

Biodiversity of Coleoptera and the Importance of Habitat Structural Features in a Sierra Nevada Mixed-conifer Forest

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ABSTRACT Beetle biodiversity, particularly of leaf litter fauna, in the Sierran mixed-conifer ecosystem is poorly understood. This is a critical gap in our knowledge of this important group in one of the most heavily managed forest ecosystems in California. We used pitfall trapping to sample the litter beetles in a forest with a history of diverse management. We identified 287 species of beetles from our samples. Rarefaction curves and nonparametric richness extrapolations indicated that, despite intensive sampling, we undersampled total beetle richness by 32–63 species. We calculated alpha and beta diversity at two scales within our study area and found high heterogeneity between beetle assemblages at small spatial scales. A nonmetric multidimensional scaling ordination revealed a community that was not predictably structured and that showed only weak correlations with our measured habitat variables. These data show that Sierran mixed conifer forests harbor a diverse litter beetle fauna that is heterogeneous across small spatial scales. Managers should consider the impacts that forestry practices may have on this diverse leaf litter fauna and carefully consider results from experimental studies before applying stand-level treatments.

KEY WORDS Coleoptera, pitfall trapping, leaf litter beetles, Sierra Nevada

The maintenance of high biodiversity is a goal shared by many conservationists and managers, either because of the increased productivity and ecosystem processes that may be associated with areas of high biodiversity (Tillman et al. 1996, McCann 2000) or because it is an 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 successful, long-term studies on the effects of management (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 and heavily managed 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 in California make this ecosystem particularly worthy of increased study. Over two thirds of the 6,000 km² of mixed-conifer forest in the

Sierras is available for timber harvesting, whereas 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, North et al. 2002), 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 beetles is particularly scant (Kimsey 1996). Beetles, as well as other litter arthropods, are of particular importance to study because of their roles as predators, decomposers, and herbivores (Petersen and Luxton 1982).

Our primary objective in this paper is to present a complete list of leaf litter beetle species captured in pitfall traps over the course of three summers of trapping in a representative Sierran mixed-conifer forest. We also analyze the richness and diversity of Coleoptera and determine the degree of spatial heterogeneity in beetle assemblage composition. 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 et al. 2001).

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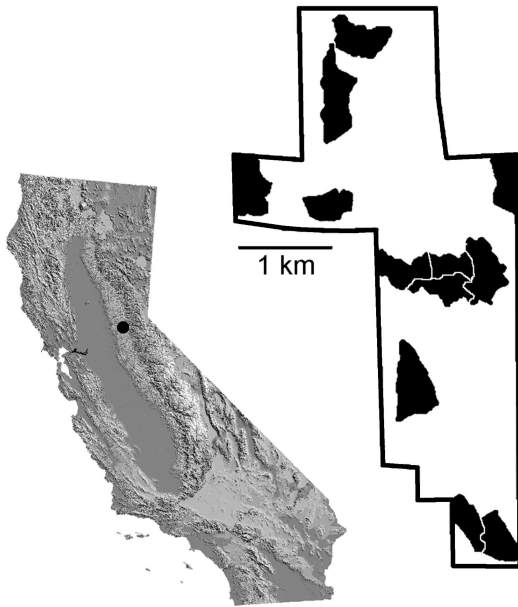


Fig. 1. Map of the study site showing location of Blodgett Forest within California. Compartments are delineated within the forest. Shaded compartments were selected for this study. Plot locations are not shown. Scale: 1 cm = 1 km.

Therefore, we also conducted a multivariate analysis of the beetle assemblages at Blodgett Forest, including relationships with several important habitat features. 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.

Materials and 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 western Sierra Nevada, between $\approx 1,200$ and $1,500$ m, near the Georgetown Divide ($38^{\circ}52'$ N, $120^{\circ}40'$ W). Olson and Helms (1996) provided a detailed description of the forest, its history, and current management regimens. 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 20th century also burned much of the forest and were a common feature of the landscape before European settlement (Stephens and Collins 2004). Otherwise, fire has been largely excluded from the property at a large scale during the 20th century. The University of California has managed Blodgett since the mid-1930s 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 (Stephens and

Moghaddas 2005a). The site is dominated by five major overstory conifer species, Douglas-fir (*Pseudotsuga menziesii* Mirbel), sugar pine (*Pinus lambertiana* Douglas), ponderosa pine (*Pinus ponderosa* Douglas ex Lawson), white fir (*Abies concolor* Gordon and Glendenning), and incense-cedar (*Calocedrus decurrens* Torrey), and one major hardwood, California black oak (*Quercus kelloggii* Newberry). The understory is dominated by a variety of shrub and herb species.

Blodgett Forest covers $\approx 1,200$ 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 inventory plots were established in each on a 60-m grid. Tree species, diameter at breast height (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. These measurements were taken as part of a larger, nationwide study on the effects of fire and fire surrogate treatments on many aspects of forest ecology. Refer to Stephens and Moghaddas (2005b, c) for a full description of plot setup and the vegetation and fuel 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 it remains 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 abundance as a function of the activity of the species, 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 five plots from each of the 12 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 4-wk intervals. Traps were kept open for 5 d 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 beetles at Blodgett with a low risk of depleting the local fauna. Traps were kept closed in the field between trapping periods to avoid a "digging in" effect (Digweed et al. 1995). Beetle samples were collected in vials of 95% ethanol for storage and sorting.

