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Original article

Local and landscape drivers of ant and carabid beetle communities during spruce forest succession

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ABSTRACT

Community composition can be determined by various factors at both local and landscape scales. We explored the question of whether ant and carabid community composition in a spruce forest is determined largely by local site conditions or by landscape factors.

Both taxonomic groups were sampled in spruce forest clear-cuts using pitfall traps in five chronosequences scattered in one large forest complex. Each chronosequence contained five neighboring patches, with each plot representing one age (ranging from recent clear-cuts with no trees or young trees to old clear-cuts with mature trees).

In total, 13 species of ants and 64 species of carabids were found. Shading was the principal factor that affected ant and carabid communities along the successional gradient. For both insect groups, however, the difference between chronosequences with different positions in the landscape was more important than differences between successional stages, i.e., landscape drivers appear to be more important that local ones. Species composition was more affected by the proportion of individual successional stages within 300 m around individual pitfall traps than successional stage in the immediate vicinity of the individual trap.

This study indicated that in addition to local conditions near the pitfall traps, species composition was strongly affected by the availability of optimal habitat in the surrounding landscape; a greater quantity of suitable habitat in the surrounding landscape increases the probability of greater abundance and diversity of ants and carabids in both optimal and suboptimal patches.

1. Introduction

Determining the mechanisms that drive community succession remains an important and interesting challenge in ecology [63]. Landscape determines the presence of potential colonizers (species pool), their population dynamics, and their ability to reach particular patches in the landscape. Local conditions determine the suitability of the habitat or patch in question [5,12,59]. Even though many studies describe succession, those quantifying the importance of both local and landscape conditions on succession in a given patch are rare. In this study, we quantified the contribution of local conditions and the surrounding landscape configuration on the development of ant and carabid beetle communities in clear-cut areas of a spruce forest.

Both ants and carabid beetles are important bioindicators of ecosystem functions, contributing significantly to the biodiversity of temperate forests [15,40,54]. Moreover, ants play a crucial role in many ecological functions of the forest [7,64], and carabids, as predators, seed predators and prey, are important components of the forest food web [6].

European temperate forests are largely represented by artificial spruce forests. In the Czech Republic, Norway spruce (*Picea abies* L.) accounts for 54% of the forested area [1] and is very often planted as a secondary forest in monocultures under clear-cut management. Environmental conditions in clear-cuts differ substantially from those in mature forests and change with patch age [43,52,53]. Clear-cutting changes many biotic and abiotic components of the environment. It induces increasing of solar radiation and soil temperature on clear-cuts [46,48]. Also plant species diversity and plant biomass are higher in the younger forest stands [49,69]. Even though individual invertebrate species may vary in response [2,23], overall invertebrate biomass often increases with forest age, which results in better food supply [32,53].

The history of forest clear-cutting also creates a mosaic of different even-aged forest patches [33,69], a mosaic that may

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influence colonization of patches during succession. Landscape composition influences colonization in two ways: (i) it determines an available species pool, and (ii) it determines landscape connectivity and thereby influences the movement of organisms between patches [5,12,59].

Although the effects of clear-cutting and different forest stands on insect communities have been extensively studied [44,45,51–53], the effects of changes in landscape structure on the occurrence and abundance of organisms (and especially of carabids) is inadequately understood [44]. Some authors have suggested that the location and the size of the remaining forests affect biodiversity, species composition, and abundances of particular species [11,36,51] but the influence of the surrounding landscape has not been studied.

The major goal of this study was to compare the effects of succession after clear-cutting on ants and carabid beetles at two spatial scales: (i) the habitat, patch, or local scale, and (ii) the landscape scale. We tested the hypotheses that: (i) at the local scale, the composition of ant and carabid beetle communities of a patch is determined by age (e.g. time since succession) and major environmental factors; and (ii) at the landscape scale, invertebrate community composition of a patch is affected by the composition of these communities in the surrounding landscape.

2. Material and methods

2.1. Study sites

The study was performed in fragmented Norway spruce (*P. abies* (L.) Karts.) forest with a whole area of several hundred ha located on the Cerna Studnice Hill (869 m asl, 50°42′29.57″N; 15°12′31.72″E). Cerna Studnice is mountain ridge with forest (10 × 3 km), somewhere the forest is fragmented by small tracks and grasslands. The forest is close to Jablonec nad Nisou (Czech Republic), at 620–760 m altitude, and has a mean annual temperature of 7 °C and a mean annual precipitation of 1000 mm. Podsols are the dominant soil types in this rugged upland, and the original beech woods have been replaced by spruce monocultures so that spruce is now the dominant species [8]. Because of previous cutting and re-planting, the large forest consisted of a mosaic of forest patches of various ages, with nearly all trees in a given patch of the same age. Typical patch size ranged from 0.5 to several ha.

