

The recovery of ant communities in regenerating temperate conifer forests

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Abstract

Although ants perform many critical functions in forested ecosystems, little is known about how they respond to timber harvesting, especially in temperate systems. We examined ground-foraging ant communities and 11 forest characteristics in temperate conifer forests of southwestern Oregon, USA that ranged in age from 5 to 427 years. Seven forest characteristics were related to stand age and were summarized using principal components analysis (PCA). In this case study, species richness was nearly three times higher in young clearcuts compared to closed-canopy and old stands, and worker number was highest in young stands, lowest in closed-canopy stands, and intermediate in old stands. Using stepwise multiple regression, we found that both species richness and worker number were significantly related to PCA axis 1, which represented the environmental changes that accompany stand development, and canopy variability. Though species richness was high in recently logged stands, our study suggests that, in this system, the ant community does not resemble those found in mature forests until over 100 years following disturbance. Because ants modify their environment and perform ecosystem functions like seed dispersal, the alteration of ant communities may cascade through other parts of ecosystems.

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1. Introduction

Widespread timber harvest in many parts of the world has resulted in a marked conversion of older, unmanaged forests to a mosaic of remnant forest fragments surrounded by regenerating stands of varying ages (U.N.E.P., 2006). Regenerating forest continues to comprise larger proportions of many landscapes, and as such has been increasingly recognized for its potential role in maintaining biological diversity across large areas (Gustafson and Gardner, 1996; Fahrig, 2001; Dunn, 2004). Given the historical focus by ecologists on intact, older forests, we know relatively little about the recovery of many taxa after disturbances such as timber harvest (Jules and Shahani, 2003). The goal of this study was to assess the response of ant communities to harvesting of conifer forests of the Pacific Northwest, USA.

Ants, in addition to performing a variety of critical ecosystem functions (Folgarait, 1998), have been used as indicators of biodiversity around the world (Alonso and Agosti, 2000). Similarly, ants have been used in several regions of the world to assess the response of biota to forest disturbances. In tropical forests, logging generally results in a decrease in ant species richness, and the recovery of species richness to mature-forest levels may occur in approximately 40 years. Species composition, however, appears to recover more slowly (Dunn, 2004). In contrast to tropical ant communities, ant species richness in the taiga of southern Finland generally increases following clearcut logging (Punntila et al., 1991). In North America, research examining the effects of logging on ant communities has been limited to broad-leaved forests of the southeastern United States. In these areas, clearcut logging reduced native ant abundance, but did not alter species richness (Zettler et al., 2004). To date, no studies have investigated the response of ant communities to logging in temperate conifer forests of the Pacific Northwest.

While the immediate response of ants to logging has been studied in several forest types, no study has yet examined community recovery over several decades or more. For

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instance, previous studies have compared ant communities in older, unlogged forests to communities in forests cleared <20 years prior to the time of study (Punttila et al., 1991, 1994; Vasconcelos, 1999; Zettler et al., 2004), and the oldest secondary forests examined were cleared less than 50 years prior (Belshaw and Bolton, 1993; Lawton et al., 1998). These studies, while useful in considering the immediate impacts of logging on ant communities, do not allow for predicting the long-term responses of communities through all stages of forest development. Temperate coniferous forest development includes three general stages: (1) young, recently initiated stands with open canopies, (2) closed-canopy stands, and (3) older, structurally diverse stands with some openings in the canopy (Franklin et al., 2002). Assessing the impacts of logging on native fauna across these stages of forest development is especially important in regions like the Pacific Northwest, where the landscape is increasingly dominated by forests entering canopy closure. This stage is characterized by low plant species richness (Halpern and Spies, 1995; Jones et al., submitted for publication) and hence, low resource abundance for many consumers. Thus, we sought to evaluate changes in ant community composition through multiple stages of forest development by using a spatial chronosequence of 11 forest stands, ranging in age from 5 to 427 years.

