

Forest canopy gaps as structural surrogates for the measure of forest floor arthropod pattern: discussion and caveat

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Abstract

'Gap dynamics' in old-growth forests is frequently cited as a mechanism by which heterogeneity is maintained in unmanaged systems, but evidence for effects on forest insect species is scarce. Here I present a discussion based on evidence from old-growth ponderosa pine forests in California, documenting that structural attributes created during natural tree death (tree corpses, canopy gaps and recovering forest) are indeed responsible for the maintenance of distinct arthropod assemblages. I also discuss evidence that through time the decay of dead trees and corresponding recovery of young forest stands provide additional attributes to promote heterogeneity. Pitfall traps were used to survey the forest floor beetle community, which consisted of 235 species from 37 families. Species-area analysis showed that the total number of species for the area might be as high as 350. Species richness was highest in gaps>tree surfaces>forest>tree interiors. Most species were caught in low numbers (<10 individuals), and all habitat types shared a portion of species with other habitat types. Indicator species analysis showed that few species were good indicators of any one environment by themselves, suggesting a high degree of mobility between habitat types. A 2-axis ordination using NMS showed that the strongest gradient in the data was between within-tree samples and all others, but also that the state of tree decay was an important factor discriminating among sites, within the same habitat type. Decay and habitat type were not completely independent of one another, and the ordination pattern suggests that with increasing decay and canopy closure, communities from the four habitats become more similar. It appears also that with canopy closure and increased log decay, the forest floor community shifts toward predator-detritivore dominance at the expense of herbivorous species. I discuss the ramifications of these results to the potential use of forest structural measures as a surrogate for the more expensive measure of forest arthropod assemblages themselves.

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Introduction

Forest canopies shape forest environments by regulating moisture (Gray et al. 2002), light (Frazer et al. 2000), temperature (Clinton 2003) and nutrient availability (Prescott 2002) at the forest floor. Alterations to canopy structure should therefore have corresponding effects on a wide array of forest biota, with forest communities strongly linked to the mosaic of exposed and shaded pattern that exists as a result of tree recruitment and mortality. The spatial and temporal scales at which gaps in the forest canopy occur in the absence of anthropogenic influence varies widely between forest types (Bartemucci et al. 2002; Connell et al. 1997). Forests that experience infrequent stand-initiating events like fire, windstorms or insect outbreaks are often characterized by individual tree deaths, creating small but distinct gaps in the forest canopy (Kneeshaw and Bergeron 1998; Lertzman et al. 1996; Spies et al. 1990; Whitmore 1978, 1989). Depending on the size of a tree at the time of death, its effect on surrounding trees and on the forest floor can be dramatic (Salvador-Van Eysenrode et al. 1999; Clinton and Boring 1993). The persistence of a tree corpse in a prostrate position, for example, provides resources for decay organisms, and influences resource regimes at the forest floor (Harmon et al. 1986). The overall importance of tree mortality in forested ecosystems is perceived with such importance that it has led some researchers to describe this phenomenon as the 'death cycle' (Franklin et al. 1987).

Forests with large, old trees occur in many biomes, including those of the Pacific Coast of North America. East of the Cascade and Sierra Nevada Mountain ranges in the United States, ponderosa pine is a dominant canopy species (Oliver and Ryker 1990) and, in the absence of catastrophic fires and industrial harvesting, grows to enormous sizes (Fig. 1). Alternatively, when these kinds of forests are heavily utilized for fibre production, their structure is dramatically altered (Fig. 1).



Figure 1. Large and old ponderosa pine trees near Hat Creek, California (left), and feller-buncher harvesting in 'eastside pine' forests (right).