Sorting and Identification. Arthropod samples were sorted in the laboratory by K. Apigian and trained technicians. All arthropods were initially sorted into “morphospecies,” and a reference collection was made. Identifications of beetles 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). Voucher specimens were placed in the collection of the University of California, Berkeley, Essig Museum.

Data Analysis. The results in this paper 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 2005b, c). For the larger study, treatments were implemented in the summer and fall of 2002 after this pretreatment work, and initial posttreatment data were collected in 2003. Pitfall trap captures from all three summers of trapping (2001, 2002, and 2003) formulate the species list presented herein. We also use data from all years of the study for total richness and diversity estimates. For the purposes of multivariate analyses of the relationships between habitat characteristics and species assemblages, we use data only from 2001, before implementation of the treatments. A previous paper focused exclusively on the effects of treatments on the leaf litter fauna at Blodgett Forest (Apigian et al. 2006).

We calculated a rarefaction curve for the year 2001 using the free EstimateS software (Colwell 2005) to determine how adequately we sampled the beetle community at Blodgett. We also constructed a curve for all years of trapping (2001, 2002, and 2003) as a comparison to the 2001 curve. Richness calculations were made at the plot or compartment level by summing together the total beetle capture for each of the traps in the sample unit (plot or compartment) across the 4 mo of sampling. We calculated alpha (α), beta (β), and gamma (γ) diversity for the beetle community. Alpha diversity was calculated at two scales: based on the mean plot species richness (sample size = 60 in 2001; 165 for all years) and the mean compartment species richness (sample size = 12 in 2001; 30 for all years). Gamma diversity was calculated as the total diversity across all of our samples and was determined separately for 2001 and the years 2001–2003 combined. We also calculated beta diversity, a measure of heterogeneity of the beetle community across sample units, at the plot and compartment scale using the equation of Whittaker (1972): $\beta = (\gamma/\alpha) - 1$.

As even very intensive sampling fails to account for all species in most insect communities, we calculated two nonparametric estimators of total species richness: the first-order jackknife estimate and the bootstrap estimate. Raw species richness totals form a lower bound of the estimate of total species richness for both estimators. The nonparametric first-order jackknife estimator predicts total species richness based on a combination of the abundance and inci-

dence of “singletons” (species represented by a single individual in the sample, see Colwell and Coddington 1994 for equation). The bootstrap method uses a resampling procedure to estimate species richness (Efron 1979). The relative bias, precision, and accuracy of these and several other estimation procedures has been reviewed at length with little overall consensus on the best procedure (Smith and van Belle 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 estimator has been found to be among the least biased (Palmer 1990, Hellman and Fowler 1999), but at larger sample sizes, all estimators show positive bias, particularly in a community with many rare species (Palmer 1995). The bootstrap procedure has been shown to be less biased than other estimators with large sample sizes or extensive sampling (Smith and van Belle 1984, Hellman and Fowler 1999) and has been shown to generally underestimate species richness relative to the jackknife estimator (Palmer 1990). We used both of these procedures to provide a high and low estimate of total diversity. We calculated both the first-order jackknife estimator and the bootstrap estimator for our beetle community for all years of sampling (2001–2003) and 2001 only and compared these estimates of gamma diversity with our raw species richness totals.

Three common indices were used to concisely describe community structure and diversity: the Shannon index (H), Simpson’s index (D), and an evenness index (E). High evenness and abundance contribute to a high Shannon Index. Simpson’s index measures dominance by giving the probability that any two individuals drawn from the community will be of the same species. The evenness index measures equitability on a scale from 0 to 1, with communities with perfect evenness approaching 1.

Nonmetric multidimensional scaling (NMS) was used to develop an ordination based on species responses, unconstrained by habitat variables, using PC-Ord (McCune and Mefford 1999). 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 2001 abundance data from species appearing in at least 20% of our plots. The data matrix consisted of these abundance data from 58 plots in 2001; Two outlier plots were not included in the final ordination as a multivariate outlier analysis indicated an average Sorenson distance >2 SD from the mean. 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. While the NMS ordination does not rely on habitat variables to construct the axes, vectors overlaid on joint plots can be used to represent the strength of

Table 1. Plot means, SDs, and max and min values for the 11 habitat variables used

| | Mean | SD | Max | Min |
|--|--------|-----------------------|----------|-------|
| Percent canopy cover | 67.13 | 18.26 | 96.00 | 24.00 |
| Percent slope | 19.45 | 9.79 | 43.00 | 2.00 |
| Percent bare mineral soil | 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 fuel vol/ha (m ³) | 59.39 | 84.88 | 375.46 | 0.00 |
| Conifer basal area (m ² /ha) | 202.99 | 75.46 | 437.32 | 65.23 |
| Hardwood basal area (m ² /ha) | 22.90 | 35.01 | 162.17 | 0.00 |
| Sapling density/ha | 724.44 | 1,282.42 | 5,930.64 | 0.00 |
| Skid trail | | (categorical, Y or N) | | |

several habitat variables in relation to the NMS axes. We selected several variables that represent the structure of the habitat at Blodgett Forest: 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 coarse woody debris (CWD) vol/ha (m³), total conifer basal area (m²), total hardwood basal area (m²), and sapling density per hectare (Table 1). Previous papers have outlined the data collection techniques for these variables (Stephens and Moghaddas 2005b, c).

