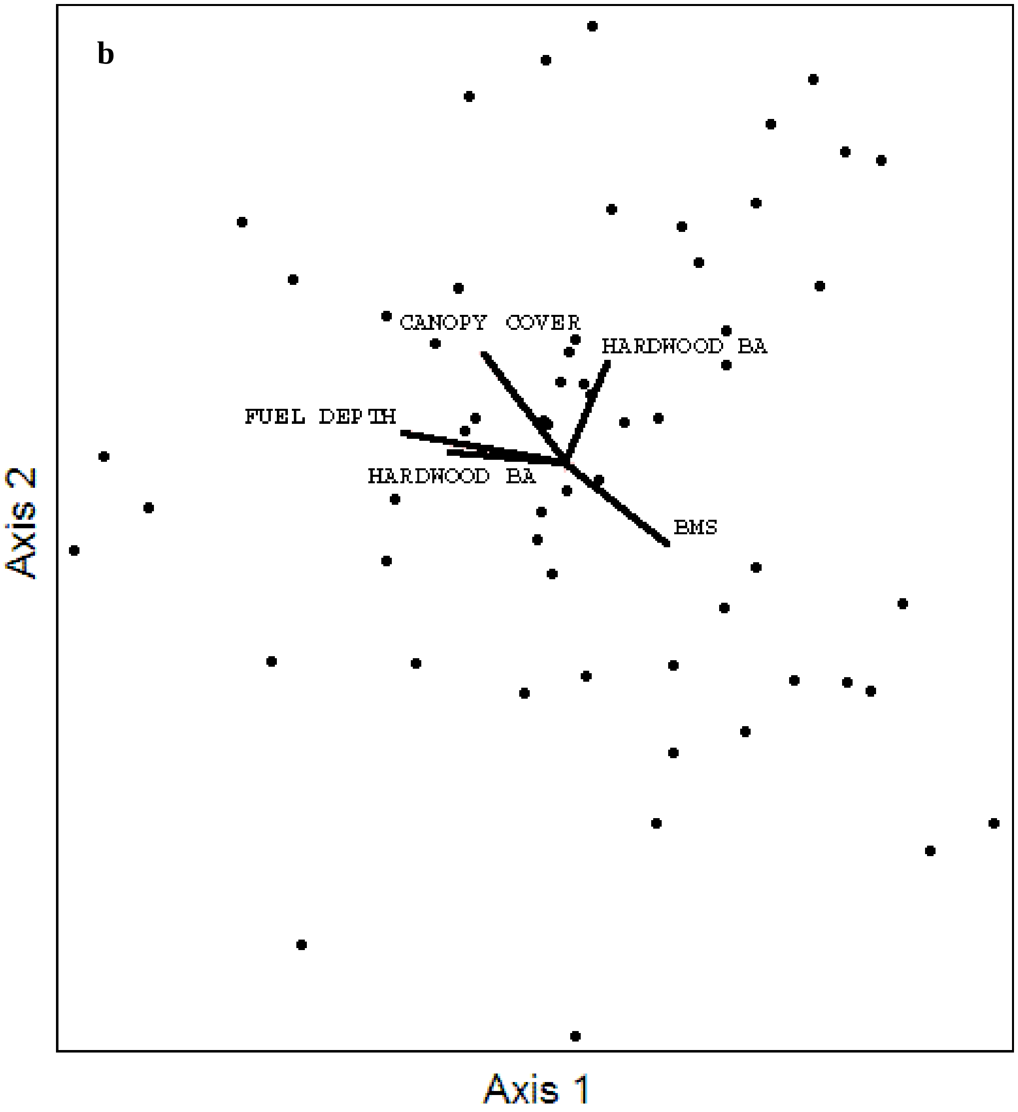

Figure 5, *cont*.

		Non-parametric estimators				
	S	Chao_1	Chao_2	Jack_1	Jack_2	Bootstrap
•$_{plot}$†	21.2	38.7	45.9	32.8	41.3	25.7
•$_{comp}$‡	53.7	88.4	94.1	79.8	97.4	64.7
•$_{plot}$	6.6	4.5	4.1	5.6	5.1	6.2
•$_{comp}$	2.0	1.4	1.5	1.7	1.6	1.8
•$_{2001}$	161	211.09	233.4	215.95	251.9	184.1
•$_{total}$	278	379.13	419.9	358.5	435.8	312.6

† = mean of the 60 compartments from 2001
‡ = mean of the 12 compartments from 2001

Table 1. Richness measures of beetles at Blodgett Forest. Species richness (S) and five methods of extrapolating total species richness were calculated. Alpha (•) diversity represents mean species richness at the plot (N=60) and at the compartment level (N=12) for 2001. Gamma (•), or landscape level diversity, was calculated for 2001 and all years of the study. Beta (•) diversity, representing the relative heterogeneity in beetle communities at Blodgett, was also calculated at the plot and compartment level.

	mean	SD	max	min
% canopy cover	67.13	18.26	96.00	24.00
% Slope	19.45	9.79	43.00	2.00
% BMS	5.87	10.69	70.00	0.00
Mean duff depth (cm)	2.81	2.34	10.75	0.00
Mean litter depth (cm)	2.43	1.16	6.00	0.50
Mean fuel depth (cm)	6.73	4.44	25.00	0.50
Total fuelVol./ha (m3)	59.39	84.88	375.46	0.00
Conifer BA (m^2/ha)	202.99	75.46	437.32	65.23
Hardwood BA (m^2/ha)	22.90	35.01	162.17	0.00
Sapling density per ha	724.44	1282.42	5930.64	0.00
Skid trail (categorical Y or N)				

Table 2. Plot means, standard deviations, and maximum and minimum values for the 11 habitat variables used.

	Summary			% canopy cover				% slope			
	r^2	F ratio	P>|F|	est	SE	F ratio	P>|F|	est	SE	F ratio	P>|F|
Total Coleoptera	-	-	-	-	-	-	-	-	-	-	-
Aleocharinae sp. 2	0.26	4.66	0.003	0.21	0.10	4.61	**0.037**	0.00	0.00	2.39	0.128
E. cordata	0.17	5.46	0.007	-	-	-	-	0.01	0.00	2.16	0.148
P. horni	0.32	3.98	0.003	-	-	-	-	-	-	-	-
M. contractus	0.07	2.11	0.131	-	-	-	-	-	-	-	-
Carabidae	0.15	3.19	0.031	-	-	-	-	-	-	-	-
Staphylinidae	0.12	4.03	0.023	0.51	0.26	3.87	*0.054*	-0.01	0.00	2.42	0.126
Tenebrionidae	0.18	2.79	0.035	-	-	-	-	-	-	-	-
Total Ants	0.10	3.08	0.054	-	-	-	-	-	-	-	-
Camponotus	0.28	3.92	0.004	-2.76	1.06	6.77	**0.012**	-0.05	0.02	6.29	**0.015**
Formica	0.19	6.38	0.003	-	-	-	-	-	-	-	-
Leptothorax	0.32	8.29	0.000	1.07	0.30	12.82	**0.001**	-	-	-	-
Liometopum	0.14	4.73	0.013	-	-	-	-	-	-	-	-
Total Spiders	0.29	3.48	0.006	-	-	-	-	-0.03	0.01	9.37	**0.004**
Lycosidae	0.36	7.73	<.0001	-	-	-	-	-0.02	0.01	9.00	**0.004**
Coleoptera richness measures											
Chao$_1$	0.25	3.26	0.013	-	-	-	-	-	-	-	-
Chao$_2$	0.24	3.37	0.010	0.22	0.13	2.90	*0.094*	-	-	-	-
Jack$_1$	0.31	4.62	0.002	8.75	4.38	4.00	*0.051*	-	-	-	-
Jack$_2$	0.26	4.53	0.003	11.42	6.26	3.33	*0.074*	-	-	-	-
Bootstrap	0.32	4.90	0.001	8.04	3.51	5.25	**0.026**	-	-	-	-
Rarefaction	0.04	2.17	0.146	-	-	-	-	-	-	-	-

Table 3. Results from stepwise multiple regression of selected taxa against 11 habitat structural variables. Analyses were done on abundances of arthropod groups per 100 traps, per month. Parameter estimates, standard errors, t-values, and P-values are listed. Dashes represent terms not included in the final models. P-values in bold are significant at the P<0.05 level, those in italics are significant at the P<0.1 level. Results from the five species richness extrapolations, as well as rarefied per plot richness values (Rarefaction) are listed below the taxonomic groups.

	% bare mineral soil				Skid trail				Mean duff depth			
	est	SE	F ratio	P>|F|	est	SE	F ratio	P>|F|	est	SE	F ratio	P>|F|
Total Coleoptera	-	-	-	-	-	-	-	-	-	-	-	-
Aleocharinae sp. 2	0.00	0.00	2.39	0.128	-	-	-	-	-	-	-	-
E. cordata	0.01	0.00	2.16	0.148	-	-	-	-	-0.13	0.09	2.11	0.152
P. horni	-	-	-	-	0.12	0.04	8.84	**0.004**	-	-	-	-
M. contractus	-	-	-	-	-	-	-	-	0.09	0.07	1.59	0.213
Carabidae	-	-	-	-	-	-	-	-	-	-	-	-
Staphylinidae	-0.01	0.00	2.42	0.126	0.13	0.10	1.56	0.217	-	-	-	-
Tenebrionidae	-	-	-	-	-	-	-	-	-	-	-	-
Total Ants	-	-	-	-	-	-	-	-	-0.48	0.26	3.35	*0.073*
Camponotus	-0.05	0.02	6.29	**0.015**	-	-	-	-	-	-	-	-
Formica	-	-	-	-	-	-	-	-	-	-	-	-
Leptothorax	-	-	-	-	-	-	-	-	-	-	-	-
Liometopum	-	-	-	-	-	-	-	-	-	-	-	-
Total Spiders	-0.03	0.01	9.37	**0.004**	0.37	0.20	3.39	*0.071*	-0.45	0.22	4.25	**0.045**
Lycosidae	-0.02	0.01	9.00	**0.004**	-	-	-	-	-0.26	0.13	4.09	**0.048**
Coleoptera richness measures												
Chao$_1$	-	-	-	-	-	-	-	-	-	-	-	-
Chao$_2$	-	-	-	-	0.09	0.06	2.80	*0.100*	-	-	-	-
Jack$_1$	-	-	-	-	3.73	1.93	3.72	*0.059*	-	-	-	-
Jack$_2$	-	-	-	-	6.04	2.58	5.46	**0.023**	-	-	-	-
Bootstrap	-	-	-	-	3.51	1.54	5.21	**0.027**	-	-	-	-
Rarefaction	-	-	-	-	-	-	-	-	-	-	-	-

Table 3, *cont*.

	Mean litter depth				Mean fuel depth				Total fuel volume			
	est	SE	F ratio	P>|F|	est	SE	F ratio	P>|F|	est	SE	F ratio	P>|F|
Total Coleoptera	-	-	-	-	-	-	-	-	-	-	-	-
Aleocharinae sp. 2	0.03	0.02	2.88	*0.096*	-0.03	0.03	1.59	0.213	-	-	-	-
E. cordata	-	-	-	-	-	-	-	-	-0.06	0.05	1.80	0.185
P. horni	-	-	-	-	-	-	-	-	-	-	-	-
M. contractus	-	-	-	-	-0.05	0.04	1.82	0.182	-	-	-	-
Carabidae	-	-	-	-	-0.08	0.05	2.64	0.110	-	-	-	-
Staphylinidae	-	-	-	-	-	-	-	-	-	-	-	-
Tenebrionidae	-	-	-	-	-	-	-	-	-0.10	0.06	2.62	0.111
Total Ants	-	-	-	-	-	-	-	-	-	-	-	-
Camponotus	-	-	-	-	-	-	-	-	0.56	0.26	4.89	**0.032**
Formica	-	-	-	-	-	-	-	-	-0.28	0.21	1.75	0.191
Leptothorax	0.10	0.05	4.59	**0.037**	-	-	-	-	-	-	-	-
Liometopum	-	-	-	-	0.61	0.25	5.91	**0.018**	-	-	-	-
Total Spiders	-	-	-	-	-	-	-	-	-	-	-	-
Lycosidae	-	-	-	-	-	-	-	-	-	-	-	-
Coleoptera richness measures												
Chao$_1$	-	-	-	-	3.69	2.00	3.40	*0.071*	3.33	2.09	2.54	0.117
Chao$_2$	-0.04	0.02	2.36	0.130	0.07	0.04	4.00	*0.051*	-	-	-	-
Jack$_1$	-	-	-	-	2.08	1.11	3.50	*0.067*	-	-	-	-
Jack$_2$	-	-	-	-	2.55	1.59	2.56	0.116	-	-	-	-
Bootstrap	-	-	-	-	1.24	0.89	1.95	0.169	-	-	-	-
Rarefaction	-	-	-	-	0.54	0.37	2.17	0.146	-	-	-	-