Lemieux and Lindgren (2004) showed that in silviculture systems containing artificially created forest patches, forest floor arthropod assemblages can exhibit pattern shift over very small distances. It follows then that structural features in forests can potentially be surrogated as measures of pattern for this group. My work in ponderosa pine forests (Lemieux 2003) led to the observation that canopy gap formation by tree death, and recovery by tree recruitment might represent a 'natural' mechanism by which heterogeneity in the distribution of forest floor arthropods is regulated. Both the interiors (Grove 2003) and surfaces (Buddle 2001) of downed trees are known to be important features for some forest arthropods. In some areas of the world, the disappearance of woody debris in forests is associated with the extirpation of saproxylic arthropod species (Siitonen and Martikainen 1994). I predicted also that the exposed forest floor would experience shifts in community structure as is commonly observed in studies of insect communities after industrial forest harvesting. Further, I predicted that with age the decay of the tree bole and recovery of the forest canopy would be accompanied by predictable changes in community structure (Fig. 2).

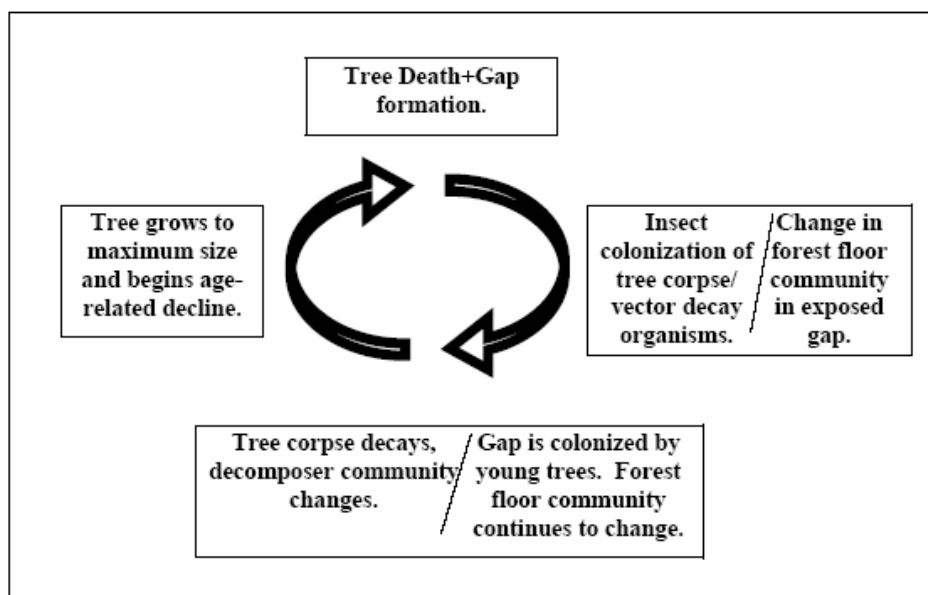


Figure 2. Hypothesized progression of community change during gap formation and recovery.

Methods

I used pitfall traps to measure arthropod communities on the forest floor of a late-seral forest at Black's Mountain Research Forest, in northern California, about 50 ha in size. I sampled four habitats characteristic of gaps: (1) beneath the bark (subcortical), and (2) on the surface of fallen trees (cortical), (3) in the gap itself 1 m distant from tree boles, and (4) at a 10 m distance at right angles from the tree bole in regenerating forest. Five trees were sampled in total, across a broad spectrum of decay stages, representing a range of time since death/gap formation. I ranked each tree on a scale from 1-5 to represent its relative state of decay according to Parks (1997). Collections were made through the summers of 1999 and 2000. All beetles were identified using morphospecies techniques that included genitalia dissection where necessary. See Lemieux (2003b) for further detail.

Results and Discussion

I caught 235 morphospecies from 37 different families of beetles, and a species-area analysis showed that the actual total could be as high as 350 beetle species. Most morphospecies were caught in very low numbers (<10). An indicator species analysis showed that morphospecies were generally not strongly associated with any particular habitat, suggesting mobility between habitat types. However, NMS ordination did indicate the following:

1. Distinct community structure among habitats, based primarily on shifts in morphospecies' relative abundance. Habitat accounted for the first ordination axis.
2. Catches from the subcortical habitat were the most distinct, while cortical and forest floor catches were more similar to one another.
3. Decay class of tree corpses at each site was an important explanatory agent for a second axis in the ordination.
4. Subcortical catches tended to be dominated by predatory morphospecies, whereas cortical catches were more strongly herbivorous, and forest floor species were dominated by detritivores.
5. Catches from inside and outside of trees (subcortical versus all other treatments) tended to be more similar to one another, dominated by decomposers, when tree corpses were in a more advanced state of decay and areas around tree corpses were shaded by a forest canopy.