Results

In all 3 yr of this study (2001–2003), we captured a total of 15,683 beetles in 51 families and 278 species (Appendix 1). Fifty-nine percent of the catch was represented by three families: Carabidae, Tenebrionidae, and Staphylinidae. Overall, we were able to identify 90% of the beetles to genus and 43% to species. Approximately one third of the unidentified species were rove beetles (Staphylinidae). In 2001 alone, gamma (overall) diversity was 161 species. Total alpha diversity at the plot level was 25.75 ± 9.67 ($N = 165$) species per plot (Table 1). Mean plot-level alpha diversity in 2001 alone was 20.62 ± 5.06 ($N = 60$ plots) species. Compartment-level diversity was predictably higher than plot-level diversity: 66.03 ± 19.61 for all years combined ($N = 30$) and 53.67 ± 8.87 species for 2001 alone ($N = 12$). The variability in number of species captured was high at both the plot and compartment level. In all years, the number of species captured at the plot level ranged from 2 to 56 species and from 10 to 97 at the compartment level. The pattern was similar for the 2001 data alone (8–35 species at the plot level, 36–66 at the compartment level). Beta diversity at the plot level was high for both the 2001 data (6.76) and the 3-yr data set (9.80), suggesting a great deal of heterogeneity in the beetle community between plots; heterogeneity was less when considered at the compartment scale (1.98 for 2001 and 3.21 for all years combined). The Shannon index was slightly higher for all years of data (3.73) versus the 2001 data alone (3.31). Simpson's index was also higher for the 2001

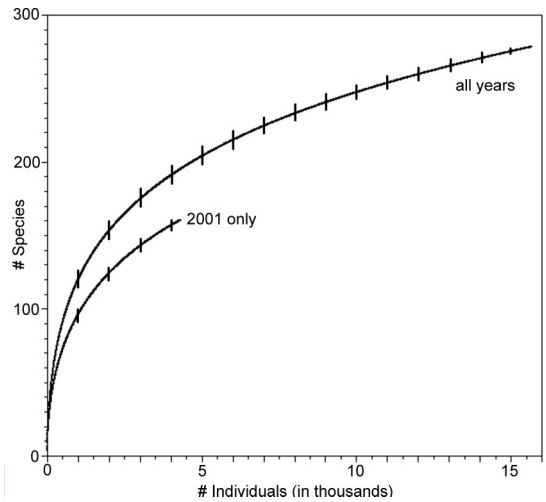


Fig. 2. Rarefaction curves of the number of species captured by plot sampled in 2001 (thin line) and all years (bold line) in mixed conifer forests at Blodgett Forest. Error bars represent SD.

data set (17.89) than for all years of data (11.64). The evenness index was similar between 2001 (0.66) and all years of data (0.65).

We calculated a rarefaction curve to determine if we had successfully sampled most of the litter 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 some continued accumulation of species even with three summers of intensive sampling. The curve for 2001 has clearly not reached an asymptote, and overall richness seems to be at least 2 SD less than the 3-yr curve, suggesting that richness was lower in 2001 relative to the other years.

Both the jackknife and bootstrap estimates of species richness estimated greater overall gamma richness than the raw species richness total (Table 2). The jackknife estimator predicted an additional 63 species in the total assemblage from the 3 yr of sampling, whereas the bootstrap estimator predicted approximately an additional 32 species. The estimator showed a similar pattern of predictions based on the 2001 data alone: 51 species were predicted by the jackknife estimate to have been missed versus 24 for the bootstrap estimate. When applied to the 2001 data, the estimators failed to predict the actual total species richness achieved in 3 yr of sampling (278); 68 (jackknife) and 94 (bootstrap) fewer species were predicted by the estimators based on 2001 data than were actually captured over 3 yr.

NMS reveals patterns of community structure based on species abundances without incorporating a second habitat matrix. The final stress for the three-dimensional NMS ordination of the 2001 data was 21.53, which is considered "poor" (Kruskal 1964) and results in an ordination diagram that is difficult to interpret (Clarke 1993); there was very little interpretable community structure based on these data. Similarly

Table 2. Richness measures of beetles in mixed conifer forests at Blodgett Forest

| | All years | | 2001 | |
|--------------------------------------|------------------|------------------|-------------------|------------------|
| Total beetles captured | 15,683 | | 4,312 | |
| Total richness (γ diversity) | 278 | | 160 | |
| Jackknife estimate | 350.97 | | 209.95 | |
| Bootstrap estimate | 310.63 | | 184.08 | |
| Shannon diversity (H) | 3.73 | | 3.31 | |
| Simpson's index (D) | 17.89 | | 11.64 | |
| Evenness (E) | 0.66 | | 0.65 | |
| | Plot level | | Compartment level | |
| | All years | 2001 | All years | 2001 |
| Mean richness (α diversity) | 25.75 \pm 9.67 | 20.62 \pm 5.06 | 66.03 \pm 19.61 | 53.67 \pm 8.87 |
| range | 2–56 | 8–35 | 10–97 | 36–66 |
| β diversity | 9.80 | 6.76 | 3.21 | 1.98 |

colored shapes on the ordination biplot indicate the four or five plots within each of the 12 compartments (Fig. 3). Notably, the plots do not cluster tightly by compartment in almost all cases, indicating that community structure is not similar over even short spatial scales. Only two habitat variables, canopy cover and fuel depth, showed even a weak correlation ($r^2 > 0.100$) with the main axes when overlaid on the NMS biplot.

