Response of beetles (Coleoptera) to repeated applications of prescribed fire and other fuel reduction techniques in the southern Appalachian Mountains

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ABSTRACT

Coleoptera are important components of forest ecosystems and can be affected by forest management schemes aimed at limiting fuel build-up. Our research objective was to determine if repeated applications of fuel reduction treatments resulted in changes in abundance or diversity of beetle (Coleoptera) families, genera, and species within upland mixed hardwood forests in the southern Appalachians Mountains, North Carolina, USA. We established three replicate blocks (~56 ha) and split each block into four fuel reduction treatments. Treatments included prescribed burning, mechanical felling, a combination of prescribed burning and mechanical felling, and a control (*i.e.*, no fuel reduction techniques applied). We implemented treatments multiple times (2 mechanical thinnings and 4 prescribed burns) over the course of a 15-year period. Using pitfall and colored pan traps, we captured 7037 coleopterans comprised of 62 families over a three-year period. Total coleopteran abundance and diversity were similar across all treatments; however, some beetle families, genera, and species responded to treatments. Nitidulidae were significantly more abundant within controls compared to all other treatments in 2015, whereas Mordellidae generally had higher abundances in mechanical and burns compared to mechanical in 2015 and mechanical and controls in 2016. Chrysomelidae was significantly more abundant in mechanical and burns compared to all other treatments over the entire duration of the study. However, Staphylinidae abundance was significantly lower in mechanical and burns compared to the other treatments. Numerous genera and species also showed variable treatment-level responses. Burn treatments killed some mature trees and reduced forest canopy cover, resulting in higher light availability and thereby greater herbaceous cover and diversity on the forest floor. This vegetation in the understory of burned treatment units may be partially responsible for many of the treatment-level responses of beetle taxa we documented. This study took place after several rounds of fuel reduction techniques were applied over a 15 year period. Some beetle abundance responses were immediate; whereas other groups seemed to be influenced by the application of treatments over time, highlighting the need to examine long-term responses to forest management practices.

1. Introduction

Humans have long used fire to alter forested landscapes for multiple purposes. In the southern Appalachian region of the United States, fire was frequently applied by Native Americans to facilitate travel, augment fruit and nut availability for forage, and attract game animals to young foliage or grasses resulting from fire-mediated disturbance (Greenberg and Collins, 2016). Later, European settlers used fire to provide suitable land for livestock grazing (Brose et al., 2001). Today, foresters use prescribed fire to reduce fuels and the risk of wildfire, and

to benefit vertebrate wildlife that feed on new plant growth. Prescribed burning is the most common fuel reduction method in forests, but it is used on a limited basis in the wildland-urban interface due to creation of smoke and risk of property damage. Fire-surrogates, such as mechanical thinnings and herbicide treatments, may accomplish many of the same management goals and are suitable for use near homes and other developed areas.

Prescribed fire and mechanical fuel reduction techniques can potentially affect invertebrates by altering forest habitat structure or by causing direct mortality during prescribed burns (McCullough et al.,

1998; Swengel, 2001). Forest managers have attempted to use arthropod indicator species (e.g., ants, beetles, spiders) to determine the sustainability and ecological soundness of forest management practices (Andersen et al., 2002; Schowalter et al., 2003; Vickers and Culin, 2014; Willett, 2001). Amongst coleopterans, Carabidae is the most frequently used family in environmental assessments of forest disturbances (Hodkinson and Jackson, 2005; Butterfield et al., 1995; Ulyshen et al., 2006). However, Cerambycidae (Maeto et al., 2002), Scarabaeidae (Davis et al., 2001), Staphylinidae (Bohac, 1999), and tiger beetles (Carabidae: Cicindellinae) (Rodriguez et al., 1998) are also used as ecological indicators. Additionally, researchers have looked to overall invertebrate community response as an indicator of forest health (Jansen, 1997; Greenberg et al., 2010).

Coleopterans comprise ~40% of all insects and are taxonomically and behaviorally diverse. Many beetles are sensitive to environmental changes, and beetles found in undisturbed forests, such as old growth forests, do not rapidly disperse, making them suitable candidates as indicators of forest condition (den Boer, 1990). Additionally, the taxonomy of many beetle families in temperate zones is well understood, making them ideal for environmental assessments with high taxonomic resolution (Werner and Raffa, 2000). Previous studies have also demonstrated beetles to be responsive to forest disturbances. When forests are cut or fragmented, some beetles may increase in abundance and richness (Lenski, 1982; Butterfield et al., 1995), especially species that are found in open habitats (Werner and Raffa, 2000).

