

Some regularities in invertebrate succession in different microhabitats on pine stumps

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Abstract. Sixty eight pine stumps felled on known dates from one to sixteen years before the moment of sampling have been studied in the San Juan de la Peña woodland (province of Huesca). Four microhabitats were distinguished: bark, subcortical space, sapwood and heartwood. The object of the study is to compare the invertebrate macrofauna succession of the different microhabitats in order to find regularities among them. The biocenosis has not been completely studied: ipidae, diptera and annelidae are the main groups not studied. The comparison has been made in terms of changes over time in the i) number of species and individuals, ii) diversity, iii) trophic structure, and iv) faunistic occupation in terms of both number of specimens and species in the different microhabitats considered. Four similar stages may be distinguished in different microhabitat. These stages occur at different paces in different microhabitats. The initial situation is characterized by few species which are very abundant, big differences in the colonization intensity, but similar specific composition of the communities. In the intermediate situation there are more species present, but they are less abundant on average; the specific composition of the communities is less similar among stumps, but the colonization intensity more uniform. At the end, the number of species and specimens decreases, and there are bigger differences in the specific composition of communities.

Resumen. *Algunas regularidades en la sucesión de invertebrados en distintos microhábitats de tocones de pino.* Se han estudiado 66 tocones procedentes de árboles cortados a lo largo de los 16 años anteriores al período de muestreo. Dicho muestreo se realizó en el bosque de San Juan de la Peña (Provincia de Huesca), durante los años 1976-77. El método de muestreo permite distinguir 4 microhábitats distintos: corteza, espacio subcortical, albura y duramen. El objetivo del estudio es comparar la sucesión de los invertebrados (únicamente macrofauna) en los distintos microhábitats a fin de encontrar regularidades en la marcha de aquella. Los coleópteros ipidos, los dípteros y los anélidos no se han estudiado. La comparación hace referencia a la evolución a lo largo del tiempo de i) número de especies y abundancia de las mismas. ii) diversidad específica, iii) estructura trófica, y iv) intensidad de la ocupación faunística en términos de número de especies y de individuos. Dicha comparación permite distinguir 4 estadios similares en los distintos microhábitats. Estos estadios no ocurren simultáneamente en todos ellos. La situación inicial se caracteriza por la presencia de pocas especies muy abundantes, grandes diferencias en la intensidad de colonización, pero una composición específica similar de las comunidades de los distintos tocones. En el estadio intermedio hay un mayor número de especies presentes si bien son menos abundantes, la composición específica de las comunidades es menos similar entre tocones, pero la

intensidad de colonización más uniforme. En el estadio final, el número de especies y su abundancia decrece, y aparecen diferencias mayores en la composición específica de las comunidades de distintos tocones.

Introduction

Dead wood is a very abundant material in many forest ecosystems, where it is present in a wide variety of sizes and situations. It has low nutrient concentration and decomposes slowly, but represents a large quantity of organic matter. For many organisms, the nutrients and energy stored in it are an important resource when decomposition releases them (Harmon et al. 1976). Although poor in nitrogen, fixation of this element in dead wood is an important nitrogen source in forest ecosystems (Cornaby & Waide 1973, Sharp & Milbank 1973, quoted by Harmon et al. 1976).

Besides its importance in nutrient-cycling, dead wood is an habitat for many invertebrates: in the ecological survey carried out by Elton (1966) at Wytham Woods, 456 species of animals were found to live on decayed wood or under bark; Fager (1968) found 182 species on fifty-one samples of oak wood and synthetic logs.

From a theoretical point of view, dead wood, cow dung, carrion, etc. are subsystems within the main system undergoing relatively quick microsuccessions inside the principal succession. «These microsuccessions permit the recognition of the same mechanisms operating in the principal succession, and may be considered as secondary successions that reconstruct, as if in a regenerating process, parts of the system. They appear continuously as less mature patches inside a more uniform ecosystem.» (Margalef 1974).

The study of insect succession on dead wood has attracted the attention of many workers (Carle 1971, Dajoz 1966, Elton 1966, Fager 1968, Franch 1985, Graham 1925, Saveli 1939, Tragardh 1930, Wallance 1953). Harmon et al. (1986) have extensively reviewed the ecology of coarse woody debris.