2. Study area

Our study was conducted in the Sucker Creek watershed, which encompasses 250 km² of the Siskiyou Mountains of southwestern Oregon (42°07'N, 123°22'W). The area has a complex fire regime; the estimated natural fire rotation is site specific and, prior to fire suppression in the mid-1900s, was characterized by frequent low- to moderate-intensity fires (Agee, 1991; Taylor and Skinner, 1998). Logging, which began in the area in the 1960s, combined with natural fires, has produced a mosaic of forest stands of varying ages (U.S.D.A., 1995). Within this mosaic, we selected eleven 50 m × 50 m plots. Each plot was located within a discrete forest stand, and stands ranged in age from 5 to 427 years (see Table 1). Plots were originally established by Kahmen and Jules (2005), who determined stand age by using increment cores sampled from the oldest cohort of trees in a site. To eliminate edge effects, all plots were at least 60 m from the nearest forest edge. To reduce

the effects of environmental factors other than stand age, all sites were located on west to northwest facing slopes at elevations between 1295 and 1495 m, where Douglas-fir (*Pseudotsuga menziesii*) and white fir (*Abies concolor*) are the dominant tree species. Within each plot, we established a grid of twenty evenly spaced circular subplots. Each subplot had a 2-m radius. In each subplot, we sampled the ant community and assessed stand characteristics.

The use of a chronosequence can be valuable in predicting the recovery of an area following a disturbance, though it relies heavily on the assumption that each site was similar prior to disturbance and that the disturbances invoked similar changes (Foster and Tilman, 2000). The four youngest stands (5, 14, 21, and 43 years old) all originated from a clearcut timber harvest. After harvesting, these sites were broadcast burned, then replanted with Douglas-fir seedlings (U.S.D.A., 1995) with the exception of the youngest site, which was not broadcast burned. Stumps present in the managed stands suggest that these sites contained mature to old-growth forest prior to timber harvesting (Kahmen and Jules, 2005). The seven older stands (98–427 years old) originated from stand replacing fires. Like clearcut logging followed by burning and replanting, natural stand replacing fires in the Siskiyou Mountains can produce an even-age cohort of Douglas-fir (Agee, 1991). Thus, although not identical, stand-replacing fires and clearcuts likely represent comparable disturbance types, except that standing dead trees are present at lower densities following logging (unpublished data). Older clearcut sites (i.e. >40 years) do not exist in the Sucker Creek watershed, as logging did not begin until the 1960s, and young unmanaged sites are not known to exist in the study area, in part due to fire suppression efforts.

3. Methods

At each of the plots, we measured elevation, slope, aspect, soil moisture, % open canopy, coarse woody debris, gravel, bare ground, litter depth, duff depth, and total number of snags. Elevation, slope, aspect and soil moisture for all 11 sites were determined by Kahmen and Jules (2005). Tree canopy cover was estimated at each of 20 subplots using a spherical densiometer. Readings were used to estimate mean canopy openness and variation in canopy openness (standard deviation) for each site. Percent cover of woody debris, exposed bare

Table 1
Worker number for all ant species sampled in each site in June and August, 2003

Species	Stand age										
	5	14	21	43	98	119	128	179	252	273	427
<i>Camponotus laevigatus</i>	43 (13)	23 (10)	10	0	0	0	0	0	0	0	0
<i>Camponotus vicinus</i>	0	3 (3)	2 (2)	0	0	0	0	0	0	0	0
<i>Camponotus modoc</i>	72 (15)	8 (3)	0	1 (1)	0	2 (2)	33 (8)	18 (8)	70 (14)	1 (1)	21 (1)
<i>Lasius pallitarsis</i>	0	10 (8)	1 (1)	1 (1)	1 (1)	5 (2)	16 (2)	1 (1)	3 (3)	1 (1)	4 (1)
<i>Tapinoma sessile</i>	22 (6)	119 (15)	44 (13)	1	0	0	0	0	0	10 (2)	0
<i>F. moki</i>	0	28 (2)	482 (8)	0	0	0	0	0	0	0	0
<i>Formica lasiodes</i>	4 (1)	17 (9)	10 (2)	0	0	0	0	0	0	4 (1)	0
<i>Myrmica discontinua</i>	6 (4)	33 (9)	4 (3)	0	1 (1)	0	0	0	0	0	0

Frequency of occurrence in 20 traps given in parentheses.

mineral soil (bare ground) and gravel were visually estimated and litter and duff depth were measured at each subplot. Finally, at each 50 m × 50 m plot, the total number of snags with >7.6 cm diameter at breast height (DBH) was counted.