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 in-

formation on the most speciose groups, specifically litter beetles and other soil arthropods, is sorely lacking. This is the first study to document leaf litter beetle biodiversity in the Sierra Nevada of California, and one of only a few studies in the western United States to report richness of beetles.

Despite the high beetle richness we found in our samples, it is clear that we have only sampled a portion of the full beetle diversity 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 rarefaction curve indicates that sampling at 60 plots for three summers (with, in fact, four collections of five traps at each of those plots) was not sufficient to result in an entirely asymptotic curve, although the curve does begin to flatten out. The question of how many leaf litter beetle species there are in this habitat is still open. The nonparametric estimators of species richness that we used to estimate total richness were not in agreement: our estimates ranged from a low of 310.63 species (the bootstrap estimate), to a high of 350.97 species (the jackknife estimator). It is quite likely that the higher jackknife estimate is positively biased as a result of the high number of rare species in our sample (Palmer 1995). The shape of the rarefaction curve also suggests that this high estimate is not conservative enough, as it does begin to flatten out at high sample sizes. 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). Overall, we believe that the jackknife and bootstrap estimates provide a reasonable upper and lower bound to the potential total species richness on our site.

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 because of lower sampling. However, both of the richness estimators underestimated the total 3-yr richness based on this 1 yr of sampling. This is an indication that there is considerable between-year variation in species presence and that multiyear sampling is necessary to approach

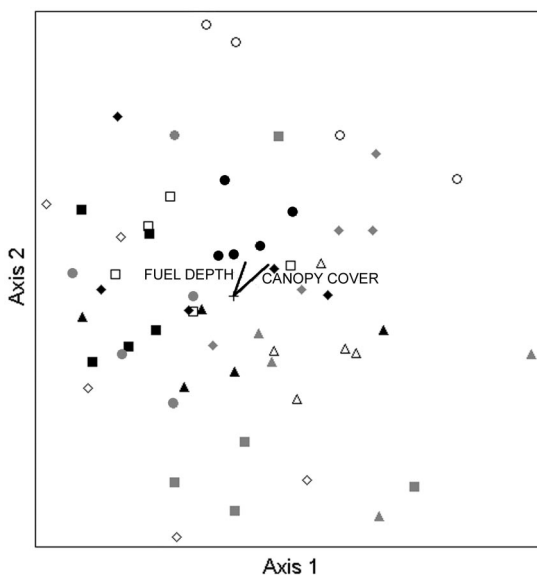


Fig. 3. Nonmetric multidimensional scaling plot of 32 beetle species and 58 plots in mixed conifer forests at Blodgett Forest. This analysis includes only the most common of the 161 total species from 2001. Habitat variables with $r^2 > 0.100$ were plotted as vectors.

a true litter beetle diversity estimate. The fact that the multiyear total was higher than the estimate based on 2001 alone is also likely to be a result of fire and harvesting treatments on the site in 2002, which may have attracted specialized species that are adapted to those disturbances. This would also explain the 2001 rarefaction curve appearing to be significantly shallower than the total curve, because more species were clearly present in the total years data set than in the 2001 alone data set, given equal sampling.

There was a high degree of variability in alpha diversity between sampling units, at both the plot and the compartment level. At the 165 plots sampled across 3 yr of sampling, we captured as few as 2 and as many as 56 species of beetle. The variability across the 30 compartment-level samples taken over the 3 yr was 10–97 species. This pattern was the same for the 2001 data alone. This indicates a great deal of heterogeneity at both very small scales (plots were frequently as few as 60 m apart) and larger scales (100s of meters at the compartment level).

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 the work of Niemela et al. (1996) on carabid beetles, who found that this family can display heterogeneity in assemblage membership over scales as small as 10–15 m. Indeed, the parts of Blodgett Forest that were sampled in 2001 were fairly homogenous at the scale of the compartments, possibly because of the long history of similar management, including logging and fire exclusion for much of the past century. This is partially an artifact of the design of this study, because compartments were randomly selected among stands with similar histories to provide similar initial conditions for testing effects of fire and logging treatments. Despite this, there is still a great deal of small-scale (plot-level) heterogeneity within the compartments, brought about by natural forest processes and small-scale management activities such as group selection harvests.

Understanding the habitat structural features that are important for insect taxa allow managers to make better predictions about the effects of treatments (Niemela et al. 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 et al. 2004), dead

trees (Kaila 1997), soil conditions (Sanderson et al. 1995), microclimate (Judas et al. 2002), and leaf litter type (Koivula et al. 1999). We found few strong correlations between the axes in our NMS ordination and the measured habitat variables, although canopy cover and fuel depth did show weak correlations with the NMS axes. Surprisingly, volume of coarse wood debris was not strongly correlated with our NMS axes. This is not consistent with many other studies that have linked CWD to high leaf litter arthropod abundance (Harmon et al. 1986, Schiegg 2000, Kehler et al. 2004). Another study examining the posttreatment responses of arthropod groups showed that the loss of conifer basal area and increased bare mineral soil after fire and harvesting treatments significantly impacted the beetle community at Blodgett forest (Apigian et al. 2006). These treatments represented significant alterations to the structural, chemical, and floristic make-up of the forest, and this multivariate analysis of the 2001 (pretreatment) data in this study would not have adequately predicted the responses of the beetle community. This result emphasizes the practical importance of large-scale, experimental studies to evaluate the potential effects of forest management, rather than relying exclusively on predictions based on pretreatment data alone.