In commercially exploited woodlands, the amount and size distribution of dead wood is quite different from that in undisturbed ones. In the former, stumps are an important fraction of the total woody remains. Moreover, it is easy to get a series of them felled on successive and known dates and in a relatively uniform environment. Therefore the study of stump succession combine practical and theoretical interest in an experimental situation not far from natural conditions.

This paper is an analysis of the invertebrate succession on pine stumps during the 16 years after the felling of the trees. The aim of this analysis is to compare the succession in the different microhabitats of the stump in order to find regularities among them. In the microhabitats considered we study the changes over time in (i) number of species and their abundances, (ii) diversity, (iii) trophic structure, and (iv) faunistic occupation in terms of both number of specimens and species.

Description of the study area

The San Juan de la Peña massif is situated in the province of Huesca in the north of Spain. It is the remains of a massive conglomerate synclinals constituting an inverted relief. Steep cliffs border the synclinals, but its interior relief is relatively smooth with an altitudinal difference of nearly 400 m between the highest and lowest points. The highest peak reaches an altitude of 1556 m above sea level. Coniferous forests occupy the upper part of the conglomerate shield, with *Abies alba* and beech trees in the depressions and drainage channels and *Pinus sylvestris* in the ridges. A forest of *Pinus sylvestris* with beech trees in the depressions and an undergrowth of holly trees occupies the lowest part. *Pinus nigra* trees appear on the steeper slopes.

Groves of evergreen oaks are found at the foot of the south facing cliffs, colonizing the colluvium and the sunny slopes. Mixed forests, with a rich variety of tree species such as beech, lime, ash, maple, and hazel appear at the foot of the north facing steep rocks. Mossy pine groves, of *Pinus sylvestris* with *Buxus sempervirens* in the undergrowth. Are found at lower altitude always on the shady side. Prickly pads of *Echinopartium horridum* occupy the crests which border the synclinals. For a more detailed description of the massif see Puigdefàbregas (1973).

Most of our research was carried out in an area occupied by a *Pinus sylvestris* forest with an undergrowth of *Ilex aquilifolium*, but in order to include pine stumps of ten years of age we also took some samples in a *Pinus sylvestris* forest with an undergrowth of *Buxus sempervirens* as well as in a mixed forest of *Pinus sylvestris* and *Fagus sylvaticus*.

Material and methods

Pine stumps were taken from fellings done periodically by ICONA (Instituto para la Conservación de la Naturaleza), thus their exact age (i.e. number of years since they had been cut off) was known. On average, pine stumps were of some 30 cm in height and 45 cm in diameter. Field work was done throughout the period 1976-1977. The sample size is summarized in Table 1. All fellings were sampled during both years (1976-77), but, with the exception of the 1975 felling, stumps from the same felling were all considered of the same age class even if sampled in different years. Monthly distribution of sampling is summarized in Franch (1985). Differences in sample sizes between different ages are a consequence of the unavailability of stumps.

The method of sampling consisted of a thorough search of the above-ground part of the stumps in an attempt to collect any invertebrate present. Sampling started with rapid removal of pieces of bark which were placed on a white cloth where all specimens were collected by one person using standard procedures (i.e. aspirator, paintbrush, forceps); meanwhile another collector was doing the same on the lateral surface of the stump just exposed. The speci-

Table 1. General characteristics of the samples. Masses expressed in kg, and area in m².

Year of felling	Stump age (years)	Number of stumps	Mass of			Area of subcortical space
			heartwood	sapwood	bark	
1975	1	3	21	42	4.4	1
1975	2	6	42	83	8.6	1.9
1972	4-5	10	66	114	14	3
1969	7-8	11	47	65	10	2.2
1966	10-11	17	98	138	22	4.7
1963	13-14	13	52	51	13	2.7
1960	16-17	8	44	42	9.8	2.1

mens collected in this way were considered to be subcortical space inhabitants. The next step was to break down the bark on the white cloth and collect all the bark-inhabiting individuals. The stump without bark was then sawn off as near to the ground as possible, cut into pieces and each piece cut by axe into 1 cm slices in order to extract the inhabitants of the sapwood and heartwood. Therefore, four different microhabitats have been considered: bark, subcortical space, sapwood and heartwood.

Results

The study of the invertebrates collected permitted to sort out 4 different stages on three of the four microhabitats considered: bark, subcortical space and sapwood (Franch 1985).