Table 3, *cont*.

	conifer basal area				hardwood basal area				sapling density			
	est	SE	F ratio	P>|F|	est	SE	F ratio	P>|F|	est	SE	F ratio	P>|F|
Total Coleoptera	-	-	-	-	-	-	-	-	-	-	-	-
Aleocharinae sp. 2	0.00	0.00	10.64	**0.002**	-	-	-	-	-	-	-	-
E. cordata	-	-	-	-	0.06	0.02	7.48	**0.009**	-	-	-	-
P. horni	-	-	-	-	-0.02	0.01	2.50	0.120	-	-	-	-
M. contractus	-	-	-	-	-	-	-	-	-	-	-	-
Carabidae	-	-	-	-	0.04	0.02	3.00	*0.089*	-0.07	0.03	5.34	**0.025**
Staphylinidae	0.00	0.00	4.69	**0.035**	-	-	-	-	-	-	-	-
Tenebrionidae	-	-	-	-	-	-	-	-	-	-	-	-
Total Ants	-	-	-	-	-	-	-	-	0.09	0.07	1.53	0.222
Camponotus	-	-	-	-	0.32	0.13	6.21	**0.016**	-	-	-	-
Formica	-	-	-	-	-0.30	0.09	10.37	**0.002**	-	-	-	-
Leptothorax	0.00	0.00	3.88	*0.054*	-	-	-	-	-	-	-	-
Liometopum	-	-	-	-	-	-	-	-	0.21	0.15	2.06	0.157
Total Spiders	-	-	-	-	-0.13	0.05	7.18	**0.010**	0.10	0.06	2.83	0.098
Lycosidae	-	-	-	-	-0.12	0.03	16.13	**<0.0001**	0.06	0.04	2.39	0.128
Coleoptera richness measures												
Chao$_1$	0.00	0.00	2.81	0.100	1.31	0.88	2.22	0.143	-	-	-	-
Chao$_2$	0.00	0.00	2.21	0.143	-	-	-	-	-	-	-	-
Jack$_1$	0.00	0.00	6.62	**0.013**	-	-	-	-	-0.84	0.66	1.64	0.206
Jack$_2$	0.00	0.00	4.37	**0.042**	-	-	-	-	-	-	-	-
Bootstrap	0.00	0.00	5.90	**0.019**	-	-	-	-	-0.85	0.53	2.58	0.115
Rarefaction	-	-	-	-	-	-	-	-	-	-	-	-

Table 3, *cont*.

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.148 *	0.093 •	0.062
Variance in species data:			
% of variance explained	8.6	5.4	3.6
Cumulative % explained	8.6	13.9	17.5
Pearson Correlation Spp-Envt	0.822 *	0.723	0.727
Kendall (Rank) Corr., Spp-Envt	0.517 *	0.479	0.489

Monte Carlo randomization test
• = P<0.10
* = P<0.05

Table 4. Results from Canonical Correspondence Analysis (CCA). Significance of eigenvalues and species-environment correlations was tested using Monte Carlo tests (99 randomizations).

CHAPTER 5

Fire and fire surrogate treatment effects on leaf litter arthropods in a western Sierra Nevada mixed-conifer forest

INTRODUCTION:

Frequent, low intensity wildfires were a common feature of Sierra Nevada forests prior to European colonization (Caprio and Swetnam 1995, Skinner and Chang 1996, Stephens and Collins 2004), and use of fire as a tool by Native Americans is well documented (Anderson and Moratto 1996). However, the federal policy of fire suppression over the past century has left millions of acres throughout the western US at risk for catastrophic wildfires (Pyne 1982, NWCG 2001). Despite considerable debate over the means and goals of fire reintroduction (Stephens and Ruth 2005), there is increasing consensus that some degree of fire management will be important in restoring ecosystem processes and reducing fire risk in our conifer forests (Stephens and Moghaddas 2005*a*). However, recent policies, most notably the "healthy forests initiative" (HFRA 2003), remain controversial, as many suggest thinning in addition to fire reintroduction as a means of reducing fire risk. The effects of thinning and burning treatments on many aspects of forest ecosystems remain poorly understood.

Arthropods are critical components of forest ecosystems, and must be considered in any forestry plan that balances management with the maintenance of biodiversity (Kremen et al 1993, Niemela et al. 1996, Perry 1998). Leaf litter arthropods in particular act as predators and prey, contribute to nutrient cycling and decomposition (Peterson and Luxton 1982, Lattin 1993), and may serve as sensitive indicators of habitat quality

(Kremen et al 1993). Leaf litter arthropods depend heavily on many structural elements in forests that may be impacted by fire management, including the amount of dead woody debris (Okland et al. 1996, Schiegg 2000), litter abundance and composition (Koivula et al. 1999), and soil moisture (Sanderson et al. 1995). In heavily managed forests, the habitat heterogeneity brought about by practices that mimic natural disturbances, such as fire and some types of thinning, may serve to increase arthropod biodiversity (Haila et al. 1994, Kaila 1997). However, other forestry practices have been shown to have negative short and long term effects on diversity and abundance of some groups (Niemela et al. 1993, Bellocq et al. 2001). Alternatively, many studies that have examined the effects of burning on various arthropod groups have found these communities to be highly resilient, showing only minor short-term changes (Holliday 1992, Niwa and Peck 2002, Collett 2003, Baker et al. 2004), or even increases in biodiversity (Beaudry et al. 1997, Villa-Castillo and Wagner 2002).

There is a notable lack of information about arthropod populations in the heavily managed Sierra Nevada conifer forests (Kimsey 1996), and little information about how communities might respond to fire and thinning treatments. In this study, we measured immediate, post-treatment responses of several arthropod groups, focusing on the Coleoptera, to fire and thinning treatments in a Sierra Nevada mixed-conifer forest. This study is part of a larger, nationwide effort, the Fire and Fire Surrogate Study (Weatherspoon and McIver 2000), to determine the effects of fire and thinning treatments on many aspects of the forest ecosystem. Previous research at the site where this work took place has shown that fire, thinning, and thinning followed by burning can all reduce the risk of catastrophic wildfire (Stephens and Moghaddas 2005*a*). Prescribed fire treatments can also significantly alter litter, duff and fuel loads and canopy density. Decayed coarse woody debris (CWD) was also significantly reduced by the fire treatments, while sound CWD was not (Stephens and Moghaddas 2005*b*). The thinning treatments resulted in significant reductions in basal area, canopy cover, and an increase in some fuel and CWD loads. A pretreatment study of arthropod biodiversity at the same sites has shown very high Coleoptera biodiversity, but that habitat factors such as volume of coarse woody debris, amount of bare mineral soil, and overstory tree basal area did not consistently or strongly predict the abundance of a variety of leaf litter groups (Chapter 4). Based on these results, and the results from other prescribed burn and thinning experiments, we expected relatively small effects of the treatments on abundance and diversity of our study fauna. However, the burning treatments on this site did substantially change the litter structure, so our results from pre-treatment studies (Chapter 4) may not adequately predict what may occur after the fire and fire surrogate treatments, as the range of differences is likely to be greater post-treatment. The mechanical alone treatments had a less dramatic effect on the litter structure, but the reduced canopy cover and basal area may impact some arthropod groups.

METHODS:

Study site:

We conducted this study at Blodgett Forest, an experimental forest owned by the University of California on the western slope of the Sierra Nevadas. Blodgett is located between approximately 1200 – 1500 m, near the Georgetown Divide (38º 52•N, 120º 40• W). Olsen and Helms (1996) provide a detailed description of the forest, its history, and current management regimes. In short, the site is typical of a highly productive Sierran mixed-conifer forest (Allen 1988). Large scale logging was undertaken between 1900 and 1913, and most of the property was harvested with the seed-tree method at that time. Large fires in the early part of the century also burned much of the forest, and were a common feature of the landscape prior to European settlement (Stephens and Collins 2004). Fire has been largely excluded from the property at a large scale since the middle of the 20th century. The University of California has managed Blodgett since the mid-1930's and has undertaken a range of harvesting practices on the property, including a variety of even- and uneven-aged management regimes, single tree selection, and retention of old growth reserve stands. The site is dominated by five major overstory conifer species, Douglas-fir (*Pseudostuga menziesii*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), and incense cedar (*Calocedrus decurrens*), and one major hardwood, black oak (*Quercus kellogii*). The understory is dominated by a variety of shrub and herb species.

Plot setup and treatments:

Twelve compartments within Blodgett Forest, ranging in size from 14 to 29 ha, were selected for this study (Fig. 1). A grid of 0.04 ha circular plots was established within a 10 ha core area of each compartment to reduce edge effects. All vegetation measurements and arthropod collections took place within these circular plots. Tree species, DBH, total height, height to live crown base, and crown position were recorded for all trees larger than 10 cm DBH. Coarse woody debris (CWD), litter, and duff measurements were made along two random azimuth transects from the center of each vegetation plot. Stephens and Moghaddas (2005*a*, *b*) detail vegetation and coarse woody debris protocols and results.

Four treatments were assigned at random to the 12 compartments (3 replicates of each): control, mechanical, fire, and mechanical followed by fire ("both"). Control compartments were untreated for the course of the study. Mechanical compartments underwent a thinning from below and crown thinning to increase crown spacing, followed by a mastication of approximately 85% of understory (2-25 cm DBH) conifers and hardwoods. Mastication was completed using an excavator mounted rotary masticator which shreds plant material into chips, which were then left on site. Fire compartments underwent a prescribed burn using strip head fires, while mechanical plus fire compartments were burned using backing fires after the mechanical treatment. Stephens and Moghaddas (2005*a*) provide more details of plot setup and the implementation of treatments.

Insect collections:

Litter dwelling arthropods were collected using pitfall traps. Pitfall traps are an efficient means of collecting arthropods over long periods of time, despite their known drawbacks (Spence and Niemela 1994). The total catch by these traps is a measure of the relative abundance of local fauna, but may be greatly influenced by the relative activity levels of different groups. Thus, results must be interpreted with some caution. Nonetheless, sufficient sampling over the length of the active period has been found to provide reasonable abundance estimates for groups such as carabid beetles (Baars 1979, Niemela et al. 1990). Our traps were constructed from 1L polypropylene cups with a removable collection cup inside that held a small amount of 50% propylene glycol as a killing and preserving agent. Holes around the rim of the trap provided entry for arthropods while preventing catches of small mammals and reptiles (Lemieux and Lindgren 1999). Five plots were selected at random in each of the 12 study compartments. A random azimuth from the plot center was chosen and five traps were arrayed along this transect at 1m intervals. We made four collections during the summer prior to treatments (2001) and four collections during the summer immediately following completion of all of the treatments (in 2003). Collections were made on a monthly basis from late May (soon after snowmelt), to mid September. For each collection, the traps were kept open for 5 days at a time, and then closed between collections and left in the field to prevent repeated site disturbance (Digweed et al. 1995). This trapping scheme allowed us to sample the full activity period of many arthropod groups at Blodgett Forest, as opposed taking a single point sample, with a low risk avoiding depletion of local fauna. Arthropod samples were placed in vials of 95% ethanol for storage and sorting.

Data analysis:

Arthropod samples were sorted in the lab by K. Apigian and trained technicians. All arthropods were initially sorted into “morphospecies”, and a reference collection was made. Identifications of beetles and ants were made by comparisons with museum reference collections, identification keys, and experts. Any groups from the reference collection that were split after identification were rechecked for accuracy. If we were unable to identify all beetles to species, we assigned them a morphospecies label. It was not feasible to identify some difficult ant genera (e.g. *Formica*) to species given the volume of ants collected. Thus, for our quantitative comparisons, we grouped ants by genus. Spiders were identified as Lycosidae or “other”, as Lycosids were by far the most abundant family captured. In several traps we collected hundreds of small, immature Lycosids that likely fell into the trap while riding on an adult; in these cases, the juveniles were later excluded from the counts and subsequent analyses.

We used rank-abundance diagrams (Whittaker 1965) to qualitatively compare diversity and evenness of the beetle community between the four treatments. We plotted pre-treatment data next to post-treatment data for each treatment type to compare relative change. These diagrams provide an effective means of comparing community structure and may provide greater detail than a single diversity statistic (Krebs 1989).