We estimated ant species richness and worker number in each plot in June and August, 2003. At each site, one pitfall trap was placed in the center of each of the 20 subplots. The traps consisted of a 50-mL plastic tube partially filled with 15 mL of propylene glycol (Sierra[®] antifreeze) and one drop of detergent. All traps remained open for 72 h during dry weather. In addition to pitfall traps, 16 bait stations with tuna in oil and shortbread cookies were used at each site in May, 2003. However, no additional species were detected at the bait stations, thus, only the pitfall trap samples will be discussed here. All ants collected were identified to species level. The measured richness is strictly speaking a measure of species density, because it is a measure of the species captured in a unit area, not the number of species that would be captured were sampling to go to exhaustion (Gotelli and Colwell, 2001).

4. Data analysis

Prior to regression analysis, we constructed a correlation matrix to examine possible relationships among forest characteristics. Of eleven site characteristics surveyed, seven (soil moisture, % open canopy, total snags, gravel, litter depth, duff depth, and bare ground) showed significant correlations ($r > 0.602$, $P < 0.05$) either directly with stand age or with other age-associated variables. Thus, we summarized these seven variables, hereafter referred to as age-associated forest characteristics, using principal components analysis. The resulting principal components represent the environmental changes that accompany stand development. We assessed the influence of the principal components and the five environmental variables not summarized using PCA on total ant species richness and worker number using forward stepwise multiple regression (P -to-enter = 0.10). Canopy variability was normalized using a log-transformation prior to analysis. The regression analysis for worker number was performed twice, once with all workers and again with two samples that appeared to be outliers removed.

Because species density increases with the number of individuals sampled, we used EstimateS (Colwell, 2005) to construct sample-based rarefaction curves. Rarefaction corrects for variation in the number of individuals or samples among assemblages. Due to the low number of individuals represented in some stands, we combined the three young sites (forest age <43 years), the closed-canopy sites (forest age = 43–119 years), and old sites (forest age >119 years) in a class-based analysis. In each of the plots, pitfall traps were samples.

5. Results

Eight species were detected from a total of 1105 individual worker ants captured (Table 1). The genus *Camponotus* accounted for three of the eight species observed and 26.9% of all individuals collected. *Formica moki* was present at only

two sites, but worker number was high ($n = 482$) in the 21-year-old stand. Specifically, two traps in this stand accounted for 63% of the *F. moki* workers at this site. This was likely due to the placement of these traps near a nest location or foraging trail, thus analyses for worker number were performed both with and without these traps for comparison. *Lasius pallitarsis* was present at 10 of 11 sites, but worker number was relatively low, accounting for only 3.7% of all ants collected. Changes in species richness and worker number across the 11 stands corresponded to the three stages of stand development, although we could not statistically assess change in worker number due to limited replication. Species richness and worker number were high in young sites and low in closed-canopy sites. In older stands, species richness remained low while worker number increased from that observed in close-canopy stands although it remained lower than in young sites. Few studies have examined ant communities in the Siskiyou Mountains, therefore it is difficult to assess what proportion of the larger regional species pool the species found here represent. Ratchford et al. (2005) sampled ants at much lower elevations (375–800 m) and in different habitats (fens, adjacent uplands), and collected 33 species, six of which were found in this study. Five of the six were restricted to young stands (<43 years old).