Stage 1, intensive consumption of the substrate by boring xilophagous larvae of a few species of families cerambycidae, curculionidae and ipidae.

Stage 2, predominance of the sproxilophagous larvae of the elaterid *Melanotus rufipes* (Hbst.)

Stage 3, occupation of the microhabitat by a very diverse and rich edaphic fauna which uses it as a place to feed, nest, grow and shelter.

Stage 4, progressive abandon of the microhabitat due to loss of food and shelter capacity, the latter due to the destruction of woody tissues and the appearance of big holes made by fungi and borrows.

Since heartwood decomposes more slowly, only the first two stages have been observed in the sampled stumps for this microhabitat, and therefore a much longer time span would be required for heartwood.

Although the different microhabitats undergo similar stages, they occur in more rapid succession in bark and subcortical space than in sapwood and heartwood. Stage 1 takes place during the first two years in bark and subcorti-

cal space and two years later in sapwood and heartwood. Stages 2 and 3 take place about six years earlier in bark and subcortical space than in sapwood. While a longer sampling period would be necessary, it seems reasonable to assume a similar six years delay for stage 4 in these three microhabitats.

Number of species and their abundances

Figure 1 represents the logarithm of the abundance of species in the different microhabitats; feeding habits are shown by the variously shaded columns.

From these figures it can be seen that all microhabitats follow a similar pattern.

Stage 1): initially there are, a few very abundant xilophagous species.

Stages 2, 3): later on, excluding heartwood, there is an increase in the number of species represented by a low number of individuals (some of them are only present) and a reduction in the densities of the xilophagous species.

Stage 4): at the end there is a general reduction on the number of species and their abundances.

These numerical changes go together with changes in the trophic structure of the community, which will be considered later.

The initial situation, in which a few species are very abundant, correspond to environments which are distant from general conditions or are fluctuant and, therefore, challenging (Margalef, 1974). In this sense we observe a gradient in microhabitats from less to more challenging: subcortical space, bark, sapwood and heartwood.

Bark and heartwood have chemical protection against their potential consumers and consequently they appear as a more hostile substrata than subcortical space and sapwood respectively. On the other hand, sapwood and heartwood, due to their mechanical resistance, are more challenging substrata than bark and subcortical space.

The abundance distributions that are observed later on, after the initial colonization, characterized by a great number of poorly represented species may be interpreted as a result of the presence of individuals of species that reach greater development in some other neighbouring system (Margalef, 1974). In our case edaphic species.

Diversity changes

The diversities of the different microhabitats have been calculated using Shannon-Weaver index and are represented in Figure 2.

Some regularities may be seen:

Stage 1): Low diversity coinciding with the initial strong invasion by a few xilophagous species.

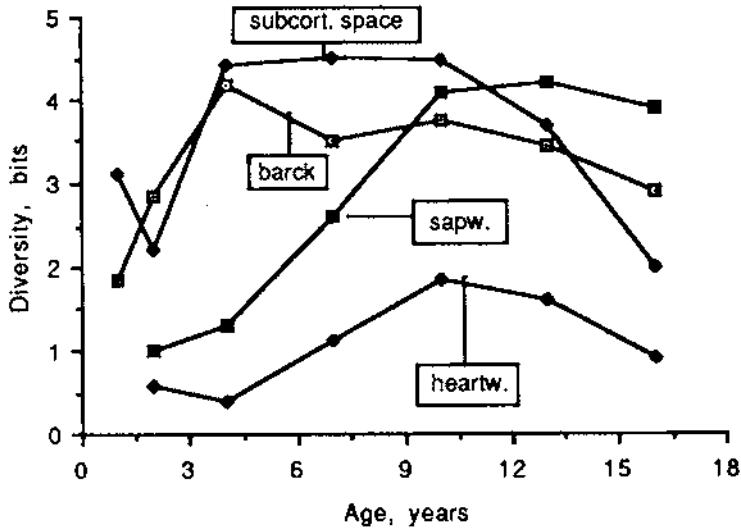


Figure 2. Changes over time in the diversity of microhabitats (Shannon-Weaver index).

Stages 2, 3): Increase in diversity until a maximum is reached when the microhabitats are used basically for shelter by an edaphic fauna.