There are likely a number of important, interacting factors that structure the beetle community at Blodgett forest. This is consistent with others who have found that abundance of groups as diverse as beetles are not well explained by only a few habitat features (Humphrey et al. 1999, Jonsson and Jonsell 1999, Rieske and Buss 2001, Jeanneret et al. 2003). Many other factors are known to be important but were simply not measured or included in our analyses, such as soil pH (Sanderson et al. 1995), moisture (Antvogel and Bonn 2001), bulk density (Rushton 1991), plant species richness (Jeanneret et al. 2003), and other factors. Future studies should focus on these and other unmeasured habitat variables, as well as the potential effects of the changes in these variables on beetle assemblages.

In conclusion, Blodgett Forest has a high diversity leaf litter beetle fauna. The community is very heterogeneous in its composition at small (plot-level) scales, but somewhat less so at larger (compartment-level) scales. It is likely that 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.

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Appendix 1. Coleoptera collected (2001–2003) in mixed conifer forests at Blodgett Forest

| Family | Species | No. individuals | |
|---|--|-----------------|--|
| Anobiidae | <i>Paralobium mundum</i> Fall 1905 | 2 | |
| | <i>Ptinus</i> sp. 1 | 114 | |
| | <i>Ptinus</i> sp. 2 | 66 | |
| | <i>Tricorynus</i> sp. | 2 | |
| | | | |
| Anthicidae | <i>Ischyropalpus nitidulus</i> LeConte 1851 | 1 | |
| Bostrichidae | <i>Scobicia declivis</i> LeConte 1857 | 6 | |
| Buprestidae | <i>Anthaxia aeneogaster</i> LaPort & Gory 1841 | 21 | |
| | <i>Anthaxia</i> sp. | 1 | |
| | <i>Chrysobothris semisculpta</i> LeConte 1859 | 1 | |
| | <i>Serropalpus substriatus</i> Haldeman 1848 | 1 | |
| Byrrhidae | <i>Amphicyrta dentipes</i> Erichson 1843 | 3 | |
| Cantharidae | <i>Malthodes</i> sp. | 36 | |
| | <i>Podabrus cavicollis</i> LeConte 1851 | 3 | |
| | <i>Podabrus</i> sp. 1 | 12 | |
| | <i>Podabrus</i> sp. 2 | 5 | |
| | <i>Podabrus</i> sp. 3 | 1 | |
| | | | |
| | | | |
| | | | |
| | | | |
| | | | |
| Carabidae | <i>Agonum</i> sp. | 1 | |
| | <i>Amara californica</i> Dejean 1828 | 3 | |
| | <i>Anisodactylus similis</i> LeConte 1851 | 1 | |
| | <i>Bembidion</i> sp. 1 | 1 | |
| | <i>Bembidion</i> sp. 2 | 14 | |
| | <i>Bembidion</i> sp. 3 | 2 | |
| | <i>Bembidion</i> sp. 4 | 1 | |
| | <i>Callisthenes discors</i> LeConte 1857 | 7 | |
| | <i>Carabus taedatus</i> F. 1787 | 7 | |
| | <i>Metrius contractus</i> Eschscholtz 1829 | 1,258 | |
| | <i>Omus californicus</i> Eschscholtz 1829 | 374 | |
| | <i>Pterostichus</i> (<i>Hypherpes</i>) sp. 1 | 215 | |
| | <i>Pterostichus</i> (<i>Hypherpes</i>) sp. 2 | 327 | |
| | <i>Pterostichus</i> (<i>Hypherpes</i>) sp. 3 | 100 | |
| | <i>Pterostichus</i> (<i>Hypherpes</i>) sp. 4 | 110 | |
| | <i>Pterostichus</i> (<i>Hypherpes</i>) sp. 5 | 56 | |
| | <i>Pterostichus</i> (<i>Leptoferomia</i>) <i>stapedius</i> Hacker 1968 | 2 | |
| <i>Pterostichus inanis</i> Horn 1891 | 20 | | |
| <i>Pterostichus lama</i> Menetries 1843 | 272 | | |

(Continued)

Appendix 1. (Continued)

