

THE ROLE OF NICHE AVAILABILITY AS A FACTOR DETERMINING THE DIVERSITY AND ABUNDANCE OF INVERTEBRATES ON SCOTS PINE, *Pinus sylvestris*

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SUMMARY

We review aspects of invertebrate biodiversity relevant to the management of Scots pine forests. At a landscape level, the area occupied by the host tree species, the length of time that species has been present, and the taxonomic relatedness of the host to other trees, all influence invertebrate biodiversity. At a stand level, tree size and above-ground architecture affect the number of niches available. Consideration needs to be given to the various feeding guilds since they exploit different components of these niches. Although there have been few published studies of invertebrate numbers in relation to niche availability in Scots pine, it would appear that the deadwood habitat is underrepresented in Scots pine forests and increasing the availability of this niche would enhance invertebrate biodiversity. An issue for managers is the need to distinguish between increasing total biodiversity and the encouragement of rare species with particular niche requirements which may also be dependent upon the continuity of that niche within a landscape.

KEY WORDS: Invertebrates
Niches
Feeding guilds
Scots pine

INTRODUCTION

Ecological theories based on observations and on both qualitative and quantitative analyses suggest that, within tree genera and, to a lesser extent, tree species, the numbers of invertebrate species are determined at wide spatial and temporal scales. However, the patterns at these wider landscape and regional scales are actually determined by much more local interactions; i.e. the invertebrates encounter their potential hosts and use local cues to determine whether they remain on the host plant or not. These direct interactions between invertebrate colonisers, their food plants and other biotic and abiotic factors therefore include elements linked to a wide range of spatial scales. Such invertebrate-host interactions occur at the tree itself, where invertebrates will encounter and use a range of

niches or micro-habitats. At a simplistic level, the presence of any invertebrate species depends on its net reproductive rate once it has encountered a potentially suitable niche and has committed itself to feeding and reproduction on the selected host.

Availability of niches is dependent on characteristics of the population of putative host plants. This involves both plant structure and size, so that trees, by virtue of their dominant physical position in the environment, offer the greatest potential for colonisation, retention and support of invertebrates. Such structural complexity is one component among many that determine invertebrate biodiversity at the invertebrate-host interface (Strong *et al.*, 1984). Other factors, at increasing scales, help to determine the likelihood of particular tree species, tree ages, etc. being present and available for exploitation by a local pool of potential invertebrate colonisers.

This paper examines invertebrate biodiversity on Scots pine, *Pinus sylvestris*, in the context of the ecology of the organisms, taking account of spatial and temporal scales, but ultimately focussing on interactions at the micro-scale within the structure of the tree itself. Such an approach allows the wider ecological context to be examined from the viewpoint of invertebrate colonisers and their ecological requirements, rather than from the more usual approach of direct numerical correlations between larger scale environmental components. The paper will first examine the wider scale ecological processes and then focus on micro-scale, niche provision within trees where direct interaction between invertebrates and their host trees take place.

AREA OCCUPIED BY TREE SPECIES

One of the most prominent ecological concepts put forward to explain the distributions and abundances of animals and plants is the species-area relationship. In summary, this states that the greater the area occupied by a particular resource, the greater the number of animals or plants associated with it. A key theory supporting this concept is the island biogeography theory of McArthur and Wilson (1967) in which larger islands have been shown to support greater biodiversity of species than smaller islands. In relation to forests, the «islands» in general are ecological rather than physical, reflecting the natural distribution of the principal forest species and, over more recent geological time, the major changes arising from commercial deforestation and, increasingly, re-forestation.

One of the most comprehensive analyses of the relationships between invertebrate species and areas occupied by their host tree genera is the study of British trees by Kennedy and Southwood (1984). The authors analysed a number of ecological factors that could potentially explain the observed diversity of insects on British trees. They made use of the extensive data on insects available in both published and unpublished sources in Britain and carried out correlation analyses of species lists against various attributes of British trees. Included in these correlates were log area (abundance), geological time since the host plant arrived in Britain, evergreenness, taxonomic relatedness, tree height, leaf length and coniferousness. Some of these factors will be discussed later in this paper but, in relation to area occupancy, there was a significant linear relationship between log abundance (an approximation to area based on presence in particular county records rather than area *per se*) and log numbers of insects recorded on the trees. The use of area data based on county records will tend to overestimate the actual occupancy by particular

tree genera and, therefore, it has been suggested that actual census data on tree area would be a better correlate. This was done by Claridge and Evans (1990) who used Forestry Commission census data (Locke, 1987) to re-analyse the insect data used by Kennedy and Southwood. In the new analysis, the species area relationship for broadleaved tree species was only weakly correlated but there was still a significant linear relationship for the main commercial conifers.