We used one-way analyses of variance to test for treatment effects at the compartment level between 2001 and 2003. Multiple comparisons were made using Dunnett's test to determine if treatment effects relative to the control. We tested for changes in abundance of several groups of arthropods: all Coleoptera, the three most common Coleoptera families (Carabidae, Tenebrionidae, and Staphylinidae), the five most common Coleoptera species (Aleocharinae sp. 2, *Dacne californica*, *Eleodes cordata*, *Metrius contractus*, and *Pactopus horni*), all ants, the four most common ant genera (*Camponotus*, *Formica*, *Leptothorax*, and *Liometopum*), all spiders, and the most common spider family, the Lycosidae. We also assigned a guild to each of our Coleoptera species, based upon feeding and life history, and tested these guilds for treatment effects. Guilds were assigned based upon Arnett et al. (2000, 2002); if no specific information was known or given about the species, we used general information about the family to assign guild membership. Means per compartments were used for analysis. In several instances traps were dislodged or destroyed by wildlife, resulting in unequal sampling effort per plot. We therefore divided our total catch per plot by the number of traps to standardize our catch. We also standardized by number of months sampled, as some compartments were inaccessible for a month during the pre-treatment period due to forestry operations. Abundance data were log (x+1) transformed when necessary to meet assumptions of normality.

We also used one-way ANOVAs to test for changes in beetle species richness as a result of the treatments. Unequal sample sizes, and the loss of some traps, made direct comparisons of richness impossible, since species richness is highly dependent on sample size. We used rarefaction to standardize our catches to the lowest number of beetle individuals captured in a single compartment (N=120). We also used the bootstrap method (Smith and Van Belle 1984), a non-parametric estimator of species richness, to compare estimated numbers of total beetle species per treatment. The bootstrap estimator worked well with this data set in the past (Chapter 4), and, while potentially underestimating overall richness (Chiarucci et al. 2003), it is still an effective means of making relative comparisons between sites (Palmer 1990, Poulin 1998). The JMP IN statistical software (SAS institute 2003) was used for these analyses.

Indicator species analysis (Dufrene and Legendre 1997) was used to determine beetle species characteristic of certain treatment types. This analysis considers species found exclusively in a single treatment type to be perfect indicators of that habitat, and would receive an indicator value of 100. A low indicator value indicates that a species is not characteristic of the habitat in question. Monte Carlo randomization tests are used to determine if the value is greater than expected by chance; thus, species with only one or a very few total individuals are unlikely to be considered indicators, even if they appear in only one habitat type (McCune and Grace 2002). PC-Ord (McCune and Mefford 1999) was used for this analysis.

We used two multivariate methods to analyze the assemblage level responses of Coleoptera to the fire and fire surrogate treatments, canonical correspondence analysis (CCA) and nonmetric multidimensional scaling (NMS). CCA is a "direct" gradient analysis (ordination) method that places plots in species space relative to a matrix of habitat variables (ter Braak 1986). We ran a CCA with a matrix of our 115 most common beetle species (species found on at least 20% of our compartments) and 24 compartments (the 12 study compartments, pre- and post-treatment). Our habitat matrix initially consisted of 11 habitat variables, but we reduced the matrix to only the four most important variables (% bare mineral soil, total fuel volume, conifer basal area, and hardwood basal area) because there was very high correlation between these and other measured variables (e.g. litter depth, canopy cover). The CCA was run using the axis scores centered and standardized to compartment variance, and compartments were plotted on diagrams using linear combination scores and the analysis was done using the PC-Ord program. NMS was used to develop an ordination based solely on species responses, unconstrained by habitat variables, as a contrast to the CCA. NMS is a non-eigenvalue based ordination technique that is appropriate for data sets that are non-normal or contain many zeros (Kruskal and Wish 1978, Clarke 1993, McCune and Grace 2002). We used the "slow and thorough" autopilot mode in PC-Ord with a Sorenson distance matrix to seek the best NMS solution by sequentially stepping down in dimensionality. The stress at each dimensionality is compared against Monte Carlo results from 50 randomized runs to determine the lowest number of appropriate dimensions. We plotted the first two axes of both the CCA and NMS ordinations as standard plots to compare changes as a result of the fire and mechanical treatments.

RESULTS:

We captured a total of 11,815 individual beetles within 49 families and 256 species during the two summers of this study (App. 1). The rank-abundance curves for all treatments and years show a pattern typical of many insect communities: very few species dominate the catch with many species represented by only one or two individuals (Fig. 2a-d). The strongest pattern in the rank-abundance plots is an increase in the number of species from 2001 to 2003. The movement of the curves to the right indicates increased evenness of the community in 2003 versus 2001. The post-fire curve (Fig. 2b) shows a different response than the control curves, as there appears to be very little change from 2001 to 2003 in the lower ranked (i.e. more common) species. This pattern is less apparrent for the mechanical (Fig. 2c) and mechanical plus fire treatment (Fig. 2d). This can be express quantitatively as the number of individuals within the ten most common species. The numbers of individuals in the most common species declined by 19.6% from 2001 to 2003 in the fire compartment, while the control and other treatments increased (control: +50.6%, mechanical: +40.9%, both: +55.6%). Most of the community change on the burned compartments is a result of increased numbers of rare species. The “right tails” of the two fire treatments, representing the numbers of rare species, is longer than for the control or mechanical treatment curves. The number of rare species (species represented by only 1 or 2 individuals) in the control group increased by 4 species from 2001 to 2003. The mechanical treatment increased by 10, the fire by 30, and the mechanical plus fire by 32 species.

Indicator species analysis revealed several species closely associated with certain treatments (App. 1). Most of the indicator species were found in the treated rather than the control compartments. Only two beetle species could be considered indicators of the control treatment, *Pterostichus lama*, a common Carabid beetle, and *Ichnosoma californicum*, a Staphylinid. In contrast, 9 species were indicators of the fire treatment, 18 for the mechanical treatment, and 17 for the combined treatment. Two Carabid beetles were the most common indicators of the fire and mechanical treatments, respectively: *Omus californicus* and *Pterostichus* sp. 1. A Cryptophagid was the most common species associated with the combined treatment, *Atomaria* sp. 1.

Several of the selected species and groups of species showed significant responses to the treatments. *Pactopus horni*, a common Throscid beetle, showed a positive response to the combined mechanical and fire treatment. The catch of the most common ground beetle, *Metrius contractus*, was negatively impacted by all of the active treatments. We were unable to detect a treatment effect for the other three beetle species. The response of the family Carabidae mirrored that of the most common ground beetle species, showing a negative response to all active treatments. The Staphylinidae catch was reduced by the fire treatment. Effects on beetles at the guild level were limited to predators and wood-borers: predators were negatively affected by all active treatments, paralleling the responses of the two most common predaceous families (Carabids and Staphylinids), while wood-borers responded positively to the combined treatment. Ant activity-abundance was generally unaffected by the treatments, save for a weak negative response of wood ants (*Formica*) to the mechanical treatment. The combined treatment significantly suppressed the catch of wolf spiders (Lycosidae) and spiders as a whole. Species richness was slightly higher in the fire treated compartments, as measured by the rarefaction estimate, and higher in the mechanical plus fire compartments as measured by the bootstrap extrapolation.

The CCA and NMS ordinations reveal similar patterns with regard to community level responses of Coleoptera to the treatments. The first axis of the CCA explained the most variance in the data, while axes 2 and 3 explained relatively little and failed the Monte Carlo test (Table 2). Vectors connecting the pre- and post-treatment compartments show the relative effects of the treatments on the beetle community (Fig. 3a). The control plots moved relatively little, and in both directions, along the second axis. The mechanical plots tended to move up the second axis. The movement of all six of the compartments treated with fire to the left along the first axis was the most distinct change between years. Notably, all of the fire only compartments moved left and down, while the mechanical plus fire compartments moved left and slightly up, suggesting a slightly different response of the community to the two treatments. The biplot of sample units and habitat variables (Fig. 3b) reveals that percent bare mineral soil was the most important variable along axis 1, increasing to the left. Total fuel volume was an important factor for the mechanically treated compartments, while the conifer basal area vector points in the vicinity of many of the pre-treatment compartments. Figure 3c shows the positions of the 115 most common beetle species in the CCA ordination space. The species are positioned relative to their abundances in the various compartments and their relationships with the habitat variables. The indicator species for each treatment (see above) tend to be positioned in the region of the ordination plot for which they are strongly associated, i.e. mechanical indicators in the upper right, along the total fuel vector, fire associated species in the lower left, indicators of the combined treatments in the middle to upper left, and the two species associated with the control treatment in the lower right.

The NMS ordination reveals inherent patterns of community structure without regard to the habitat variables. Final stress for a three-dimensional NMS ordination was 9.55, which is considered "good" and results in an easily interpretable ordination diagram (Kruskal 1964, Clarke 1993). The pattern of change on our compartments relative to the treatments was similar for the NMS as for the CCA (Fig. 4). The control compartments, and, to a lesser degree, the mechanical compartments, moved down along the second axis. The fire treated compartments all moved strongly to the right along the first axis. The mechanical compartments moved along axis 1 as well, but not as dramatically as the fire treatments. Axis 1 can be interpreted as an "increasing disturbance" axis, with fire as the primary disturbance, while axis 2 represents time.

DISCUSSION:

Community-level ecological studies of arthropod assemblages in California are surprisingly rare, considering the diversity of arthropods in the state in general and the importance of the Sierran mixed-conifer ecosystem. This is the first study to examine the impacts of a variety of fire management methods on the leaf litter fauna in the Sierra Nevada. Past work has shown that while the conifer forests of the Sierras hold relatively few endemic species (Kimsey 1996), these forests harbor a high diversity of beetle and other insect fauna (Chapter 4). Only 8 percent of the mixed conifer forest in the Sierras is formally protected for conservation, while 67 percent is available for timber management (Davis and Stoms 1996). Studies like these are keys to understanding how we can maintain biodiversity while sustainably managing our forests (Perry 1998).

It is important to note that the results from this study focus on a particular group of species only: the active, litter-dwelling arthropod fauna. The clearest limitation of the pitfall trapping method is that catches are a function of activity levels of the collected fauna, as well as abundance. Relative abundances of the same species in different habitats may be a result of changes in activity due to a more complex litter structure, for example, as much as changes in numbers of individuals. This problem has been well-documented (Spence and Niemela 1994), however changes in “activity-density” may still be as ecologically important as changes to absolute abundance.

Some of our focal study groups or species were significantly impacted by the treatments. Numerical responses were, in general, negative. The two most common beetle families, Carabidae and Staphylinidae, were both negatively impacted by fire. Carabids, and the most common carabid, *Metrius contractus*, were negatively affected by both the fire and mechanical treatments. This is a response that would not have been predicted based on previous work at the same site (Chapter 4) which found that few environmental factors were important predictors for this group, including such factors as the amount of bare mineral soil, litter, and fuel, which were impacted by the treatments. However, the differences in litter layer habitat between treated and control compartments were much greater than any inter-plot differences before treatment (Stephens and Moghaddas 2005*a*). In addition to the structural changes, the fire and thinning treatments likely changed soil moisture and chemistry conditions, and this may be partially responsible for the differences seen in these common families. Spiders, including the most common family, the Lycosidae, were also negatively impacted by the combined thin and burn treatment.

Pactopus horni, a Throscid beetle, showed a positive response to the combined thinning and burning treatment. This small, litter-dwelling beetle is thought to feed largely on ectomycorrhyzal fungi, but its habits are poorly known (Arnett et al. 2002). This species may be attracted to fire, as it has been collected in burned logs (Yensen 1975). The wood-borer guild increased as a response to the thin and burn treatment. This response is largely due to an increase in bark beetles (Scolytidae, *Hylurgops* sp., *Hylastes* sp., and *Xyleborus* sp., in particular) in these compartments. Some species of bark beetles are attracted specifically to burning (Hanula et al. 2002, Sullivan et al. 2003), and thinning treatments have been shown to be attractive to these beetles as well (Witcosky et al. 1986). The two measures of species richness showed positive responses to different treatments, but neither response was strong. The rarefaction corrected estimate of richness was higher in the fire treatment, while the bootstrap estimate was higher in the combined treatment. These estimates of higher richness in burned areas are consistent with other studies of areas experiencing prescribed burns (Beaudry et al. 1997, Villa-Castillo and Wagner 2002).

Both the rank-abundance diagrams and the indicator species analysis support the conclusion that the treated compartments harbor a unique beetle community relative to the control compartments. There were considerably more “rare” species (species represented by one or two individuals) on the treated compartments than on the control compartments. There were also several species closely associated with the treatments, as measured by indicator species analysis, while only two species were control indicators. A previous analysis of pretreatment collection data (Chapter 4) found a great deal of small-scale (plot-level) spatial heterogeneity at Blodgett Forest, but much lower heterogeneity at the compartment level. These results suggest that these treatments increase habitat heterogeneity at the compartment level, and provide opportunities for slightly different beetle communities to coexist.