In earlier studies, we examined initial effects of prescribed burning and mechanical fuel reduction on pollinators (Campbell et al., 2007) and arthropod communities (Greenberg et al., 2010). However, response of beetle communities after multiple applications of fire and fire surrogate treatments is largely unknown. We assessed how beetle abundance and diversity responded to repeated fuel-reduction treatments including: (1) low-intensity prescribed burns; (2) mechanical understory reductions; (3) a combination of mechanical understory reduction followed by a high-severity burn and subsequent lower-intensity prescribed burns; and (4) controls in the southern Appalachian Mountains, USA. The vast majority of studies that examined arthropod responses to fuel reduction practices, primarily focused on the immediate responses of various treatments. Although we did collect beetles shortly after one round of treatments, our study was primarily interested in longer-term impacts of repeated applications of fuel reduction techniques. We hypothesized that some beetles that prefer disturbed habitats would increase in abundance immediately after treatments but would decrease in abundance over time. Additionally, these beetles' abundances may remain relatively high in treatments that resulted in canopy and shrub reduction. Alternatively, other beetle groups that are fungivores or use duff material for sheleter may decrease in abundance among treatments that allowed more sunlight to penetrate the canopy. Fungal growth should decrease within the hotter/drier conditions and prescribed burns could lead to the destruction of leaf litter and other coarse woody debris.

2. Methods

2.1. Study sites and design

We conducted this study on the 5841-ha Green River Game Land (GRGL) (35° 17′0900 N, 82° 19′42″W and 35°15′42″N, 82° 17′27″W) in Polk County, North Carolina, USA. GRGL lies within the mountainous Blue Ridge Physiographic Province of western North Carolina. The region receives an average of 164 cm of precipitation annually that is distributed evenly throughout the year, and the average annual temperature is 17.6 °C. Soils in GRGL are composed primarily of the Evard series (*i.e.*, fine-loamy, oxidic, mesic, Typic Hapludults); they are very deep (> 1 m) and well-drained in mountain uplands (Keenan, 1998). Elevation ranges from approximately 366 to 793 m. Oaks (*Quercus* spp.) and hickories (*Carya* spp.) were the primary trees in the upland

hardwood forest. Shortleaf pine (*Pinus echinata* Mill.) and Virginia pine (*P. virginiana* Mill.) were dominant ridgetop species, and white pine (*P. strobus* L.) occurred in moist coves. The age of the forest within experimental units ranged from ~85–125 years old. Mountain laurel (*Kalmia latifolia* L.) was the predominant shrub along ridgetops and on upper southwest-facing slopes, and rhododendron (*Rhododendron maximum* L.) was the most common shrub in mesic habitats. Prior to the 2003 prescribed burns conducted in this study, none of the study sites had been thinned or burned for a minimum of 20 years.

We selected three replicate study areas (hereafter "blocks") within GRGL. To ensure consistency in baseline conditions among the blocks, we considered size (*i.e.*, capacity to accommodate four experimental units each), forest age, cover type, and management history. Each of the three blocks was either bordered or traversed by perennial streams.

In order to accommodate a 10-ha "core" area surrounded by 20-m wide buffers, experimental units within blocks were a minimum of 14-ha. Some experimental units were separated by dirt roads or fire lines. A number of experimental units were traversed by wooded trails, but none were crossed by roads or fire lines. Within each of the three blocks, we randomly assigned three fuel reduction treatments and an untreated control (C), resulting in a total of 12 experimental units. Treatments were: (1) repeated prescribed burns (four times, in February or March 2003, 2006, 2012, and 2015; B); (2) repeated mechanical felling of all shrubs and small trees > 1.4 m tall and < 10.2 cm in diameter at breast height (dbh) with a chainsaw (twice, winters 2001–2002 and 2011–2012; M), and; (3) initial mechanical cutting of the understory (winter 2001–2002), followed by four prescribed burns (as for B, above; MB); and (4) untreated controls. Cut trees and shrubs were left scattered onsite in MB and M.