Stage 4): Diversity decrease observed when the microhabitats are abandoned due to the loss of their shelter capacity and food reserves.

Changes in trophic structure

Microhabitats also show a similar sequence of changes in their trophic structure (See Fig. 1).

Stage 1): At the beginning of the process xilophagous species reach maximum abundance.

Stages 2, 3): Later on, there is a peak of sapiroxilophagous species, and at the end, predators and species with other feeding habits reach a peak.

Stage 4): The general decrease in abundance is not followed by changes in the trophic structure.

The different microhabitats, excluding heartwood, also show similarities in the number of species with similar feeding habits:

- Two or three abundant xilophagous species and two or three not abundant ones.
- One or two abundant sapiroxilophagous species and three or four not abundant ones
- A lot of predator species: few of them very abundant, some of them less abundant and most of them very scarce or only present.

Variability on the faunal occupation of the stumps

Figures 3 and 4 show some regularities:

Stage 1): The mean number of individuals per stump, its standard deviation and the amplitude of the oscillation of the number of individuals present is maximum. The ratio between the mean number of species per stump, and the total number of species found on stumps of the corresponding age class reaches a peak

Stages 2, 3): Mean number of species per stump and the total number of species collected on stumps of the same age class show a peak and their ratio tends to decrease. Mean number of individuals per stump and the oscillation of the number of individuals per stump also diminish.

Stage 4): There is a general decrease in mean numbers of individuals and species per stump and total number of species on stumps of the same age class.

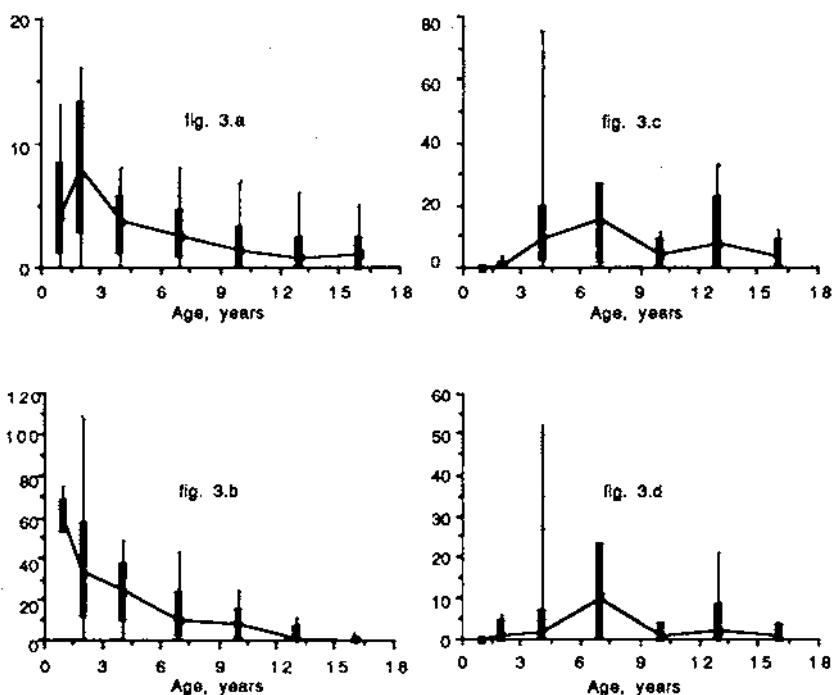


Figure 3. Changes over time in the mean number of individuals per stump present in different microhabitats. Thick vertical lines represent the standard deviation for this mean. Thin vertical lines represent the total range in the numbers of individuals present on stumps. Fig. 3.a: bark, fig. 3.b: subcortical space, fig. 3.c: sapwood, fig. 3.d: heartwood.