The CCA and NMS ordinations show similar patterns of beetle community response to treatments. The response was strongest to the fire treatments, and the increased bare mineral soil, resulting from an almost complete loss of a duff and litter layer, was the most significant habitat variable explaining the change. The change due to the mechanical only treatment was less apparent, and associated with an increase in fuel volume. The CCA also suggests that the community level response to the thin and burn treatment was slightly different than the fire alone treatment, signifying that the mastication and harvesting procedures do have a distinct impact.

Management recommendations from this work must be made in light of the history of Blodgett Forest. This study was conducted on a site that has more than a century-long history of timber management. While fire has been largely excluded for decades (Stephens and Collins 2004), the site has experienced a variety of harvesting regimes, including several types of even and uneven-aged management (Olsen and Helms 1996). While the compartments chosen for this study were randomly selected from a group of stands that had experienced relatively moderate management in the form of group selection, the structure and history is very different than undisturbed stands in the

Sierras, and even from the reserve stands at Blodgett Forest. Thus, while the specific treatment regimes were unique compared to what had been previously experienced on the site, it is likely that they were within the range of disturbances frequently encountered at Blodgett Forest. This is particularly true of the mechanical treatment, though perhaps less so of the fire treatment, due to fire exclusion from Blodgett Forest.

Considering the management history at Blodgett Forest, it is likely that the differences seen in this study are minimal relative to the differences that might be seen if an unmanaged or old-growth forest were treated similarly. The beetle community at our study site probably contains few, if any, species that could be classified as old-growth specialists. It is best described as a community of forest generalists with fairly wide tolerances for disturbance, mixed with some more open-adapted species from adjacent clear-cuts or group selection cuts. The short-term effect on the leaf-litter community at Blodgett Forest from these fire and fire surrogate treatments can be considered moderate. If recovery from these treatments is similar to that in other studies (Holliday 1992, Abbott et al. 2003, Baker et al 2004), it is likely that recovery can be expected within several years, and implementation of these treatments would be well-justified in terms of the impact on leaf litter arthropod communities. However, care should be taken when extrapolating these results to other forest types under different management regimes. Blodgett Forest is a forest managed with a variety of strategies, resulting in a mosaic of habitat types for a range of species. Applied to an even-aged stand, the local fauna may respond in an entirely different manner. Indeed, overall diversity may be increased by the introduction of different overstory, understory, and litter structures (Haila et al 1994). Alternatively, applied liberally to old growth stands, the treatments may result in the loss of some specialists (Niemela 1996). The scale of the impact should also be considered when implementing treatments. A smaller edge to interior ratio may reduce the ability of the local fauna to recolonize the impacted areas, or at least increase the time until recolonization.

In conclusion, while the thinning, burning, and combination treatments did result in declines of some common species, other species showed the opposite response. Species richness slightly increased after the fire treatments, while all of the treated compartments appear to have gained some rare species. Overall beetle community composition changed as a result of the treatments, but remained diverse and abundant. Use of fire and fire surrogate treatments, applied at similar spatial scales, appears to be justified on sites similar to Blodgett Forest in the Sierra Nevada, from the standpoint of the leaf litter arthropod community. Differences between the treatments used in this study appear to be small, and the choice of which technique to use should be based on management goals.

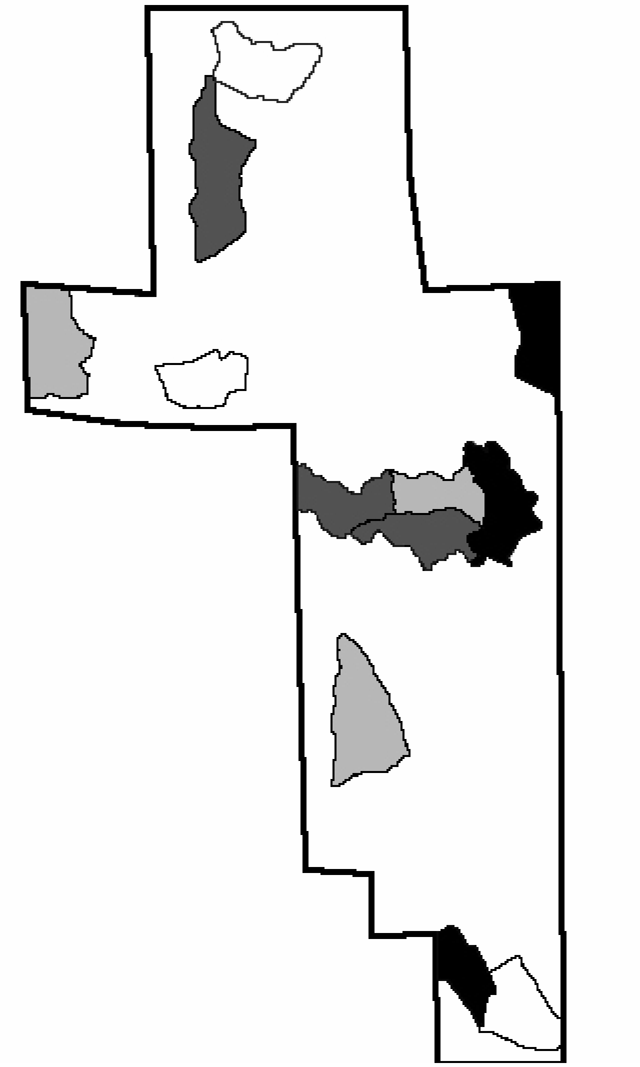

Figure 1. Map of Blodgett Forest showing its location within California and the treatments applied to the 12 study compartments. Empty = control, black = mechanical followed by fire, dark grey = fire, light grey = mechanical.

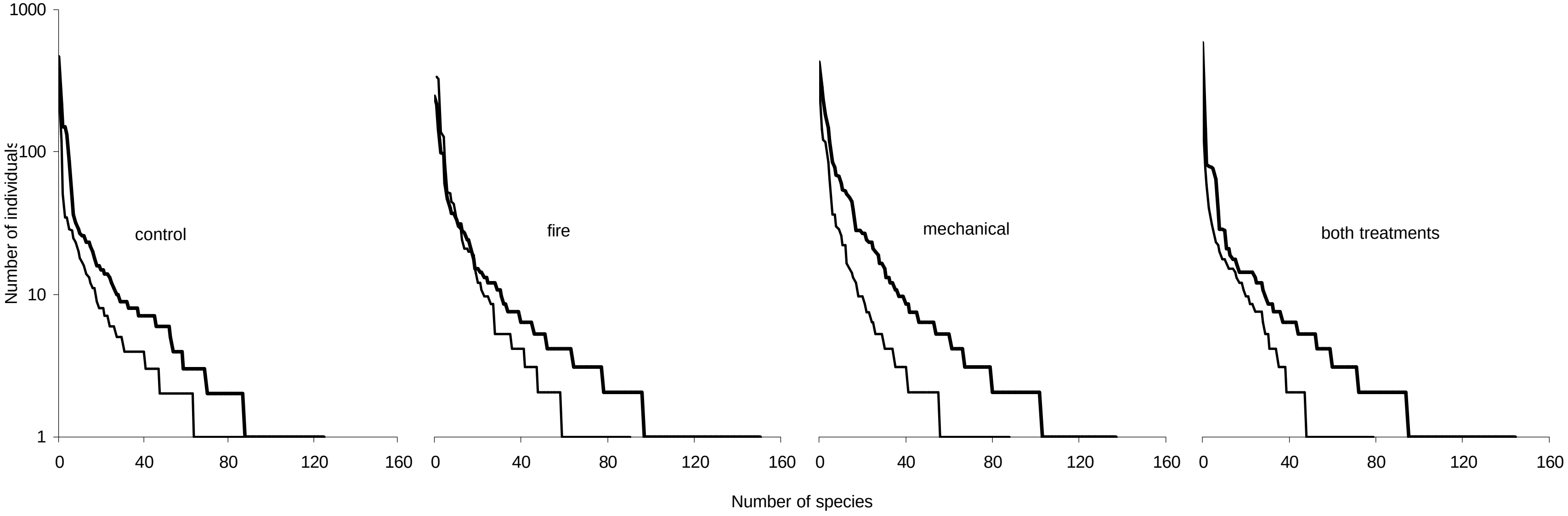

Figure 2. Rank-abundance diagrams showing the structure of the beetle assemblage at Blodgett Forest for each treatment type pre- (thin lines) and post- treatment (bold lines). The shift in the line reflects changes in beetle assemblage between years.

Figure 3. *a* Canonical correspondence analysis (CCA) ordination diagram of the fire and fire surrogate compartments pre- and post- treatments. Open symbols are pre-treatment, filled symbols are post-treatment. Circles are control compartments (untreated for both years), triangles are fire only compartments, diamonds are mechanical, squares are the combined mechanical and fire compartments. Vectors represent change from 2001 to 2003 (pre- to post-treatment). *b* Overlay of habitat variables on ordination diagram. Only variables with correlation coefficients greater than 0.200 are displayed. Direction and length of the habitat vectors show the importance of each variable. bms = % bare mineral soil, tfuel = total fuel volume, conba = conifer basal area. *c* Common beetle species displayed in ordination space. See Appendix 1 for species codes and note the different scale relative to the habitat vectors.

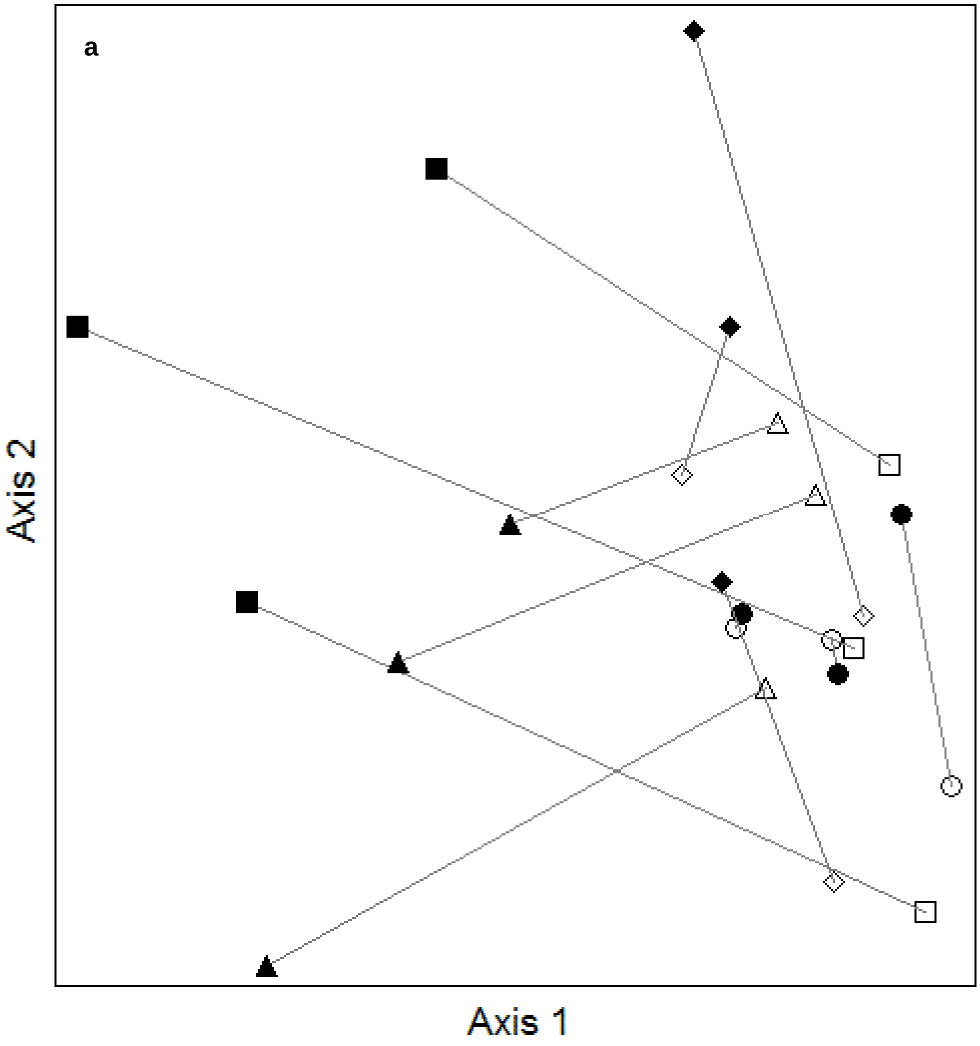

Figure 3*a*.