Canopy cover was strongly and positively related to decay class of tree corpses, presumably reflecting recruitment of young trees inside of canopy gaps, concurrent with the development of decomposition in tree corpses.

The emergent patterns from these data suggest that my hypotheses were correct: that each of the habitat types created during gap formation helps to create heterogeneity in catches of forestdwelling arthropods when observed using pitfall traps. Secondly, I verified the importance of decay stage in tree boles, and gap recovery as mechanisms that are associated with heterogeneity in arthropod catches: both spatial and temporal elements are important.

The conversion of old-growth forests to even-aged management, even with the retention of forest patches, can be expected to change the prevalence of gap-oriented community shifts in forest floor arthropods. Although the prudent management approach would be to create large reserves in which gap dynamics are allowed to persist as a forest disturbance regime, further study of the kind presented here should eventually be made against anthropogenic disturbance regimes. Because it is plausible that both individual species and the overall community patterns in gap creation/recovery might be maintained under even-aged management, specific tests should be carried out to compare arthropod patterns under natural and even-aged disturbance types.

Some important research issues in this regard are:

1. Can these spatial and temporal patterns be maintained in forests that are managed with early-mid versus late-seral rotation ages?

The primary factors that regulate the variation in community pattern in this study were the presence of dead woody substrate, and changes to light and moisture regimes by canopy alteration. All of these same factors are induced by even-aged management, though the spatial and temporal variation of them is quite different. Study should focus on whether smaller trees and larger gaps are sufficient habitat features for forest floor arthropods.

Assessment of tree interiors (subcortical dwelling species) is difficult to gauge, however, and on smaller trees pitfall traps might prove impractical, necessitating the development of alternative sampling mechanisms. Ideally any method that is used to measure within trees should be also applicable to the forest floor to maintain a standard sampling effort among all treatments.

2. Are there particular gap-dependent species that are at risk from the conversion of late-seral forests to managed stands?

It is possible that gaps organize a common suite of species in a particular fashion, and that alternative harvesting regimes would conserve the fauna but allow it to assemble in different taxonomic, spatial and temporal patterns. Study in this regard should focus on classical entomology, with concerted effort made to determine species using more extensive methods than morphospecies approaches. Understanding life history, spatial distribution and habitat requirements of individual species is not furthered when morphospecies methods are used to generate data sets, though in many cases this is the only practical approach when dealing with the inherent taxon richness of this group.

3. Does the retention of old forest patches within young-mid seral stands assist in conserving gap-related patterns?

A slightly different hypothesis is that gap-related species thrive under gap dynamic disturbance regimes, and persist to a lesser extent in traditional, even-aged management. If this is true then retention patches with large, old trees might serve to populate developing forest as it matures outside of patches. This is important because current practices invoking variable retention stipulate that patches themselves are ephemeral, subject to natural disturbance, and eventually scheduled harvesting.

4. Are the patterns observed in ponderosa pine forests attributable to other forest types typified by gap dynamics?

Both the presence of dead wood, and strong environmental gradients through gaps to intact forest are presumably responsible for the strong variation of pattern in insect communities observed in this study. All of these elements are likely to be observed in all forest types, though the direction and strength of environmental gradients, and the persistence of woody substrates may vary dramatically. For example, forests typified by ponderosa pine are very dry, in marked contrast to the wetter conditions of many tropical and temperate rainforests where gap dynamics have been reported as important disturbance patterns. Soil moisture regimes in ponderosa pine forests following logging (canopy depletion) are variable (Keppeler et al. 1994), but can include both wetting and drying depending on slope and time of year. Alternatively, gaps from coastal Douglas-fir forests are known to possess increased soil moisture levels, light, and temperature levels; the former presumably from decreased evapotranspiration (Gray et al. 2004). All evidence suggests that gaps created by large, old trees should generate sufficient heterogeneity in forest floor conditions to create similar patterns to those observed in this study.

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