2.2. Sampling

During 2005 and 2006, ants and carabid beetles were sampled in five areas, each area containing five study plots located in forest patches representing five age classes of spruce forest (0–2, 3–5, 8–12, 26–41, and 85–105 years old). Each age class is different in high and thickness rise in trunk and crown parties. It causes light and moisture differences of forest [31]. Thus, the five forest patches in each area formed a chronosequence. The five areas were separated by at least 800 m but typically by several km. The study plots within an area were <100 m apart. Younger forest patches (up to 40 year-old) occupied about 0.5 ha while mature forest patches occupied 1–2 ha. Study plots were located at least 5 m from edge of the patch. In each study plot (20 × 20 m), ants and carabid beetles were sampled with pitfall traps, which is suitable method [65]. Six traps were placed equidistantly along the margin of the plot. Plastic pitfall traps (10 cm high × 7 cm diameter) were filled with 3% formaldehyde. Pitfall traps were deployed at each area for 2 weeks in June, July, and August in both years. After each 2-week period, pitfall traps were removed from the field, and ants and other invertebrates were stored in 80% ethanol. All ants collected were identified using the taxonomic key of Czechowski et al. [10], and all Carabidae collected were identified using Hurka [24].

Table 1
Average proportion of age classes of spruce forest area in the surroundings of study plots (in %).

Surrounding zone	Forest age (years)					Non-forest
	0–2	3–5	8–12	26–41	85–105	
50 m	3.4	20.1	16.3	6.1	43.1	11.1
300 m	3.0	10.6	6.7	14.3	51	14.4

On days when traps were deployed, invertebrates in the nearby vegetation were collected by sweeping (50 sweeps per area going diagonally across the study plot). The number of invertebrates was assumed to be an indicator of the potential food for ants and Carabidae, and was designated as “sweeping food”. Invertebrates other than ants and Carabidae were also recorded in the pitfall traps; the number of these other invertebrates was also assumed to be an indicator of the potential food for ants and carabids, and was designated as “pitfall food”. The sum of sweeping food and pitfall food is referred to as “total food”.

Relative light penetration was measured in each plot as the ratio of light penetrating through the canopy in comparison with light penetrating in the absence of a canopy in a nearby non-forested area. Light was measured when pitfalls were deployed and removed with a light meter (Voltcraft LX 1108, Conrad Electronic SE, Wernberg-Köblitz).

Temperature at the soil surface was measured using data loggers (Comet R0122, Comet System s.r.o., Roznov pod Radhostem). The extent of ground vegetation cover was rated as 0–20, 21–40, 41–60, 61–80, or 81–100%. Landscape features were evaluated by the proportion of patches belonging to the individual age classes (see above) within the radius 50, or 300 m which were compared to local features represented by age class on each plot.

These distances could reflect differences in the dispersal abilities of species and mosaic of different age forest. For example 1 m radius is close to the average foraging distance of *Myrmica* spp (*Myrmica* workers forage up to 2 m from the nest, [13]) and 50 m is common territory of wood ants. Similarly dependences are valid for carabids [38,62]. The age classes within a radius of 50 and 300 m, which were recorded as proportions because the age class often changed with location in the circular areas defined by these radii. Average proportion of areas of age classes in the surroundings of study plots are shown in Table 1.

In other words, the circular areas often included patches of different ages. The proportion of non-forested area within the area defined by each radius was also recorded. The software Geomedia Professional 6.0 from database of Forest Management Institute Brandys nad Labem was used for landscape evaluation.

2.3. Statistical analysis

Only abundant species were analyzed. Two-way ANOVA was used to evaluate the contribution of area of sampling (there were five large areas; see Sampling subsection) and age of forest patch to the variation in total numbers of all carabids and ants, as well as numbers of abundant species, captured in the pitfall traps. Proportion of variability explained by individual factors or combination of factors was calculated as the proportion of sum of squares accounted for by that factor (or its interaction) relative to the total sum of squares [56]. SPSS 10.0 was used for ANOVA calculations.

CCA (canonical correspondence analysis) and variation partitioning were used to evaluate the proportion of variability in data