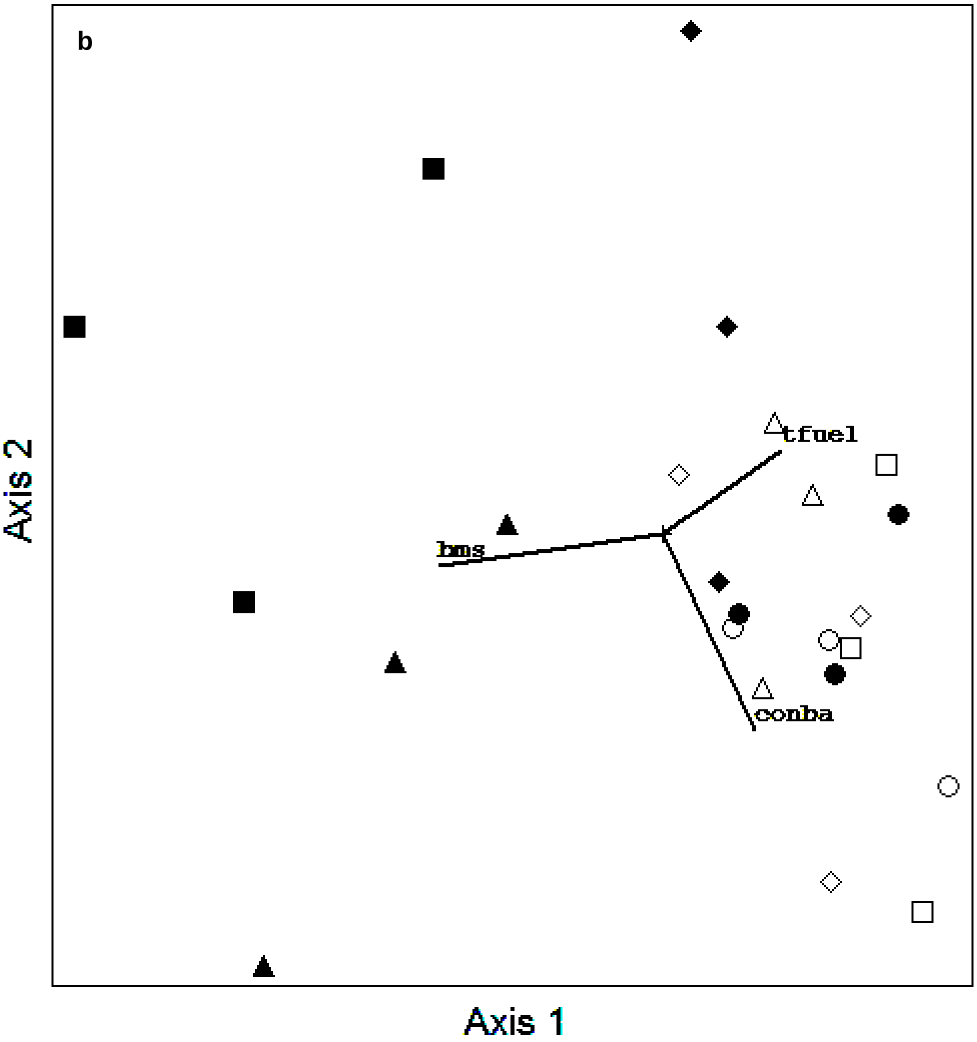

Figure 3*b*.

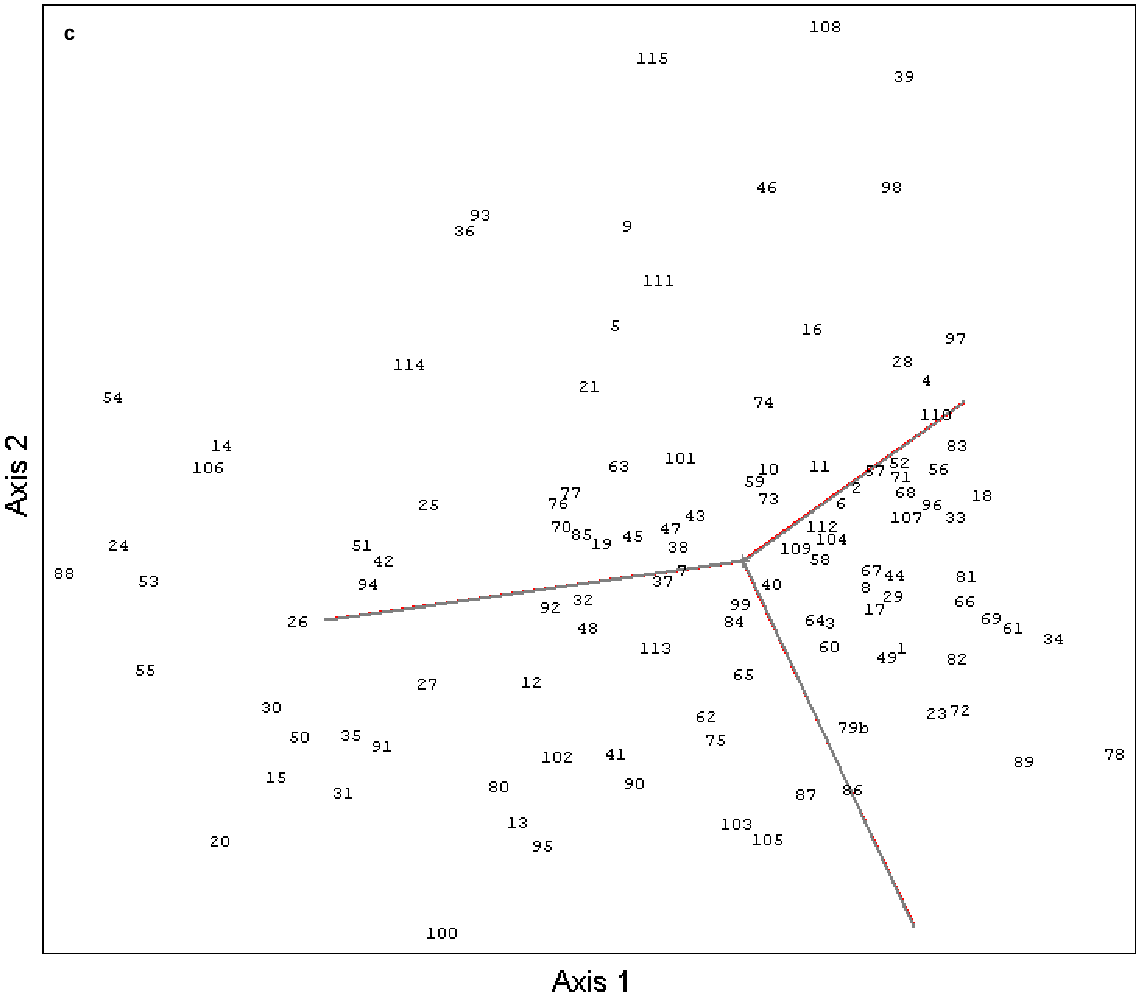

Figure 3*c*.

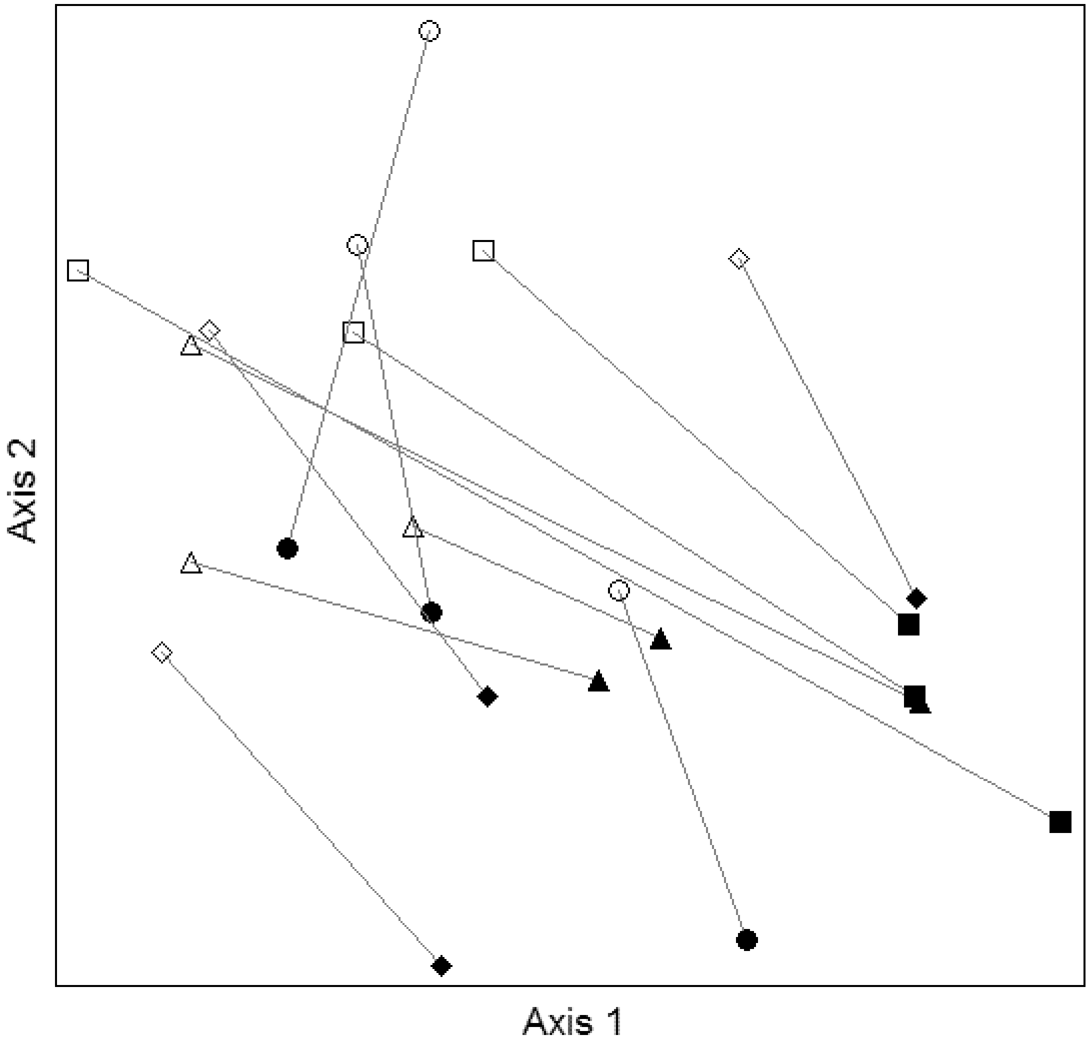

Figure 4. Nonmetric multidimensional scaling (NMS) ordination of the fire and fire surrogate compartments pre- and post- treatments. Open symbols are pre-treatment, filled symbols are post-treatment. Circles are control compartments (untreated for both years), triangles are fire only compartments, diamonds are mechanical, squares are the combined mechanical and fire compartments. Vectors represent change from 2001 to 2003 (pre- to post-treatment). The NMS was based on a species matrix of 115 beetle species by 24 compartments (12 compartments pre- and post-treatment).

	Treatment						
	control	fire	mech	both	F	P	Dunnett's test
Total Coleoptera	330.67 ± 76.16	36.33 ± 191.66	285.22 ± 436.15	254.44 ± 219.53	0.730	0.563	-
Aleocharinae sp. 2	6.97 ± 3.7	-79.17 ± 126.46	-22.69 ± 53.3	4.1 ± 9.34	1.586	0.267	-
Dacne californica	46.75 ± 51.96	37.24 ± 17.17	48.05 ± 34.77	17.43 ± 7.49	0.469	0.712	-
Pactopus horni	5.15 ± 5.1	29.19 ± 48.55	82.84 ± 90.11	139.46 ± 54.73	3.466	*0.071*	**both (+)**
Metrius contractus	140.04 ± 152.78	-26.88 ± 18.1	-10.98 ± 12.06	-18.38 ± 20.83	10.469	**0.004**	**mech (-)**; **both (-)**; **fire (-)**
Eleodes cordata	-28.05 ± 106.08	-18.77 ± 13.51	-28.43 ± 79.91	-43.9 ± 42.08	0.959	0.458	-
Carabidae	132 ± 134.01	-49.33 ± 27.06	-48.11 ± 54.55	-38.11 ± 13.15	5.564	**0.023**	**both (-)**; **fire (-)**; *mech (-)*
Tenebrionidae	-19.67 ± 126.08	0.67 ± 33.01	1.22 ± 169.8	-32.56 ± 47.31	0.445	0.728	-
Staphylinidae	39.33 ± 17.16	-112.67 ± 133.1	40.67 ± 79.78	-1.89 ± 29.25	4.080	**0.050**	**fire (-)**
Coprophages	-1.43 ± 1.29	-4.13 ± 3.47	-6.42 ± 8.37	-2.82 ± 5.42	4.931	**0.032**	-
Fungivores	-59.88 ± 20.74	-51.14 ± 43.02	-75.2 ± 23.13	-52.58 ± 11.35	1.347	0.326	-
Herbivores	-27.33 ± 11.59	-13.67 ± 18.58	-49.55 ± 12.06	5.44 ± 23.02	1.551	0.275	-
Omnivores	-1.15 ± 1.45	-3.85 ± 0.82	-1.13 ± 3.16	-1.3 ± 0.8	1.090	0.407	-
Predators	5.48 ± 78.27	-18.57 ± 57.77	22.26 ± 14.69	9.03 ± 18.34	10.236	**0.004**	**mech (-)**; **both (-)**; **fire (-)**
Scavengers	-9.53 ± 22.38	-24.82 ± 69.8	-8.93 ± 37.42	15.06 ± 34.78	0.226	0.876	-
Wood-borers	-16.84 ± 13.64	-9.64 ± 5.22	-37.04 ± 12.91	-14.83 ± 13.1	3.818	*0.058*	**both (+)**

Table 1. Means and standard deviations of differences between pre- and post-treatment years. Positive values indicate that a group increased in abundance, negative values indicate a decline. Means are derived from the three replicates per treatment. Abundances represent the mean number of individuals captured per compartment per summer of trapping. F and P-values are based on one-way ANOVAs testing for differences between treatments. Multiple comparisons were tested using Dunnett’s test versus the control group. A significant ANOVA with a non-significant Dunnett’s test indicates that while there were differences between treatments, there were no changes in abundance relative to the control compartments.