We conducted prescribed burns (*i.e.*, B and MB) by hand-ignition using spot fire and strip-head fire techniques, as well as helicopter-assisted spot fire ignition. The initial prescribed burns in March 2003 resulted in flame lengths of 1–2 m throughout all burn units. However, topography and intersecting flame fronts contributed to localized areas of erratic fire behavior where flame lengths reached up to 5 m in height (Waldrop et al., 2010). As a result of these high intensity burns, numerous trees were killed in MB, resulting in a dramatic alteration of forest structure (e.g., canopy openings). Felling of the shrub layer on MB contributed to a load of fine woody fuels that was approximately 2-fold larger than C and B, thus contributed to the higher intensity fires. Average fire temperature at 30 cm aboveground was much hotter in MB than B (370 °C and 180 °C, respectively; Waldrop et al., 2010). Subsequent burns of the MB produced lower-intensity fires than the initial burn (Waldrop et al., 2010). The second burn (March 2006) produced flame lengths generally < 1.5 m, and the average temperature 30 cm aboveground was 155 °C in B and 222 °C in MB (Waldrop et al., 2016). The third and fourth burns were of low-intensity, producing flame lengths < 2 m, but measurements of fire temperature were not collected.

2.2. Sampling procedure

Within each treatment unit, we established two pitfall trap arrays spaced > 50 m apart. Arrays consisted of a 4 oz (118 ml) cup filled halfway with soapy water, with three 30-cm long aluminum flashing drift fences trenched into the ground that radiated from the center of the cup and were oriented at 120° to the neighboring drift fence. We also used sets of colored pan traps filled with soapy water, both in the midstory and on the ground to capture beetles unlikely to be captured in pitfall traps. For the colored pan traps, we attached blue, red, white, and yellow pans at each corner of a 66 cm square of metal remesh (Nucoar) with binder clips (Campbell et al., 2018). Colored pan traps have been successfully used to sample forest Coleoptera (Meng et al., 2013), and many beetle groups are known to be attracted to various colors (Francese et al., 2005; Campbell and Hanula 2007). At each of the two locations (> 50 m apart) within each treatment unit, we hoisted one

Table 1

Mean (± SE) relative abundance of beetle families, subfamilies, genera, species, family richness, and Shannon-Weaver indices within three fuel reduction treatments and controls, at Green River Game Land, Polk County, NC (2014–2016). † indicates treatment × year interaction. Different letters within a family, subfamily, genera, and species indicates a significant difference ($P \leq 0.05$).