Sample-based rarefaction, which corrected for variation in sampling, indicated that species richness was significantly higher in the youngest stands than in the closed-canopy or old stands (Fig. 1). The overlapping 95% confidence intervals for closed-canopy and old stands indicate that species richness in those plots did not differ significantly from one another.

Principal components analysis using seven forest characteristics produced two axes that together explained 82% of the total variance. The first axis accounted for 67% of the variance and was strongly correlated with all seven forest characteristics (Fig. 2). The corresponding correlation coefficients were: soil moisture, 0.842; open canopy, -0.886; total snags, 0.723; gravel, -0.810; litter depth, 0.935; duff depth, 0.621; bare

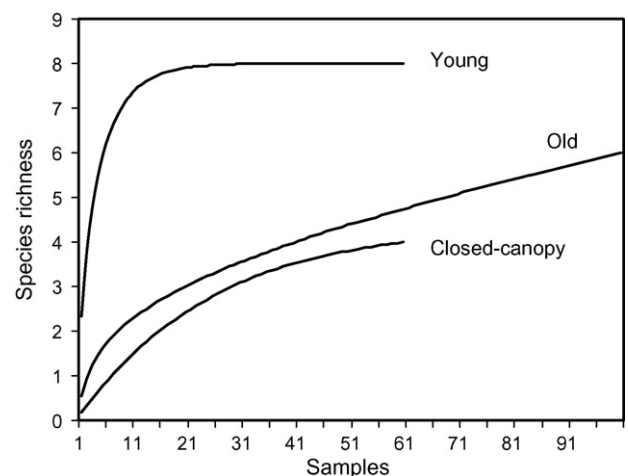


Fig. 1. Results of sample-based rarefaction for young, closed-canopy and old sites. For clarity, we omitted the 95% confidence intervals, though confidence intervals overlap between closed-canopy and old sites.

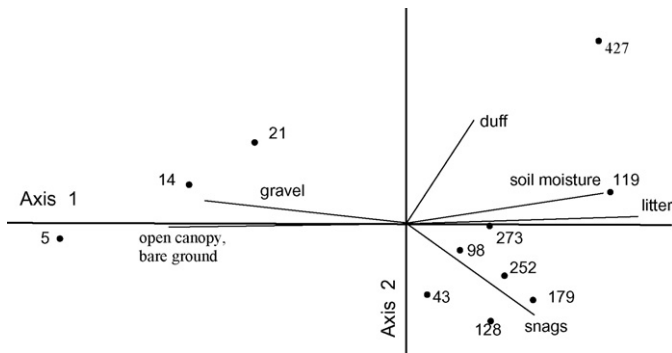


Fig. 2. Principal components for age-associated variables across a 427-year chronosequence. Filled circles and numbers represent the sites and their ages. The lengths of the lines represent the strength of the correlation between each variable and the PCA axes. Because correlations for open canopy and bare ground were nearly identical, one line represents both. The first axis explained 67% of the variation and the second axis explained an additional 15%.

ground, -0.883 . The second axis explained an additional 15% and showed a significant relationship only with duff depth ($R = 0.678$) and total snags ($R = -0.622$; Fig. 2). Only Axis 1 was correlated with stand age ($R = 0.708$). The ordination illustrates that the three youngest sites (5, 14, 21 years) form a loose group (i.e. were similar in forest characteristics). Intermediate and older sites appear dissimilar from young sites and similar to each other, although the oldest site (427 years) was distinct.