	Treatment						
	control	fire	mech	both	F	P	Dunnett's test
Total Formicidae	756.44 ± 1189.43	531.33 ± 572.62	-866.22 ± 2146.98	742 ± 685.4	1.118	0.397	-
Camponotus	188.64 ± 355.16	-54.14 ± 31.48	-49.34 ± 126.71	97.54 ± 234.92	0.849	0.505	-
Formica	510.9 ± 394.11	370.8 ± 530.46	-44.09 ± 208.05	224.83 ± 145.88	2.873	0.103	*mech (-)*
Leptothorax	-170.26 ± 136.45	-84.37 ± 54.48	-299.72 ± 133.08	23.86 ± 74.22	1.680	0.248	-
Liometopum	169.66 ± 64.29	124.32 ± 235.25	-601.34 ± 1895.7	-18.7 ± 74.54	0.412	0.749	-
Total Spiders	43.27 ± 64.63	-103.03 ± 21.27	132.09 ± 81.91	-122.54 ± 69.02	11.009	**0.003**	*fire (-)*; **both (-)**
Lycosidae	-0.03 ± 18.42	-36.3 ± 41.61	27.39 ± 8.27	-69.65 ± 23.07	8.048	**0.008**	**both (-)**
Coleoptera richness							
Rarefied, N=171	-4.65 ± 13.58	14.82 ± 2.43	11.02 ± 9.6	8.84 ± 5.79	2.725	0.114	*fire* (+)
Bootstrap est.	25.16 ± 14.27	34.36 ± 8	39.13 ± 7.03	49.49 ± 10.99	2.811	0.108	*both (+)*

Table 1, *cont*.

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.229 *	0.080	0.051
Variance in species data:			
% of variance explained	16.5	5.7	3.7
Cumulative % explained	16.5	22.2	25.9
Pearson Correlation Spp-Envt	0.912 *	0.883 *	0.792
Kendall (Rank) Corr., Spp-Envt	0.696 *	0.572 *	0.717

Monte Carlo randomization test
* = P<0.05

Table 2. Results from the Canonical Correspondence Analysis (CCA) of the beetle community at Blodgett Forest. The CCA was based on a species matrix of 115 beetle species by 24 compartments (12 compartments pre- and post-treatment). The habitat matrix was 4 environmental variables by 24 compartments. The first axis explained most of the variance in the data and was the only significant axis based on a Monte Carlo test.

CONCLUSIONS

anthropogenic disturbances

negative vs positive view of disturbances

one disturbance may require management, while another is management

recap results

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Appendix 1. From Chapter 4, the list of beetle species and number captured at Blodgett Forest over three summers of trapping (2001-2003).

Family	**Species**	**# individuals**
Anobiidae	*Paralobium mundum* Fall. 1905	2
	Ptinus sp. 1	114
	Ptinus sp. 2	66
	Tricorynus sp.	2
Anthicidae	*Ischyropalpus nitidulus* Lec. 1851	1
Bostrichidae	*Scobicia declivis* Lec. 1857	6
Buprestidae	*Anthaxia aeneogaster* LaPort & Gory 1841	21
	Anthaxia sp.	1
	Chrysobothris semisculpta Lec. 1859	1
	Serropalpus substriatus Haldeman 1848	1
Byrrhidae	*Amphicyrta dentipes* Erichson 1843	3
Cantharidae	*Malthodes* sp.	36
	Podabrus cavicollis Lec. 1851	3
	Podabrus sp. 1	12
	Podabrus sp. 2	5
	Podabrus sp. 3	1
Carabidae	*Agonum* sp.	1
	Amara californica Dej. 1828	3
	Anisodactylus similis Lec. 1851	1
	Bembidion sp. 1	1
	Bembidion sp. 2	14
	Bembidion sp. 3	2
	Bembidion sp. 4	1
	Callisthenes discors Lec. 1857	7
	Carabus taedatus Fabr. 1787	7
	Metrius contractus Esch. 1829	1258
	Omus californicus Esch. 1829	374
	Pterostichus (*Hypherpes*) sp. 1	215
	Pterostichus (*Hypherpes*) sp. 2	327
	Pterostichus (*Hypherpes*) sp. 3	100
	Pterostichus (*Hypherpes*) sp. 4	110
	Pterostichus (*Hypherpes*) sp. 5	56
	Pterostichus (*Leptoferonia*) stapedius Hacker 1968	2
	Pterostichus inanis Horn 1891	20
	Pterostichus lama Menetries 1843	272
	Pterostichus morionides Chaudoir 1868	6
	Scaphinotus marginatus Fischer 1822	3
	Sericoda bembidioides Kirby 1837	1
	Tanystoma striata Dej. 1828	8
	Trachypacus holmbergi Mann. 1853	21
	Trechus sp.	1
Cerambycidae	*Callidium antennatum* Casey 1912	1
	Centrodera spurca Lec. 1860	10
	Clytus planifrons Lec.	27

Appendix 1, *cont.*

Family	**Species**	**# individuals**
Cerambycidae, *cont.*	*Phymatodes decussatus* Lec. 1857	2
	Phymatodes hirtellus Lec. 1873	1
	Pidonia gnathoides Lec. 1873	2
	Spondylis upiformis Mann. 1843	13
	Strophiona laeta Lec. 1857	14
	unknown Cerambycid sp. 1	2
	unknown Cerambycid sp. 2	1
Chrysomelidae	*Pachybrachis* sp.	1
Cicindellidae	*Cicindela* sp.	4
Ciidae	*Sulcacis curtulus* Casey 1898	17
Cleridae	*Cymatodera ovipennis* Lec. 1859	7
	Phyllobaenus scaber Lec. 1852	2
Coccinellidae	*Coccinella* sp.	1
	Hippodamia convergens Guerin-Meneville 1842	1
	Psyllobora vigintimaculata Say 1824	1
	unknown Coccinellid sp. 1	1
	unknown Coccinellid sp. 2	1
	unknown Coccinellid sp. 3	1
Colydiidae	*Lasconotus* sp.	2
	Oxylaemus californicus Crotch 1875	1
Cryptophagidae	*Atomaria* sp. 1	181
	Atomaria sp. 2	1
	Cryptophagus sp. 1	2
	Cryptophagus sp. 2	4
	Henoticus sp.	9
	unknown Cryptophagid sp.	16
Curculionidae	*Agronus cinerarius*	23
	Cossonus crenatus Horn 1873	1
	Dyslobus lecontei Casey 1895	74
	Dyslobus sp.	100
	Lechirops sp.	1
	Nemocestes montanus Van Dyke 1936	45
	Rhyncolus oregonensis Horn 1873	39
	Rhyncolus sp.	1
	Sitonia sp.	4
	Thricolepis simulator Horn 1876	91
	Tychius sp.	3
	unknown Curculionid sp. 1	5
	unknown Curculionid sp. 2	6
	unknown Curculionid sp. 3	319
	unknown Curculionid sp. 6	33
Dermestidae	*Trogoderma glabrum* Hbst 1783	24
Diphyllostomatidae	*Diphyllostoma linsleyi* Fall 1932	9
Elateridae	*Ampedus mixtus* Herbst 1806	4
	Ampedus phoenicopterus Germar 1843	1
	Ampedus rhodopus Lec. 1857	3
	Athous imitans Fall 1910	31

Appendix 1, *cont*.

Family	**Species**	**# individuals**
Elateridae, *cont*.	*Athous limbatus* Lec. 1861	1
	Athous opilinus Candeze 1860	14
	Athous scissus Candeze 1860	3
	Cardiophorus sp. 1	35
	Cardiophorus sp. 2	28
	Cardiophorus sp. 3	2
	Ctenicera imitans Brown 1935	36
	Ctenicera mendax Lec. 1853	32
	Ctenicera pallidipes Brown 1936	5
	Limonius humeralis Candeze 1960	13
	Limonius maculicollis Motschulsky 1859	2
	Megapenthes stigmosus Lec. 1853	1
	unknown Elaterid sp. 1	1
	unknown Elaterid sp. 2	2
	unknown Elaterid sp. 3	18
	unknown Elaterid sp. 4	3
	unknown Elaterid sp. 5	27
	unknown Elaterid sp. 6	1
Endomychidae	*Mycetina horni* Crotch 1873	3
	unknown Endomychid sp.	2
Erotylidae	*Dacne californica* Horn 1870	834
Euchnemidae	*Melasis rufipennis* Horn 1886	1
Geotrupidae	*Bolboceras obesus* Lec. 1859	20
Histeridae	*Bacanius* sp.	3
	Psiloscelis subopacus Lec. 1863	1
	Stictostix californica Horn 1870	40
Lampyridae	*Phausis riversi* Lec. 1884	28
Latridiidae	*Ardius* sp.	1
	Cartodere sp.	16
	Corticarina sp.	3
	Enicmus tenuicornis Lec. 1878	59
	Latridius sp. 1	85
	Latridius sp. 2	7
	Latridius sp. 3	2
	Metophthalmus sp.	113
	Migrogramme sp.	1
Leiodidae	*Agathidium* sp. 1	3
	Agathidium sp. 2	1
	Agathidium sp. 3	3
	Anisotoma nevadensis Brown 1937	4
	Anisotoma sp.	3
	Colon sp.	21
	Hydnobius sp. 1	7
	Hydnobius sp. 2	33
	Hydnobius sp. 3	7
	Ptomaphagus sp.	535
	unknown Leiodid sp.	1

Appendix 1, *cont*.

Family	**Species**	**# individuals**
Lucanidae	*Platyceroides latus* Fall 1901	53
Lyctidae	*Lyctus* sp. 1	1
	Lyctus sp. 2	2
Melandryidae	*Abdera bicinctus* Horn 1888	3
	unknown Melandryid sp.	3
Melyridae	*Dasyrhadus* sp. 1	6
	Dasyrhadus sp. 2	1
	Dasytini sp. 1	1
	Dasytini sp. 2	40
	Pseudasydates inyoensis Blaisdell 1938	1
	Trichochrous sp.	9
Monotomidae	*Hesperobaenus* sp.	35
Mordellidae	*Mordella* sp.	25
Mycetophagidae	*Mycetophagus californicus* Horn 1878	91
	Mycetophagus sp.	8
	Typhaea stercorea Linn. 1758	1
Nemonychidae	*Cimberis comptus* Lec. 1876	5
Nitidulidae	*Carpophilus* sp. 1	11
	Carpophilus sp. 2	9
	Pityophagus rufipennis Horn 1872	13
	Soronia guttulata Lec. 1863	15
	Thalycra sp. 1	37
	Thalycra sp. 2	4
	Thalycra sp. 3	5
Ochodaeidae	*Pseudochodaeus estriatus* Carlson and Richter 1974	1
Phalacridae	*Phalacrus* sp.	1
Ptiliidae	unknown Ptiliid sp. 1	569
	unknown Ptiliid sp. 2	2
	unknown Ptiliid sp. 3	40
	unknown Ptiliid sp. 4	85
	unknown Ptiliid sp. 5	21
	unknown Ptiliid sp. 6	11
Rhysodidae	*Clinidium calcaratum* Lec. 1875	33
Salpingidae	*Elacitus* sp.	2
Scarabaeidae	*Aphodius* sp.	126
	Canthon simplex Lec. 1857	3
	Cremastochelius sp.	1
	Dichelonyx crotchi Horn 1876	37
	Dichelonyx lateralis Fall 1901	17
	Serica anthracina Lec. 1856	1
	Serica curvata Lec. 1856	42
Scolytidae	*Dendroctonus valens* Lec. 1860	1
	Gnathotrichus retusus Lec. 1868	1
	Gnathotrichus sulcatus Lec. 1868	1
	Hylastes gracilis Lec. 1868	24
	Hylastes macer Lec. 1868	78
	Hylurgops pinifex Fitch 1851	1

Appendix 1, *cont*.