| Family | Species | No. individuals |
|--------------------|--|-----------------|
| | <i>Pterostichus morionides</i> Chaudoir 1968 | 6 |
| | <i>Scaphinotus marginatus</i> Fischer 1822 | 3 |
| | <i>Sericoda bembidioides</i> Kirby 1837 | 1 |
| | <i>Tanystoma striata</i> Dejean 1828 | 8 |
| | <i>Trachypacus holmbergi</i> Mannerheim 1853 | 21 |
| | <i>Trechus</i> sp. | 1 |
| Cerambycidae | <i>Callidium antennatum</i> Casey 1912 | 1 |
| | <i>Centrodera spurca</i> LeConte 1860 | 10 |
| | <i>Clytus planifrons</i> LeConte 1874 | 27 |
| | <i>Phymatodes decussatus</i> LeConte 1857 | 2 |
| | <i>Phymatodes hirtellus</i> LeConte 1873 | 1 |
| | <i>Pidonia gnathoides</i> LeConte 1873 | 2 |
| | <i>Spondylis upiformis</i> Mannerheim 1843 | 13 |
| | <i>Strophiona laeta</i> LeConte 1857 | 14 |
| | Unknown Cerambycid sp. 1 | 2 |
| | Unknown Cerambycid sp. 2 | 1 |
| Chrysomelidae | <i>Pachybrachis</i> sp. | 1 |
| Cicindellidae | <i>Cicindela</i> sp. | 4 |
| Ciidae | <i>Sulcacis curtulus</i> Casey 1898 | 17 |
| Cleridae | <i>Cymatodera ovipennis</i> LeConte 1859 | 7 |
| | <i>Phyllobaenus scaber</i> LeConte 1852 | 2 |
| Coccinellidae | <i>Coccinella</i> sp. | 1 |
| | <i>Hippodamia convergens</i> Guerin-Meneville 1842 | 1 |
| | <i>Psyllobora vigintimaculata</i> Say 1824 | 1 |
| | Unknown Coccinellid sp. 1 | 1 |
| | Unknown Coccinellid sp. 2 | 1 |
| | Unknown Coccinellid sp. 3 | 1 |
| Colydiidae | <i>Lasconotus</i> sp. | 2 |
| Cryptophagidae | <i>Oxylaemus californicus</i> Crotch 1875 | 1 |
| | <i>Atomaria</i> sp. 1 | 181 |
| | <i>Atomaria</i> sp. 2 | 1 |
| | <i>Cryptophagus</i> sp. 1 | 2 |
| | <i>Cryptophagus</i> sp. 2 | 4 |
| | <i>Henoticus</i> sp. | 9 |
| | Unknown Cryptophagid sp. | 16 |
| Curculionidae | <i>Agronus cinerarius</i> | 23 |
| | <i>Cossonus crenatus</i> Horn 1873 | 1 |
| | <i>Dyslobus lecontei</i> Casey 1895 | 74 |
| | <i>Dyslobus</i> sp. | 100 |
| | <i>Lechirops</i> sp. | 1 |
| | <i>Nemocestes montanus</i> Van Dyke 1936 | 45 |
| | <i>Rhyncholus oregonensis</i> Horn 1873 | 39 |
| | <i>Rhyncholus</i> sp. | 1 |
| | <i>Sitonia</i> sp. | 4 |
| | <i>Thricolepis simulator</i> Horn 1876 | 91 |
| | <i>Tychius</i> sp. | 3 |
| | Unknown Curculionid sp. 1 | 5 |
| | Unknown Curculionid sp. 2 | 6 |
| | Unknown Curculionid sp. 3 | 319 |
| | Unknown Curculionid sp. 6 | 33 |
| Dermestidae | <i>Trogoderma glabrum</i> Herbst 1783 | 24 |
| Diphyllostomatidae | <i>Diphyllostoma linsleyi</i> Fall 1932 | 9 |
| Elateridae | <i>Ampedus mixtus</i> Herbst 1806 | 4 |
| | <i>Ampedus phoenicopterus</i> Germar 1843 | 1 |
| | <i>Ampedus rhodopus</i> LeConte 1857 | 3 |
| | <i>Athous imitans</i> Fall 1910 | 31 |
| | <i>Athous limbatus</i> LeConte 1861 | 1 |
| | <i>Athous opilinus</i> Candeze 1860 | 14 |
| | <i>Athous scissus</i> Candeze 1860 | 3 |
| | <i>Cardiophorus</i> sp. 1 | 35 |
| | <i>Cardiophorus</i> sp. 2 | 28 |
| | <i>Cardiophorus</i> sp. 3 | 2 |
| | <i>Ctenicera imitans</i> Brown 1935 | 36 |
| | <i>Ctenicera mendax</i> LeConte 1853 | 32 |
| | <i>Ctenicera pallidipes</i> Brown 1936 | 5 |
| | <i>Limonius humeralis</i> Candeze 1960 | 13 |
| | <i>Limonius maculicollis</i> Motschulsky 1859 | 2 |
| | <i>Megapenthes stigmatosus</i> LeConte 1853 | 1 |
| | Unknown Elaterid sp. 1 | 1 |
| | Unknown Elaterid sp. 2 | 2 |
| | Unknown Elaterid sp. 3 | 18 |
| | Unknown Elaterid sp. 4 | 3 |

(Continued)

Appendix 1. (Continued)