Beetle taxa	Treatments			
	Control	Burn	Mechanical	Mechanical & Burn
All beetles	654.00 (61.61)	667.33 (90.14)	521.67 (46.32)	502.67 (11.67)
Richness	76.67 (5.69)	86.00 (8.39)	75.00 (5.74)	72.44 (2.61)
Shannon-Weaver	2.70 (0.10)	2.95 (0.17)	3.01 (0.07)	3.02 (0.17)
Carabidae				
Cicindela sexguttata	0.67 (0.33)	3.67 (2.03)	2.67 (1.76)	3.67 (1.86)
Pterostichus spp.	5.67 (2.03)	3.00 (1.00)	2.00 (0.58)	1.67 (1.20)
Chrysomelidae	2.33[b] (0.67)	2.00[b] (1.53)	2.33[b] (0.67)	7.00[a] (4.04)
Cleridae				
Phyllobaenus pallipennis	1.00[b] (1.00)	4.67[ab] (1.67)	5.67[a] (0.33)	5.33[a] (2.19)
Coccinellidae	2.67[ab] (0.67)	3.67[ab] (3.18)	1.33[b] (0.88)	5.33[a] (1.76)
Curculionidae[†]				
2014	1.67[b] (1.20)	3.33[ab] (1.33)	4.00[ab] (1.00)	9.00[a] (1.73)
2015	17.67[ab] (9.94)	38.33[a] (8.45)	16.00[b] (7.21)	30.00[ab] (9.45)
2016	11.00[b] (3.46)	13.33[b] (7.36)	11.00[b] (4.04)	32.33[a] (13.97)
Scolytinae	48.00[b] (2.31)	131.00[a] (40.43)	53.33[b] (10.99)	48.00[b] (13.53)
Erotylidae				
***Triplax* spp.**	1.00[b] (0.58)	7.67[a] (3.18)	3.00[ab] (1.53)	3.67[ab] (1.20)
Tritoma spp.	5.33 (2.96)	5.67 (2.60)	2.00 (1.53)	2.00 (0.58)
Eucenemidae	3.67 (1.20)	5.33 (1.45)	4.00 (1.00)	4.33 (1.33)
Histeridae	2.00[b] (1.15)	8.67[a] (3.84)	4.00[ab] (3.06)	3.00[ab] (1.00)
Hydrophilidae	17.67[a] (7.67)	4.00[bc] (1.73)	10.00[b] (4.58)	0.67[bc] (0.33)
Lycidae				
***Plateros* spp.**	2.33[ab] (0.88)	2.33[ab] (0.88)	1.67[b] (0.67)	6.00[a] (5.51)
Mordellidae[†]				
2014	15.33 (4.33)	18.67 (6.67)	12.33 (5.90)	7.33 (1.33)
2015	14.00[ab] (4.58)	31.00[a] (3.51)	12.00[b] (3.06)	28.00[a] (1.53)
2016	10.00[b] (2.08)	20.00[ab] (9.07)	11.00[b] (3.06)	32.67[a] (10.53)
Nitidulidae[†]				
2014	4.33 (2.40)	4.33 (1.86)	4.33 (2.03)	2.00 (2.00)
2015	149.67[a] (33.93)	13.67[b] (5.36)	68.33[b] (22.70)	7.33[b] (2.67)
2016	13.33 (3.38)	13.67 (5.21)	8.67 (1.45)	5.33 (1.86)
Ptinidae	10.00 (3.06)	14.33 (5.55)	9.00 (6.03)	13.33 (6.96)
Scarabaeidae				
Aphodiinae	2.67[b] (1.76)	3.00[b] (3.00)	1.00[b] (0.58)	8.67[a] (4.81)
Ateuchus histeroides	0.33[b] (0.33)	8.67[a] (4.63)	2.33[b] (2.33)	3.33[ab] (1.76)
Canthon spp.	3.67 (2.72)	4.00 (2.65)	6.00 (5.03)	1.33 (0.88)
Canthon viridis	26.00 (7.55)	40.00 (2.89)	23.67 (3.18)	34.33 (14.25)
Onthophagus spp.	21.33 (5.93)	13.33 (1.33)	9.67 (2.73)	8.33 (3.33)
Scraptiidae	1.67 (0.88)	6.00 (2.65)	1.67 (0.88)	2.33 (1.86)
Silphidae				
***Nicrophorus* spp.**	10.67[a] (3.33)	4.33[b] (2.85)	5.67[ab] (0.67)	6.33[ab] (5.33)
Staphylinidae	75.33[a] (16.76)	70.33[a] (11.79)	61.33[a] (3.84)	25.67[b] (3.93)
Tenebrionidae[†]				
2015	2.67[b] (0.88)	4.33[ab] (2.60)	2.00[b] (0.58)	8.00[a] (3.46)
2016	0.33[bc] (0.33)	7.00[ab] (3.51)	3.00[b] (1.00)	11.33[a] (6.96)
Alleculinae	3.33[ab] (1.33)	6.33[a] (4.91)	1.00[b] (0.58)	4.67[a] (1.67)
Throscidae	33.33 (16.17)	35.33 (18.48)	20.67 (6.49)	22.00 (16.80)

pan set (one square wire remesh with four pans) into the midstory (mean height 9.1 m ± 0.3 m) and placed another set on the forest floor. At a given trapping site, the pitfall trap array, midstory pan set, and forest floor pan set were spaced < 10 m (horizontal distance) apart. We sampled monthly for a 72-hour period during summer and early fall (4 months; May-August 2014, June-August and October 2015, and June-September 2016) for a total of twelve sampling periods. We chose to sample during these months because they coincide with the primary growing season in the region and because most beetles would be active during this time period. The 2014 trapping occurred prior to the 4th burn and 2nd mechanical treatment and the 2015 and 2016 insect trapping ensued after the 4th burn and 2nd mechanical treatment.

2.3. Beetle identification

We used Arnett et al. (2002) for family-level identification and determining feeding guilds of all beetles, and standard keys for genus and species level identification (Arnett and Thomas, 2000; Ciegler, 2000; Harpootlian, 2001; Arnett et al., 2002; Lingafelter, 2007). The research collection at the Florida State Collection of Arthropods (FSCA) was also utilized for specimen comparisons. Guilds were assigned based on natural history information in Arnett and Thomas (2000), Arnett et al. (2002), and Evans (2014).

2.4. Statistical analysis

We plotted relative abundances of all captured beetle taxa and

visually binned them into one of the following three abundance levels: (1) superabundant; (2) abundant; and (3) rare (Grodsky et al., 2018a). We considered taxon with <32 captures rare, taxon with ≥32 and ≤158 captures abundant, and taxon with >158 captures superabundant. We set the cutoff for inclusion of individual beetle taxa in analyses at the break between abundant and rare beetle groups, thereby excluding all rare beetles with relatively low relative abundances from analyses. For example, the cutoff between abundant and rare beetles in treatments was $n = 32$ because counts of beetle captures dropped from $n = 33$ to $n \leq 15$ at that point on the plot.