Family	**Species**	**# individuals**
Scolyitdae, *cont*.	*Hylurgops porosus* Lec. 1868	155
	Hylurgops reticulatus Wood 1971	2
	Hylurgops subscostulatus Mann. 1853	4
	Monarthrum scutellare Lec. 1860	1
	Phloeosinus punctatus Lec. 1876	5
	Phloeosinus sp.	1
	Pityophthorous sp.	1
	Pseudopityopthorus pubipennis Lec. 1878	3
	Scolytus ventralis Lec. 1868	5
	Xyleborinus saxeseni Ratz. 1837	58
	Xyleborus scopulorum Hopkins	168
Scraptiidae	*Anaspis* sp. 1	13
	Anaspis sp. 2	8
Scydmaenidae	*Lophioderus* sp.	5
	Veraphis sp. 1	3
	Veraphis sp. 2	17
Staphylinidae	*Actium* sp. 1	94
	Actium sp. 2	1
	Actium sp. 3	1
	Aleochara sp.	11
	Aleocharinae sp. 1	85
	Aleocharinae sp. 2	848
	Aleocharinae sp. 3	10
	Aleocharinae sp. 5	6
	Aleocharinae sp. 7	1
	Aleocharinae sp. 8	1
	Aleocharinae sp. 9	50
	Aleocharinae sp. 10	1
	Aleocharinae sp. 11	1
	Aleocharinae sp. 12	9
	Aleocharinae sp. 13	16
	Aleocharinae sp. 14	6
	Aleocharinae sp. 15	181
	Aleocharinae sp. 16	3
	Aleocharinae sp. 17	2
	Aleocharinae sp. 19	38
	Aleocharinae sp. 20	8
	Aleocharinae sp. 22	2
	Aleocharinae sp. 23	4
	Aleocharinae sp. 24	13
	Aleocharinae sp. 25	44
	Aleocharinae sp. 26	2
	Amphichroum maculatum Horn 1882	7
	Astenus sp.	1
	Batrisodes cicatricosis Brendel 1890	22
	Bryoporus sp.	6
	Deinopteroloma pictum Fauvel	42

Appendix 1, *cont.*

Family	**Species**	**# individuals**
Staphylinidae, *cont.*	*Eusphalerum* sp. 2	238
	Gabrius sp.	4
	Habrocerinae sp.	1
	Habrolinus sp.	2
	Hesperolinus sp.	8
	Ichnosoma californicum Berhauer and Schubert	149
	Lathrobium sp. 1	7
	Lathrobium sp. 2	1
	Mipseltyrus mirus Schuster 1956	2
	Omaliinae sp. 1	1
	Omaliinae sp. 2	4
	Oropus sp.	1
	Philonthus sp. 1	1
	Philonthus sp. 2	13
	Platydracus rutilicanda Horn	5
	Quedius sp. 1	13
	Quedius sp. 3	3
	Quedius sp. 4	5
	Quedius sp. 5	1
	Quedius sp. 6	1
	Renardia sp.	1
	Stenus vespertinus Casey 1884	3
	Stictolinus sp.	1
	Tachinus semirufus Horn 1877	387
	Tachyporus californicus Horn 1877	88
	Tyrus corticinus Casey 1897	1
	unknown Staphylinid sp. 1	2
	unknown Staphylinid sp. 2	1
	unknown Staphylinid sp. 3	4
Tenebrionidae	*Cibdelis blaschkei* Mann. 1843	17
	Cnemeplatia sericea Horn 1870	60
	Coelocnemis californica Mann. 1843	187
	Coniontis sp.	145
	Eleodes cordata Esch. 1833	2369
	Helops punctipennis Lec. 1866	5
	Helops simulator Blaisdell 1921	113
	Iphthminus serratus Mann. 1843	8
	Megeleates sequoiarum Casey 1895	1
	Mycetochara sp.	3
	Nyctoporis sponsa Casey 1907	213
	Scotobaenus parallelus Lec. 1859	16
Tetratomidae	*Eustrophinus tomentosus* Say 1827	11
Throscidae	*Pactopus horni* Lec. 1868	1842
Trogossitidae	*Eronyxa* sp.	1
Zopheridae	*Phellopsis porcata* Lec. 1853	5
	Usechimorpha montana Doyen 1979	7

Appendix 2. From Chapter 4, the list of ant species captured and total number of each genus captured at Blodgett Forest over three summers of trapping.

Species	**# individuals**
Amblyopone	2
Amblyopone oregonensis Cole 1938	
Aphaenogaster	3446
Aphaenogaster occidentalis Emery 1895	
Camponotus	11842
Camponotus essigi Smith 1923	
Camponotus laevigatus Smith 1858	
Camponotus modoc Wheeler 1910	
Camponotus quercicola Smith 1953	
Camponotus vicinus Mayr 1870	
Formica	10408
Formica accreta Francoeur 1973	
Formica argentea Wheeler 1912	
Formica aserva Forel 1901	
Formica fusca L. 1758	
Formica sp. cf. *sybilla*	
Lasius	1357
Lasius flavus Fab. 1781	
Lasius pallitarsis Provancher 1881	
Leptothorax	4732
Leptothorax nitens Emery 1895	
Leptothorax rudis Emery 1895	
Liometopum	9887
Liometopum luctuosum Wheeler 1905	
Liometopum occidentale Emery 1895	
Myrmica	22
Myrmica tahoensis Weber 1948	
Polyergus	210
Polyergus breviceps Emery 1895	
Prenolepis	427
Prenolepis imparis Say 1836	
Stenamma	121
Stenamma sp. cf. *snellingi*	
Stenamma sp.	
Tapinoma	4199
Tapinoma sessile Say 1836	

Appendix 3. From Chapter 5, the species of Coleoptera captured during the study and total abundance of each species. This list represents two summers of trapping effort (2001 and 2003). Guild assignments are as follows: C = coprophage, F = fungivore, H = herbivore, O = omnivore, P = predator, S = scavenger, and W = wood-borer. Indicator values represent the percent indication of each species for a given treatment type. Treatment indicates the habitat type for which a species was representative, based on a Monte Carlo randomization test. • $P<0.10$, * $P<0.05$, ** $P<0.01$, *** $P<0.00$

Family	Species	total	guild	code	indicator value	treatment
Anobiidae	*Paralobium mundum* Fall. 1905	1	W	-	33.3	-
	Ptinus sp. 1	99	S	83	49.8	-
	Ptinus sp. 2	55	S	84	39.7	-
Anthicidae	*Ischyropalpus nitidulus* Lec. 1851	1	O	-	33.3	-
Bostrichidae	*Scobicia declivis* Lec. 1857	6	W	88	66.7	both *
Buprestidae	*Anthaxia aeneogaster* LaPort & Gory 1841	21	W	15	34.4	-
	Serropalpus substriatus Haldeman 1848	1	W	-	33.3	-
Byrrhidae	*Amphicyrta dentipes* Erichson 1843	3	H	-	22.2	-
Cantharidae	*Malthodes* sp.	30	O	67	48.8	-
	Podabrus cavicollis Lec. 1851	3	P	-	23.8	-
	Podabrus sp. 1	8	P	80	35.7	-
	Podabrus sp. 2	5	P	-	15.9	-
	Podabrus sp. 3	1	P	-	33.3	-
Carabidae	*Agonum* sp.	1	P	-	6.7	-
	Amara californica Dej. 1828	3	P	-	15.2	-
	Anisodactylus similis Lec. 1851	1	P	-	6.7	-
	Bembidion sp. 1	1	P	-	6.7	-
	Bembidion sp. 2	13	P	20	70.2	fire *
	Bembidion sp. 3	2	P	-	6.7	-
	Bembidion sp. 4	1	P	-	33.3	-
	Callisthenes discors Lec. 1857	5	P	-	29.4	-
	Carabus taedatus Fabr. 1787	5	P	-	13.3	-

Appendix 3, *cont*.

Family	Species	total	guild	code	indicator value	treatment
Carabidae, *cont*.	*Metrius contractus* Esch. 1829	951	P	69	50.3	-
	Omus californicus Esch. 1829	276	P	75	54.1	fire *
	Pterostichus (*Hypherpes*) sp. 1	193	P	56	62.9	mech ***
	Pterostichus (*Hypherpes*) sp. 2	290	P	57	37.5	-
	Pterostichus (*Hypherpes*) sp. 3	80	P	58	32	-
	Pterostichus (*Hypherpes*) sp. 4	98	P	59	35.4	-
	Pterostichus (*Hypherpes*) sp. 5	49	P	60	63.6	mech *
	Pterostichus (*Leptoferonia*) stapedius Hacker 1968	2	P	-	13.3	-
	Pterostichus inanis Horn 1891	18	P	81	26.7	-
	Pterostichus lama Menetries 1843	228	P	82	47	control •
	Pterostichus morionides Chaudoir 1868	3	P	-	60.6	mech •
	Scaphinotus marginatus Fischer 1822	3	P	-	13.3	-
	Sericoda bembidioides Kirby 1837	1	P	-	22.7	-
	Tanystoma striata Dej. 1828	7	P	98	58	mech *
	Trachypacus holmbergi Mann. 1853	21	P	-	81	both *
	Trechus sp.	1	P	-	6.7	-
Cerambycidae	*Callidium antennatum* Casey 1912	1	W	-	33.3	-
	Centrodera spurca Lec. 1860	9	W	27	67.6	fire *
	Clytus planifrons Lec.	24	W	30	51.7	-
	Phymatodes decussatus Lec. 1857	2	W	-	27.8	-
	Phymatodes hirtellus Lec. 1873	1	W	-	33.3	-
	Pidonia gnathoides Lec. 1873	2	W	-	33.3	-
	Spondylis upiformis Mann. 1843	13	W	92	60.6	both •
	Strophiona laeta Lec. 1857	14	W	94	37	-
	unknown Cerambycid sp. 1	2	W	-	27.8	-
	unknown Cerambycid sp. 2	1	W	-	33.3	-
	Pachybrachis sp.	1	H	-	33.3	-
Cicindellidae	*Cicindela* sp.	4	P	-	13.9	-
Ciidae	*Sulcacis curtulus* Casey 1898	8	F	95	47.6	-
Cleridae	*Cymatodera ovipennis* Lec. 1859	7	P	-	92.6	both **
	Phyllobaenus scaber Lec. 1852	1	P	-	33.3	-
Coccinellidae	*Coccinella* sp.	1	P	-	6.7	-
	Psyllobora vigintimaculata Say 1824	1	P	-	33.3	-

Appendix 3, *cont*.

Family	Species	total	guild	code	indicator value	treatment
Coccinellidae, *cont*.	unknown Coccinellid sp. 1	1	P	-	33.3	-
	unknown Coccinellid sp. 2	1	P	-	33.3	-
Colydiidae	*Lasconotus* sp.	2	P	-	27.8	-
	Oxylaemus californicus Crotch 1875	1	F	-	33.3	-
Cryptophagidae	*Atomaria* sp. 1	171	F	14	80.4	both *
	Atomaria sp. 2	1	F	-	33.3	-
	Cryptophagus sp. 1	2	F	-	33.3	-
	Cryptophagus sp. 2	4	F	-	13.9	-
	Henoticus sp.	7	F	49	11.1	-
	unknown Cryptophagid sp.	5	F	-	19.6	-
Curculionidae	*Agronus cinerarius*	21	H	2	20.5	-
	Cossonus crenatus Horn 1873	1	H	-	33.3	-
	Dyslobus lecontei Casey 1895	58	H	42	38.6	-
	Dyslobus sp.	88	H	43	25.1	-
	Nemocestes montanus Van Dyke 1936	40	H	73	32.4	-
	Rhyncolus oregonensis Horn 1873	34	H	87	29.1	-
	Rhyncolus sp.	1	H	-	33.3	-
	Sitonia sp.	4	H	-	13.9	-
	Thricolepis simulator Horn 1876	58	H	100	74.3	fire •
	Tychius sp.	3	H	-	23.8	-
	unknown Curculionid sp. 1	5	H	103	15.9	-
	unknown Curculionid sp. 2	6	H	104	55.6	fire •
	unknown Curculionid sp. 3	237	H	-	35.8	-
	unknown Curculionid sp. 6	30	H	105	44.9	-
Dermestidae	*Trogoderma glabrum* Hbst 1783	20	S	102	24.5	-
Diphyllostomatidae	*Diphyllostoma linsleyi* Fall 1932	8	H	-	59.5	both *
Elateridae	*Ampedus mixtus* Herbst 1806	3	H	-	13.3	-
	Ampedus phoenicopterus Germar 1843	1	H	-	33.3	-
	Ampedus rhodopus Lec. 1857	2	H	-	33.3	-
	Athous imitans Fall 1910	28	H	17	27.5	-
	Athous opilinus Candeze 1860	13	H	18	21.3	-
	Athous scissus Candeze 1860	3	H	-	15.2	-
	Cardiophorus sp. 1	32	H	22	47.6	-

Appendix 3, *cont*.