| Family | Species | No. individuals |
|----------------|---|-----------------|
| | Unknown Elaterid sp. 5 | 27 |
| | Unknown Elaterid sp. 6 | 1 |
| Endomychidae | <i>Mycetina horni</i> Crotch 1873 | 3 |
| | Unknown Endomychid sp. | 2 |
| Erotylidae | <i>Dacne californica</i> Horn 1870 | 834 |
| Euchnemidae | <i>Melasis rufipennis</i> Horn 1886 | 1 |
| Geotrupidae | <i>Bolboceras obesus</i> LeConte 1859 | 20 |
| Histeridae | <i>Bacanius</i> sp. | 3 |
| | <i>Psiloscelis subopacus</i> LeConte 1863 | 1 |
| | <i>Stictostix californica</i> Horn 1870 | 40 |
| Lampyridae | <i>Phausis riversi</i> LeConte 1884 | 28 |
| Latridiidae | <i>Ardius</i> sp. | 1 |
| | <i>Cartodere</i> sp. | 16 |
| | <i>Corticarina</i> sp. | 3 |
| | <i>Enicmus tenuicornis</i> LeConte 1878 | 59 |
| | <i>Latridius</i> sp. 1 | 85 |
| | <i>Latridius</i> sp. 2 | 7 |
| | <i>Latridius</i> sp. 3 | 2 |
| | <i>Metopthalmus</i> sp. | 113 |
| | <i>Microgramme</i> sp. | 1 |
| Leiodidae | <i>Agathidium</i> sp. 1 | 3 |
| | <i>Agathidium</i> sp. 2 | 1 |
| | <i>Agathidium</i> sp. 3 | 3 |
| | <i>Anisotoma nevadensis</i> Brown 1937 | 4 |
| | <i>Anisotoma</i> sp. | 3 |
| | <i>Colon</i> sp. | 21 |
| | <i>Hydnobius</i> sp. 1 | 7 |
| | <i>Hydnobius</i> sp. 2 | 33 |
| | <i>Hydnobius</i> sp. 3 | 7 |
| | <i>Ptomaphagus</i> sp. | 535 |
| | Unknown Leioidid sp. | 1 |
| Lucanidae | <i>Platyceroides latus</i> Fall 1901 | 53 |
| Lycidae | <i>Lyctus</i> sp. 1 | 1 |
| | <i>Lyctus</i> sp. 2 | 2 |
| Melandryidae | <i>Abdera bicinctus</i> Horn 1888 | 3 |
| | Unknown Melandryid sp. | 3 |
| Melyridae | <i>Dasyrhadus</i> sp. 1 | 6 |
| | <i>Dasyrhadus</i> sp. 2 | 1 |
| | <i>Dasytini</i> sp. 1 | 1 |
| | <i>Dasytini</i> sp. 2 | 40 |
| | <i>Pseudasydates inyoensis</i> Blaisdell 1938 | 1 |
| | <i>Trichochrous</i> sp. | 9 |
| Monotomidae | <i>Hesperobaenus</i> sp. | 35 |
| Mordellidae | <i>Mordella</i> sp. | 25 |
| Mycetophagidae | <i>Mycetophagus californicus</i> Horn 1878 | 91 |
| | <i>Mycetophagus</i> sp. | 8 |
| | <i>Typhaea stercorea</i> L. 1758 | 1 |
| Nemonychidae | <i>Cimberis comptus</i> LeConte 1876 | 5 |
| Nitidulidae | <i>Carpophilus</i> sp. 1 | 11 |
| | <i>Carpophilus</i> sp. 2 | 9 |
| | <i>Pityophagus rufipennis</i> Horn 1872 | 13 |
| | <i>Soronia guttulata</i> LeConte 1863 | 15 |
| | <i>Thalycra</i> sp. 1 | 37 |
| | <i>Thalycra</i> sp. 2 | 4 |
| | <i>Thalycra</i> sp. 3 | 5 |
| Ochodaeidae | <i>Pseudochodaenus estriatus</i> Carlson & Richter 1974 | 1 |
| Phalacridae | <i>Phalacrus</i> 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 | <i>Clinidium calcaratum</i> LeConte 1875 | 33 |
| Salpingidae | <i>Elacitus</i> sp. | 2 |
| Scarabaeidae | <i>Aphodius</i> sp. | 126 |
| | <i>Canthon simplex</i> LeConte 1857 | 3 |
| | <i>Cremastochelius</i> sp. | 1 |
| | <i>Dichelonyx crotchi</i> Horn 1876 | 37 |
| | <i>Dichelonyx lateralis</i> Fall 1901 | 17 |
| | <i>Serica anthracina</i> LeConte 1856 | 1 |
| | <i>Serica curvata</i> LeConte 1856 | 42 |

(Continued)

Appendix 1. (Continued)