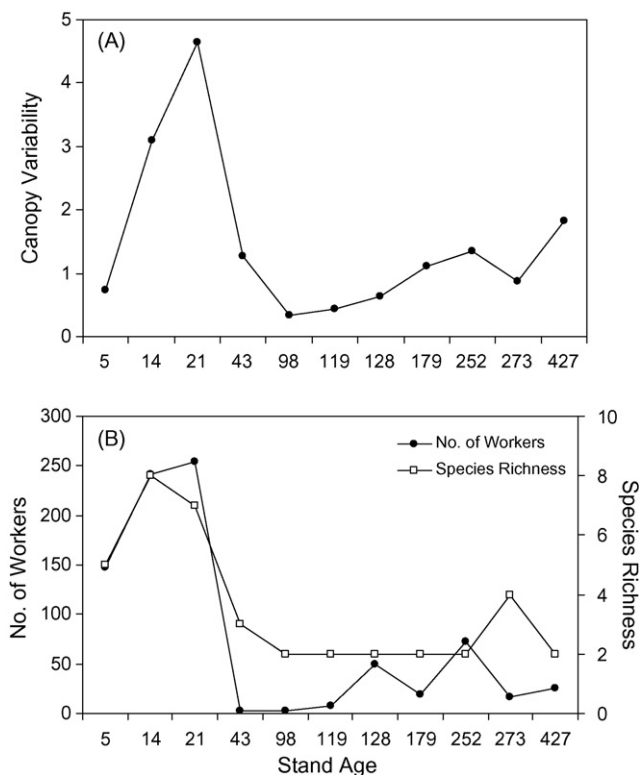


Fig. 3. Canopy variability (A), worker number and species richness (B) across stand ages. Canopy variability and principal components axis 1, which represented a suite of forest characteristics associated with stand age, were significant predictors of ant species richness and worker number. Two traps containing 306 *Formica moki* workers in the 21-year-old site are not included here.

The final regression model explained 82.4% of the variance in ant species richness ($F_{2,8} = 18.76$, $P = 0.001$) and included PCA axis 1 ($\beta = -0.649$, $t_8 = 4.09$, $P = 0.003$) and canopy variability ($\beta = 0.442$, $t_8 = 2.78$, $P = 0.024$; Fig. 3). Both regression models for worker number (all workers included and without two samples from the 21-year-old stand) also included PCA axis 1 and canopy variability. The regression model for all workers explained 68% of the variance (PCA 1: $\beta = -0.405$, $t_8 = 1.90$, $P = 0.094$; canopy variability: $\beta = 0.590$, $t_8 = 2.771$, $P = 0.024$; $F_{2,8} = 8.66$, $P = 0.01$). The regression model with outliers removed explained 84% of the variance (PCA 1: $\beta = -0.617$, $t_8 = 4.14$, $P = 0.003$; canopy variability: $\beta = 0.0495$, $t_8 = 3.32$, $P = 0.01$; $F_{2,8} = 21.8$, $P = 0.001$).

6. Discussion

Our results show that clearcut logging significantly alters the structure of ground-foraging ant communities in temperate conifer forests of the Pacific Northwest. Two species occurred independently of stand age, while the rest were confined to young stands, though two of these seemed able to inhabit older stands as well. Such a pattern resembles that found in North European boreal forests with the exception that there, territorial wood ant species dominate the old growth stages (Punntila, 1996). Ant species richness was higher in young sites than in closed-canopy or old sites, and though we could not statistically assess this due to low replication, worker number appeared highest in young sites, low in closed-canopy sites, and intermediate in old sites. Community composition did not appear similar to those communities found in older forests for over 100 years. These results contrast findings in tropical forests, where ant species richness is low following logging, and temperate broad-leaved forests where ant abundance is low following clearcut logging, while mirroring results found in boreal forests of southern Finland where ant species richness increased following clearcut logging (Punntila et al., 1991, 1994).