Family	Species	total	guild	code	indicator value	treatment
Elateridae, *cont*.	*Cardiophorus* sp. 2	19	H	23	16.1	-
	Cardiophorus sp. 3	2	H	-	16.7	-
	Ctenicera imitans Brown 1935	36	H	35	72.4	fire *
	Ctenicera mendax Lec. 1853	28	H	36	64.5	both •
	Ctenicera pallidipes Brown 1936	2	H	-	27.8	-
	Limonius humeralis Candeze 1960	8	H	66	20.8	-
	Limonius maculicollis Motschulsky 1859	2	H	-	33.3	-
	unknown Elaterid sp. 1	1	H	-	6.7	-
	unknown Elaterid sp. 2	2	H	-	27.8	-
	unknown Elaterid sp. 3	15	H	-	24.9	-
	unknown Elaterid sp. 4	3	H	-	23.8	-
	unknown Elaterid sp. 5	24	H	106	41.7	-
	unknown Elaterid sp. 6	1	H	-	6.7	-
Endomychidae	*Mycetina horni* Crotch 1873	2	F	-	75.3	mech *
	unknown Endomychid sp.	1	F	-	6.7	-
Erotylidae	*Dacne californica* Horn 1870	572	F	37	39.2	-
Euchnemidae	*Melasis rufipennis* Horn 1886	1	F	-	33.3	-
Geotrupidae	*Bolboceras obesus* Lec. 1859	9	U	21	30.3	-
Histeridae	*Bacanius* sp.	1	P	-	33.3	-
	Psiloscelis subopacus Lec. 1863	1	P	-	6.7	-
	Stictostix californica Horn 1870	39	P	-	33.3	-
Lampyridae	*Phausis riversi* Lec. 1884	28	P	-	6.7	-
Latridiidae	*Ardius* sp.	1	F	-	6.7	-
	Cartodere constrictus	11	F	26	38.8	-
	Corticarina sp.	2	F	-	16.7	-
	Enicmus tenuicornis Lec. 1878	52	F	45	59.8	fire •
	Latridius sp. 1	76	F	64	34.6	-
	Latridius sp. 2	7	F	65	14.5	-
	Latridius sp. 3	2	F	-	16.7	-
	Metophthalmus sp.	91	F	68	54.1	mech *
	Microgramme sp.	1	F	-	33.3	-
Leiodidae	*Agathidium* sp. 1	3	F	-	44.4	-
	Agathidium sp. 2	1	F	-	33.3	-

Appendix 3, *cont*.

Family	Species	total	guild	code	indicator value	treatment
Leiodidae, *cont*.	*Agathidium* sp. 3	2	F	-	16.7	-
	Anisotoma nevadensis Brown 1937	1	F	-	6.7	-
	Anisotoma sp.	2	F	-	27.8	-
	Colon sp.	19	F	33	23.3	-
	Hydnobius sp. 1	5	F	-	6.7	-
	Hydnobius sp. 2	17	F	52	75.5	mech *
	Hydnobius sp. 3	7	F	-	32.3	-
	Ptomaphagus sp.	442	S	85	53.2	-
Lucanidae	*Platyceroides latus* Fall 1901	41	H	79	22.3	-
Lyctidae	*Lyctus* sp. 2	2	F	-	66.7	both *
Melandryidae	*Abdera bicinctus* Horn 1888	3	F	-	20	-
	Eustrophinus tomentosus Say 1827	8	F	47	13.9	-
	unknown Melandryid sp.	3	F	-	33.3	-
Melyridae	*Dasyrhadus* sp. 1	5	O	-	33.3	-
	Dasytini sp. 1	1	O	-	28.5	-
	Dasytini sp. 2	26	O	38	19.6	-
	Pseudasydates inyoensis Blaisdell 1938	1	O	-	6.7	-
	Trichochrous sp.	8	O	101	11.9	-
Monotomidae	*Hesperobaenus* sp.	27	F	50	33.1	-
Mordellidae	*Mordella* sp.	15	H	70	53.2	both •
Mycetophagidae	*Mycetophagus californicus* Horn 1878	33	F	71	11.1	-
	Mycetophagus sp.	7	F	72	27.8	-
Nemonychidae	*Cimberis comptus* Lec. 1876	5	F	-	31.7	-
Nitidulidae	*Carpophilus* sp. 1	11	F	24	30.3	-
	Carpophilus sp. 2	6	F	25	33.3	-
	Pityophagus rufipennis Horn 1872	13	P	-	100	both **
	Soronia guttulata Lec. 1863	15	F	91	45.8	-
	Thalycra sp. 1	22	F	99	51.7	fire •
	Thalycra sp. 2	4	F	-	20	-
	Thalycra sp. 3	4	F	-	41.7	-
Ochodaeidae	*Pseudochodaeus estriatus* Carlson and Richter 1974	1	U	-	33.3	-
Phalacridae	*Phalacrus* sp.	1	F	-	33.3	-
Ptiliidae	unknown Ptiliid sp. 1	304	F	107	33.1	-

Appendix 3, *cont*.

Family	Species	total	guild	code	indicator value	treatment
Ptiliidae, *cont*.	unknown Ptiliid sp. 2	2	F	-	33.3	-
	unknown Ptiliid sp. 3	20	F	108	48.2	-
	unknown Ptiliid sp. 4	72	F	109	55.8	mech •
	unknown Ptiliid sp. 5	19	F	110	87.3	mech **
	unknown Ptiliid sp. 6	7	F	111	37	-
Rhysodidae	*Clinidium calcaratum* Lec. 1875	20	F	29	41.7	-
Salpingidae	*Elacitus* sp.	2	S	-	16.7	-
Scarabaeidae	*Aphodius* sp.	82	C	16	67.1	mech *
	Canthon simplex Lec. 1857	2	C	-	16.7	-
	Dichelonyx crotchi Horn 1876	36	H	40	37.5	-
	Dichelonyx lateralis Fall 1901	15	H	41	28.4	-
	Serica anthracina Lec. 1856	1	H	-	6.7	-
	Serica curvata Lec. 1856	31	H	90	33.3	-
Scolytidae	*Hylastes gracilis* Lec. 1868	23	W	53	77.7	both *
	Hylastes macer Lec. 1868	71	W	54	82.6	both *
	Hylurgops porosus Lec. 1868	129	W	55	53.9	-
	Hylurgops subscostulatus Mann. 1853	2	W	-	27.8	-
	Phloeosinus punctatus Lec. 1876	2	W	-	33.3	-
	Phloeosinus sp.	1	W	-	6.7	-
	Pityophthorous sp.	1	W	-	6.7	-
	Pseudopityopthorus pubipennis Lec. 1878	1	W	-	33.3	-
	Scolytus ventralis Lec. 1868	4	W	-	16.7	-
	Xyleborinus saxeseni Ratz. 1837	26	W	114	43.9	-
	Xyleborus scopulorum Hopkins	74	W	115	49.3	-
Scraptiidae	*Anaspis* sp. 1	10	H	13	19.2	-
	Anaspis sp. 2	7	H	-	30.9	-
Scydmaenidae	*Lophioderus* sp.	4	P	-	41.7	-
	Veraphis sp. 1	3	P	-	15.2	-
	Veraphis sp. 2	11	P	113	16.1	-
Staphylinidae	*Actium* sp. 1	85	P	1	47	-
	Actium sp. 2	1	P	-	6.7	-
	Actium sp. 3	1	P	-	6.7	-
	Aleochara sp.	4	P	-	50	both •

Appendix 3, *cont*.

Family	Species	total	guild	code	indicator value	treatment
Staphylinidae, *cont*.	Aleocharinae sp. 1	75	P	3	46.8	-
	Aleocharinae sp. 2	523	P	8	40.4	-
	Aleocharinae sp. 3	10	P	-	26.7	-
	Aleocharinae sp. 5	2	P	-	13.3	-
	Aleocharinae sp. 7	1	P	-	6.7	-
	Aleocharinae sp. 8	1	P	-	6.7	-
	Aleocharinae sp. 9	49	P	11	69.4	mech *
	Aleocharinae sp. 10	1	P	-	6.7	-
	Aleocharinae sp. 11	1	P	-	6.7	-
	Aleocharinae sp. 12	7	P	4	22.2	-
	Aleocharinae sp. 13	14	P	-	92.9	both **
	Aleocharinae sp. 14	6	P	5	38.5	-
	Aleocharinae sp. 15	159	P	6	50.6	mech **
	Aleocharinae sp. 16	3	P	-	20	-
	Aleocharinae sp. 17	2	P	-	33.3	-
	Aleocharinae sp. 19	27	P	7	36.8	-
	Aleocharinae sp. 20	6	P	-	64.1	mech *
	Aleocharinae sp. 22	2	P	-	27.8	-
	Aleocharinae sp. 23	4	P	-	20.8	-
	Aleocharinae sp. 24	13	P	9	34	-
	Aleocharinae sp. 25	36	P	10	23.3	-
	Aleocharinae sp. 26	2	P	-	13.3	-
	Amphichroum maculatum Horn 1882	6	H	12	18.5	-
	Astenus sp.	1	P	-	33.3	-
	Batrisodes cicatricosis Brendel 1890	19	P	19	29.5	-
	Bryoporus sp.	6	P	-	90.9	mech **
	Deinopteroloma pictum Fauvel	39	F	39	56	mech •
	Eusphalerum sp. 2	84	H	46	72.3	mech •
	Gabrius sp.	4	P	-	62.5	fire •
	Habrocerinae sp.	1	P	-	33.3	-
	Habrolinus sp.	2	P	-	16.7	-
	Hesperolinus sp.	7	P	51	64.5	both *
	Ichnosoma californicum Berhauer and Schubert	118	S	61	59.8	control **

Appendix 3, *cont*.

Family	Species	total	guild	code	indicator value	treatment
Staphylinidae, *cont*.	*Lathrobium* sp. 1	7	P	63	37	-
	Lathrobium sp. 2	1	P	-	33.3	-
	Mipseltyrus mirus Schuster 1956	2	P	-	27.8	-
	Omaliinae sp. 2	2	P	-	13.3	-
	Oropus sp.	1	P	-	33.3	-
	Philonthus sp. 1	1	P	-	33.3	-
	Philonthus sp. 2	10	P	78	40	-
	Platydracus rutilicanda Horn	5	P	-	25.6	-
	Quedius sp. 1	8	P	86	16.7	-
	Quedius sp. 3	3	P	-	15.2	-
	Quedius sp. 4	4	P	-	20.8	-
	Quedius sp. 6	1	P	-	33.3	-
	Renardia sp.	1	F	-	33.3	-
	Stenus vespertinus Casey 1884	3	P	-	60.6	both •
	Stictolinus sp.	1	P	93	35.5	-
	Tachinus semirufus Horn 1877	153	P	97	51.8	mech *
	Tachyporus californicus Horn 1877	76	P	96	75.3	mech **
	Tyrus corticinus Casey 1897	1	P	-	6.7	-
	unknown Staphylinid sp. 1	2	P	-	30.3	-
	unknown Staphylinid sp. 2	1	P	-	6.7	-
	unknown Staphylinid sp. 3	3	P	-	33.3	-
Tenebrionidae	*Cibdelis blaschkei* Mann. 1843	15	S	28	34.2	-
	Cnemeplatia sericea Horn 1870	59	S	31	38.4	-
	Coelocnemis californica Mann. 1843	174	S	32	36	-
	Coniontis sp.	113	S	34	47.9	-
	Eleodes cordata Esch. 1833	1737	S	44	32.5	-
	Helops punctipennis Lec. 1866	5	S	-	26.7	-
	Helops simulator Blaisdell 1921	92	S	48	42.7	-
	Iphthminus serratus Mann. 1843	8	P	62	20.8	-
	Megeleates sequoiarum Casey 1895	1	S	-	33.3	-
	Mycetochara sp.	2	S	-	27.8	-
	Nyctoporis sponsa Casey 1907	198	S	74	51.6	-
	Scotobaenus parallelus Lec. 1859	10	S	89	30	-

Appendix 3, *cont*.

Family	Species	total	guild	code	indicator value	treatment
Throscidae	*Pactopus horni* Lec. 1868	1529	F	76	42.9	-
Zopheridae	*Phellopsis porcata* Lec. 1853	5	F	77	39.2	-
	Usechimorpha montana Doyen 1979	6	F	112	60.6	both •