We conducted Poisson generalized linear models (GLMs) with number of captured individuals for each beetle taxon and Shannon-Weaver indices of diversity (generated from package 'Vegan in R; Oksanen et al., 2013) as dependent variables to test response of beetles and the beetle community to fuel reduction treatments (Grodsky et al., 2018b). For all models, we tested for correlation among covariates and assumed overdispersion when the residual deviance divided by the residual degrees of freedom was > 1.0. We ran quasi-Poisson GLMs when we detected overdispersion. For categorical treatment covariates in all models, we performed *post-hoc* Tukey's pair-wise comparisons of means with a Bonferroni adjustment to reduce probability of Type 1 errors using general linear hypothesis testing (glht function; single-step method; $\alpha = 0.05$) in the R package "multcomp" (Hothorn et al., 2017).

We considered a sampling station as the collection of 2 pitfall traps on the ground, 4 pan traps on the ground, and 4 pan traps in the midstory in each treatment ($n = 10$ traps/sampling station). We used treatment as the experimental unit and number of captured individuals of each beetle taxon pooled over all traps in each sampling station in each treatment plot and Shannon-Weaver indices of diversity calculated for each treatment plot as dependent variables. We first included a year × treatment interaction term, treatment, year, and block as explanatory variables in each model. If we detected a significant year × treatment interaction, we consequently developed a model for each year separately and included treatment and block as explanatory variables. Otherwise, we included treatment, year, and block as explanatory variables.

3. Results

We captured 7037 beetles from 62 families and identified at least 210 individual beetle species over the three year study (Appendix A). Curculionidae was the most commonly captured beetle family, comprising 20% of the overall captures; over half of these (11.9% of the total) were in the subfamily Scolytinae. Nitidulidae was the second most commonly captured family (12.9%), followed by Elateridae (10.7%), Scarabaeidae (10%), Staphylinidae (10%), and Mordellidae (9.1%). The most common adult feeding guild were fungivores (28.9% of all beetles captured), followed by phytophagous/fungivores (12.8%), phytophagous (11.9%), and sap/sugar feeders (11.5%).

Total coleopteran abundance, family richness, and Shannon-Weaver indices of diversity were not significantly different among the fuel reduction treatments. However, abundance of several coleopteran families, subfamilies, genera, and species differed among fuel reduction treatments (Table 1). For example, Nitidulidae were significantly more abundant within C compared to all other treatments in 2015; whereas Mordellidae generally had higher abundances in MB compared to M in 2015 and M and C in 2016 (Table 1). Chrysomelidae was significantly more abundant in MB compared to all other treatments during the duration of the study. However, Staphylinidae abundance was significantly lower in MB compared to the other treatments. Subfamily Scolytinae were much more abundant in B compared to all other treatments. Numerous genera and species also showed variable treatment-level responses (Table 1). *Phyllobaenus pallipennis* Say, a clerid species, was significantly more abundant in the B and MB compared to C treatments. *Ateuchus histeroides* Weber, a scarab, was more abundant in B compared to M and C.

4. Discussion

Given the diversity of beetles collected in this study, it is not surprising that we documented variable responses to fuel reduction treatments among beetle families, subfamilies, genera, and species. However, the total abundance of beetles, the abundance of the beetles groups tested, and the species richness did not differ among did not differ in abundance among the fuel reduction treatments. This result is of particular interest because many of these beetle taxa serve as prey for numerous wildlife species (Pechacek and Kristin, 2004; Young, 2015) and contribute to nutrient cycling in forested habitats (Grove, 2002). Therefore, despite the fact that some individual beetle groups demonstrated treatment-level responses to fuel reduction treatments, the overall beetle food base for wildlife was likely unchanged. However, some beetle groups are probably more important as a vertebrate food source compared to others and caution should be taken when examining overall beetle abundance within a forest ecosystem.