The contrasting response of ants in different forest types may reflect differences in disturbance dynamics of the forest types and/or land-management practices following forest clearing. Boreal and temperate conifer forests have similar disturbance dynamics compared to more stable tropical forests. Some ant species in boreal and temperate conifer forests are likely adapted to recurrent disturbances like fire, and thus are able to quickly colonize early successional stands. Boreal and temperate conifer forests are also comparable in regards to land-management practices following logging. Studies of tropical ant communities have focused primarily on logged sites that, prior to secondary forest formation, were converted to pasture or agricultural land where native plant species richness is reduced (Guariguata and Ostertag, 2001). Likewise, native plant species richness can be reduced when temperate broad-leaved forests are cleared and replanted with pines (Zettler et al., 2004). Conversely, in both boreal and temperate conifer forests, where stands are often replanted or naturally revegetated, native plant species richness may be higher in young clearcuts than in mature forest (Halpern and Spies, 1995; Reich et al., 2001; Jones et al., submitted for publication). Plant

species richness has been positively linked to faunal richness for a number of taxa, including insects (Gaston, 1992; Wright and Samways, 1996; Panzer and Schwartz, 1998) and mammals (Andrews and O'Brien, 2000; Boone and Krohn, 2000), however, this association may not be causal as plant and animal species richness gradients are usually correlated with environmental factors like temperature and moisture (Hawkins et al., 2003; Hawkins and Pausas, 2004).

We found that ant species richness was significantly related to canopy variability and a suite of age-associated forest characteristics. Of the seven characteristics examined, light availability is likely of particular importance. Punttila et al. (1991) suggest that the increase in ant species richness that follows logging is the result of decreasing canopy cover. In our study, species richness was highest in young, open stands and lowest in closed-canopy stands, where light availability is low. Diminished species richness or diversity in closed-canopy forest has been shown to occur for multiple taxa, including ants, spiders, carabid beetles, and birds (Koivula et al., 2002; Keller et al., 2003; Oxbrough et al., 2005; Lassau and Hochuli, 2004). This may be of concern, as landscapes in the Pacific Northwest are increasingly dominated by closed-canopy forests.

For ants, the influence of canopy cover may be through its effect on temperature. Some ant species may be restricted to open sites due to warmer temperature requirements for brood rearing (Hölldobler and Wilson, 1990), and increased shade and soil moisture in older stands has been associated with harmful fungal infections at nest sites (Clark and Prusso, 1986; Chen et al., 2002). Differing temperature preferences of dominant ant species may also play a role (Cerdá et al., 1998). Daily variation in temperature is greater in open sites, allowing dominant ant species with a lower thermal tolerance to forage during the cooler periods between dusk and dawn, while permitting subordinate ant species to forage during the day (Retana and Cerda, 2000). While foraging data were not available for all species encountered in our sites, the two species that were prevalent in older stands, *Camponotus modoc* and *L. pallitarsis*, are known to forage primarily in cooler temperatures. These two species co-occurred in younger stands with other species, including *Camponotus laevigatus* which is known to be a diurnal forager (Chen et al., 2002). The importance of temperature variation for maintaining ant species richness may also explain the significant role of canopy variability. While temporal segregation is important in the coexistence of dominant and subordinate species in sites with low canopy variability (Albrecht and Gotelli, 2001; Dunn et al., in press), these species may be able to segregate foraging efforts spatially in sites with high canopy variability.

Because ants modify their physical and chemical environment and perform critical ecosystem functions like seed dispersal, the alteration of ant communities following clearcut logging likely has consequences for other species. For example, members of the genus *Camponotus* removed high numbers of *Trillium ovatum* seeds in young stands (Millard, 2002). These seeds are likely not dispersed to safe sites for germination, but instead transported to nests in stumps or logs where germination is unlikely. Recruitment of *T. ovatum* in young

stands is reduced (Jules, 1998) and may be limited, in part, by diminished seed dispersal.

This study adds to the growing body of work aimed at assessing the effects of timber harvest on ants. Though our study is limited to only 11 stands within a single watershed, the results are striking and highlight the need for future studies in other temperate conifer regions. We showed that logging results in a marked spike in ant species richness and worker number that is then followed by a suppression of species richness and worker number in closed-canopy forests. This later stage is likely to last until forest development produces older forest characteristics, including greater variation in light levels, a process which takes over a century in our sites. Because ants play key roles in ecosystems there are likely to be interactions among ant communities, timber harvesting, and forest development. These interactions are largely unknown and provide an interesting avenue for future study.

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