| Family | Species | No. individuals | |
|-----------------------|---|-----------------------|----|
| Scolytidae | <i>Dendroctonus valens</i> LeConte 1860 | 1 | |
| | <i>Gnathotrichus retusus</i> LeConte 1868 | 1 | |
| | <i>Gnathotrichus sulcatus</i> LeConte 1868 | 1 | |
| | <i>Hylastes gracilis</i> LeConte 1868 | 24 | |
| | <i>Hylastes macer</i> LeConte 1868 | 78 | |
| | <i>Hylurgops pinifex</i> Fitch 1851 | 1 | |
| | <i>Hylurgops porosus</i> LeConte 1868 | 155 | |
| | <i>Hylurgops reticulatus</i> Wood 1971 | 2 | |
| | <i>Hylurgops subscostulatus</i> Mannerheim 1853 | 4 | |
| | <i>Monarthrum scutellare</i> LeConte 1860 | 1 | |
| | <i>Phloeosinus punctatus</i> LeConte 1876 | 5 | |
| | <i>Phloeosinus</i> sp. | 1 | |
| | <i>Pityophthorus</i> sp. | 1 | |
| | <i>Pseudopityophthorus pubipennis</i> LeConte 1878 | 3 | |
| | <i>Scolytus ventralis</i> LeConte 1868 | 5 | |
| | <i>Xyleborinus saxeseni</i> Ratz. 1837 | 58 | |
| | <i>Xyleborus scopulorum</i> Hopkins 1902 | 168 | |
| | Scraptiidae | <i>Anaspis</i> sp. 1 | 13 |
| | | <i>Anaspis</i> sp. 2 | 8 |
| | Scydmaenidae | <i>Lophoderus</i> sp. | 5 |
| <i>Veraphis</i> sp. 1 | | 3 | |
| Staphylinidae | <i>Veraphis</i> sp. 2 | 17 | |
| | <i>Actium</i> sp. 1 | 94 | |
| Staphylinidae | <i>Actium</i> sp. 2 | 1 | |
| | <i>Actium</i> sp. 3 | 1 | |
| | <i>Aleochara</i> sp. | 11 | |
| | <i>Aleocharinae</i> sp. 1 | 85 | |
| | <i>Aleocharinae</i> sp. 2 | 848 | |
| | <i>Aleocharinae</i> sp. 3 | 10 | |
| | <i>Aleocharinae</i> sp. 5 | 6 | |
| | <i>Aleocharinae</i> sp. 7 | 1 | |
| | <i>Aleocharinae</i> sp. 8 | 1 | |
| | <i>Aleocharinae</i> sp. 9 | 50 | |
| | <i>Aleocharinae</i> sp. 10 | 1 | |
| | <i>Aleocharinae</i> sp. 11 | 1 | |
| | <i>Aleocharinae</i> sp. 12 | 9 | |
| | <i>Aleocharinae</i> sp. 13 | 16 | |
| | <i>Aleocharinae</i> sp. 14 | 6 | |
| | <i>Aleocharinae</i> sp. 15 | 181 | |
| | <i>Aleocharinae</i> sp. 16 | 3 | |
| | <i>Aleocharinae</i> sp. 17 | 2 | |
| | <i>Aleocharinae</i> sp. 19 | 38 | |
| | <i>Aleocharinae</i> sp. 20 | 8 | |
| | <i>Aleocharinae</i> sp. 22 | 2 | |
| | <i>Aleocharinae</i> sp. 23 | 4 | |
| | <i>Aleocharinae</i> sp. 24 | 13 | |
| | <i>Aleocharinae</i> sp. 25 | 44 | |
| | <i>Aleocharinae</i> sp. 26 | 2 | |
| | <i>Amphichroum maculatum</i> Horn 1882 | 7 | |
| | <i>Astenus</i> sp. | 1 | |
| | <i>Batrisodes cicatricosis</i> Brendel 1890 | 22 | |
| | <i>Bryoporus</i> sp. | 6 | |
| | <i>Deinopteroloma pictum</i> Fauvel 1878 | 42 | |
| | <i>Eusphalerum</i> sp. 2 | 238 | |
| | <i>Gabrius</i> sp. | 4 | |
| | <i>Habrocerinae</i> sp. | 1 | |
| | <i>Habrolinus</i> sp. | 2 | |
| | <i>Hesperolinus</i> sp. | 8 | |
| | <i>Ichnosoma californicum</i> Bernhauer & Schubert 1912 | 149 | |
| | <i>Lathrobium</i> sp. 1 | 7 | |
| | <i>Lathrobium</i> sp. 2 | 1 | |
| | <i>Mipseltyrus mirus</i> Schuster 1956 | 2 | |
| | <i>Omalinae</i> sp. 1 | 1 | |
| | <i>Omalinae</i> sp. 2 | 4 | |
| | <i>Oropus</i> sp. | 1 | |
| | <i>Philonthus</i> sp. 1 | 1 | |
| | <i>Philonthus</i> sp. 2 | 13 | |
| | <i>Platydracus rutilicauda</i> Horn 1879 | 5 | |
| | <i>Quedius</i> sp. 1 | 13 | |
| <i>Quedius</i> sp. 3 | 3 | | |
| <i>Quedius</i> sp. 4 | 5 | | |
| <i>Quedius</i> sp. 5 | 1 | | |

(Continued)

Appendix 1. (Continued)

| Family | Species | No. individuals |
|---------------|--|-----------------|
| | <i>Quedius</i> sp. 6 | 1 |
| | <i>Renardia</i> sp. | 1 |
| | <i>Stenus vespertinus</i> Casey 1884 | 3 |
| | <i>Stictolinus</i> sp. | 1 |
| | <i>Tachinus semirufus</i> Horn 1877 | 387 |
| | <i>Tachyporus californicus</i> Horn 1877 | 88 |
| | <i>Tyrus corticinus</i> Casey 1897 | 1 |
| | Unknown Staphylinid sp. 1 | 2 |
| | Unknown Staphylinid sp. 2 | 1 |
| | Unknown Staphylinid sp. 3 | 4 |
| Tenebrionidae | <i>Cibdelis blaschkei</i> Mannerheim 1843 | 17 |
| | <i>Cnemeplatia sericea</i> Horn 1870 | 60 |
| | <i>Coelocnemis californica</i> Mannerheim 1843 | 187 |
| | <i>Coniontis</i> sp. | 145 |
| | <i>Eleodes cordata</i> Eschscholtz 1833 | 2,369 |
| | <i>Helops punctipennis</i> LeConte 1866 | 5 |
| | <i>Helops simulator</i> Blaisdell 1921 | 113 |
| | <i>Iphthminus serratus</i> Mannerheim 1843 | 8 |
| | <i>Megeleates sequoiarum</i> Casey 1895 | 1 |
| | <i>Mycetochara</i> sp. | 3 |
| | <i>Nyctoporis sponsa</i> Casey 1907 | 213 |
| | <i>Scotobaenus parallelus</i> LeConte 1859 | 16 |
| Tetratomidae | <i>Eustrophinus tomentosus</i> Say 1827 | 11 |
| Throscidae | <i>Pactopus horni</i> LeConte 1868 | 1,842 |
| Trogossitidae | <i>Eronyxa</i> sp. | 1 |
| Zopheridae | <i>Phellopsis porcata</i> LeConte 1853 | 5 |
| | <i>Usechimorpha montana</i> Doyen 1979 | 7 |