Relative abundance of many beetle families was not affected by the fuel reduction treatments. Our results are generally consistent with earlier studies on the overall arthropod community (Greenberg et al., 2010) and saproxylic beetles (Campbell et al., 2008) conducted within the same study sites after initial treatment application. However, Greenberg et al. (2010) found no treatment response by any of the 11 coleopteran families examined, including six families (Curculionidae, Elateridae, Histeridae, Nitidulidae, Staphylinidae, and Tenebrionidae) that did exhibit a treatment response in our study. The abundance trends we found with these six families could have been due to the multiple rounds of treatments that were applied over the 15-year period. Indeed, other groups of arthropods require multiple rounds of forest disturbance or management treatments before effects on abundance or richness are detected (Campbell et al., 2018). Apigian et al. (2006) also examined beetle assemblages within forest stands that were thinned, burned, or had combinations of thinning and burning in a mixed conifer forest in the Sierra Nevada mountains of California, USA. Similar to our findings, they reported that some groups of coleopterans differed in abundance among forest management treatments. However, these treatment responses did not show any general pattern, and most statistically significant changes were taxon-specific (Apigian et al., 2006). Additionally, like Greenberg et al. (2010), we found no significant differences for Scarabaeidae. However, we did find differences for a scarab subfamily (Aphodiinae) and species (*Ateuchus histeroides*), highlighting the benefit of greater taxonomic resolution for detecting treatment-level responses. Although we examined some beetles at a species or genus level, we performed most analyses on beetle families, potentially masking treatment effects on some genera or species within families.

Reduced canopy cover caused by initial high-severity fires in MB and by delayed overstory mortality in B allowed more sunlight to reach the forest floor relative to other treatments (Waldrop et al., 2016). Within the MB and B, canopy openness ranged from 25.5 to 34.4% and 8.2–9.0%, respectively, compared to 2.3–6.2% for C and M during the duration of this study (Greenberg et al., 2018). Reduced canopy cover could have resulted in less fungal growth and thereby fewer fungivorous beetles (e.g., many Staphylinidae species) within MB due to drier conditions from increased sunlight. Alternatively, many phytophagous beetles (e.g., Chrysomelidae) were more abundant in MB compared to the other treatments, most likely due to the increased herbaceous growth resulting from prescribed burning and higher light levels in the treatment (Waldrop et al., 2016).

Mordellidae, which feed on nectar and pollen as adults, generally were more abundant in MB and B than in M or C (2015 and 2016). This response was likely due to increases in diversity and abundance of flowering forbs and shrubs after repeated burning and reductions in canopy cover. In 2014, the previous prescribed burn was applied two years before, and the lack of response in 2014 by Mordellidae could be related to a decrease in forbs, as woody plants would have reestablished

themselves within the burn treatments. Shrub density was shown to decrease in the MB and B by 40.5% and 44.6%, respectively, between 2014 and 2015 (Greenberg et al., 2018). In contrast, Nitidulidae, which includes many fungivores, were more abundant in C than in B or MB in 2015, potentially due to the cooler, shadier, and moister conditions at the forest floor in C that promoted fungal growth relative to the open, drier conditions in burned sites. This trend was only observed in 2015, when the prescribed burns had recently been used, suggesting that some of the changes in coleopteran abundances may be temporary and short-lived.

Although our trapping methods captured numerous beetles (7000 +), our methods could have disproportionately captured certain beetle taxa. For example, pitfall traps have been shown to be more likely to capture beetles that are more mobile (Morrill et al., 1990). Additionally, some beetle taxa could be completely missed due to our sampling scheme and schedule. However, we used multiple trap types (pitfalls and pan traps placed at different elevations) to limit any potential biases and to sample the entire beetle community that might respond to treatments. Additionally, we collected only one or two individuals of several genera or species within some families and, therefore, we could not statistically analyze these groups due to low sample size.

Whereas the abundances of some beetle groups decreased in response to fuel reduction treatments, we documented positive treatment-level responses for other beetles. We suggest that reduced canopy cover, higher light levels, and increased herbaceous plant cover in B and MB increased (or decreased) the suitability of those sites for some taxa. Several studies indicate that many arthropod species tend to be more abundant in disturbed habitats (Niemelä et al., 1993). In fact, some beetle species have only been collected from disturbed habitats (Ulyshen et al., 2006). While we detected abundance effects of the fuel reduction practices on many beetle groups, as a whole, coleopteran communities remained abundant and diverse after 15 years of repeated thinning and prescribed fire. Our study highlights the importance of examining long-term impacts of fuel reduction techniques over time. Many invertebrate responses to fuel reduction techniques are immediate but some species may have delayed responses or repeated applications may change forest structure over time resulting in invertebrate community or abundance changes.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.07.022.

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