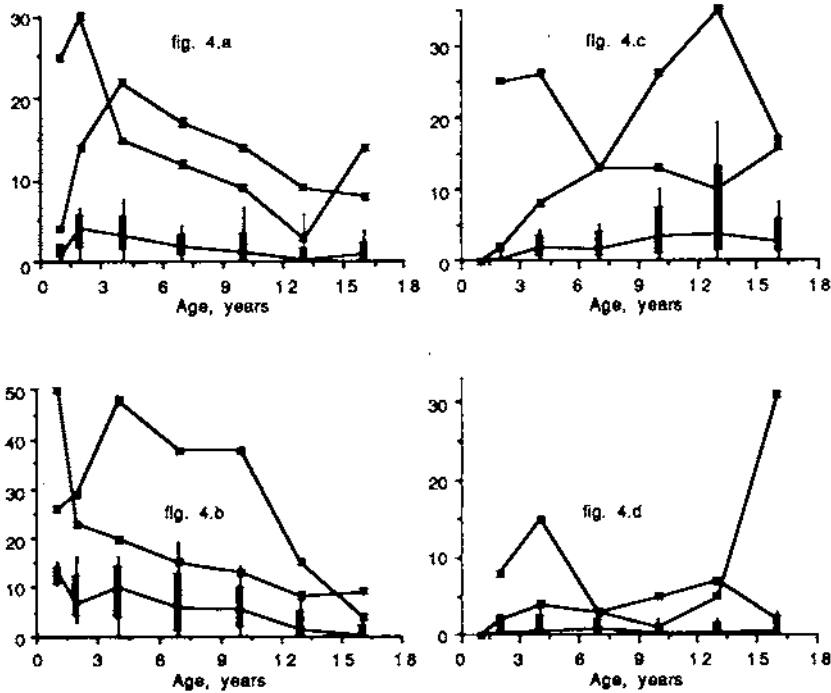


Figure 4. Changes over time in: (□) total number of species present; (—) mean number of species per stump (the standard deviation for this mean is represented by thick vertical lines) and the range of the total number of species present on stumps by thin vertical lines); (■) ratio between the mean number of species per stump \times 100, and the total number of species found on the stumps of the corresponding age class. Fig. 4.a: bark, fig. 4.b: subcortical space, fig. 4.c: sapwood, fig. 4.d: heartwood.

The considered ratios may be used as an index to measure the variability of the specific composition of the stumps' fauna over time. At the beginning of the decomposition process (stage 1) stumps have more similar fauna than later (stage 2, 3) when they are being colonized by edaphic fauna.

Discussion

Odum (1969) distinguished autotrophic and heterotrophic successions by means of the initial value of the ratio P/R (where P = primary production and R = respiration). In the former $P/R > 1$ while in the latter $P/R < 1$, but theoretically in final stages of both cases the ratio tends to equal 1. The problem with dead wood—as well as in other heterotrophic subsystems like carrion, dung etc.—is that they will not even approach that value as long as they subsist as identifiable entities. Heterotrophic successions are «downhill» successions

with a decreasing energy gradient without any possibility of reaching a stable situation (Odum 1969) and obviously, in these cases we can not talk about climax, because the final stage is the disappearance of the subsystem and its integration into the succession of the main system in which they are placed (Margalef 1974). This is an important difference with autotrophic successions and also a big limitation when trying to illustrate, through the study of heterotrophic microsuccessions, the general mechanisms operating in successions.

However, the regularities observed comparing the succession in the different microhabitats of the stump, are of interest. From this comparison it can be observed that:

- a) The invertebrate succession in the different microhabitats of the stump follow similar steps; although differences in food availability, chemical protection and mechanical resistance lead to different succession velocity.
- b) At the beginning there are few species in each microhabitat, and they are very specialized and abundant. The specific composition of the community is very similar in the same microhabitats of different stumps, but there are big differences in the colonization intensity. These differences may be the result of unequal physiological state of trees when felling was done, together with a narrow adaptation capacity of potential colonizers. Part of the energy initially stored in the stump is used by the first invaders in the construction of a system of holes and galleries, with consequent diversification of the microenvironments offered to potential colonizers and visitors. This structuration of the substrata amplifies its niche offerings and allows a bigger diversity.
- c) After the initial invasion, the number of species present increases but they are less abundant and, in general, less microhabitat specialists. Visitors become more important and food webs more complex. At this stage the specific composition of the community is less uniform in the same microhabitats of different stumps than before, but there are not big differences in the colonization intensity.
- d) This stage is followed by a progressive abandonment of the microhabitat. Due to loss of food and shelter capacity there are less species and specimens and the diversity also decreases. The differences in the specific composition in the same microhabitats of different stumps continues to increase.
- e) The stump may be considered in relation with the invertebrate succession as a substract that offers food but demands high specialization, which then turns into a substract that offers less food but more diverse, and a complex spatial structure in which to live.

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