Amongst the conifers, pine has the greatest diversity of insect associates, despite the fact that, in Britain, it now occupies a smaller area than spruce. However, the other factors, particularly time in Britain, provide an explanation for this apparent contradiction with the species-area theory (see below). It has not been possible to obtain invertebrate species area information for the major conifer species across the whole of Europe but it is known that pine is an important species in relation to listed insect associates (see, for example, Schwenke (1978) for comprehensive coverage of the principal insect associates of trees in Europe). In relation to the potential of pine to harbour insects of biodiversity interest, the role of area is probably of relatively peripheral interest in relation to modern forest management practice that tends to artificially affect both area and continuity of forests. Such an observation was made by Evans (1987) with specific reference to Sitka spruce (*Picea sitchensis*) insects. He also analysed species area relationships for conifers and pointed out that the numbers of species associated with spruce were much lower than predicted by area, reflecting the extensive planting of Sitka spruce in Britain during the past 50 years. He also predicted that the numbers of insect associates is likely to rise rapidly in relation to the wide availability of spruce within the relatively impoverished British tree flora. Taxonomic relatedness is likely to have a significant role in this (see below).

TIME

The time that a tree species has been represented within a region appears to be a significant feature in determining species richness on that tree species. This has been analysed by Strong (1974), Kennedy and Southwood (1984) and others. Within the stepwise regression analysis carried out by Kennedy and Southwood, time added significantly to the predictive value of the relationship. In the case of British trees, time that tree species have been continuously present has been influenced strongly by the period since the last ice age, approximately 13000 years ago, an event that removed trees from the landscape leading to major discontinuity in availability for invertebrates. While many areas of continental Europe will have been similarly affected, the southern distribution of Scots pine in mainland Europe, for example, has had a longer period of continuous presence and, thus, would be expected to have greater species diversity of invertebrates. While there are certainly a number of invertebrate species present specifically in southerly areas (e.g. pine processionary moth, *Thaumetopoea pityocampa* (Martínez-Álvarez, 1991) and pine scale, *Matsuccoccus feytaudi* (Schvester and Ughetto, 1986)), there are no definitive studies to compare species patterns between regions that would enable time to be considered as a co-variable over a Europe-wide scale. The major co-variate of warmer climate in southerly areas would also need to be considered in such an analysis.

TAXONOMIC RELATEDNESS

Invertebrates show a range of preferences for host plants that spans polyphagy, in which the species are opportunistic and consume a wide range of plants, through to monophagy in which they specialise on a single host plant species or genus. In fact, it is more usual for preferences to be expressed at the plant genus rather than at the species level such that, for example, many invertebrates can be found within the genus *Pinus* but are capable of colonising and breeding on most species within the genus. Such preferences illustrate the role of taxonomic relatedness in determining the biodiversity of invertebrates on a given tree species. This is well illustrated when exotic tree species are introduced into regions where they are not native and, hence, would be expected to be free of most of their normal complement of invertebrate associates. An excellent example is the colonisation of the exotic *Nothofagus* species following its introduction to Britain. Many insect species normally associated with other members of the Fagaceae have rapidly colonised the new genus so that, in this case, close taxonomic relatedness has had an overwhelming influence compared with area and time as potential co-variables (Welch and Greatorex-Davies, 1993). In the case of pine dwelling invertebrates, Scots pine tends to be a source of insects in relation to colonisation of other, exotic pine species, especially where extensive plantations have been established within areas where Scots pine is endemic. For example the extensive plantations of *Pinus radiata*, a north American species, in northern Spain have been colonised by a range of bark beetles and lepidopteran defoliators normally associated with Scots pine in that region (Amezaga, 1997). Similarly, the planting of lodgepole pine, *P. contorta*, in Scotland has resulted in extension to the range of pine beauty moth (*Panolis flammea*) that was absent from Caithness and Sutherland in northern Scotland. *P. flammea* is now a major forest pest of lodgepole pine plantations in this area, but, interestingly, is less of a problem on Scots pine, a fact that is partially attributable to greater diversity of natural enemies in Scots pine plantations (Walsh *et al.*, 1993). With the continuing expansion of forestry and the greater use of exotic tree species, we can expect to observe many more switches of host plants by invertebrates, particularly if the trees are closely related to native species. This will add to the general biodiversity of our forests but will also carry the risk of pest outbreaks because of the potential absence of natural enemies and other natural regulatory factors.

DECIDUOUS AND EVERGREEN TREE GENERA

In ecological terms, the presence of leaves as one of the primary sources of nutrients and micro-habitat components of a tree is one of the characteristics that provides seasonal variability in niche provision for a range of invertebrates that utilise the resources on the tree. Scots pine is classified as evergreen and, as such, will offer provision of leaf resources during both the active growing season and during those periods of the year when deciduous trees shed their leaves. Kennedy and Southwood (1984) considered «evergreenness» in their multiple regression analysis of the insects on British trees. They concluded that the factor was a significant contributor (third behind Log abundance (area) and Time) to the total species richness of insects. Although the slope of the evergreen re-

gression line was positive, implying that more insect species are associated with evergreen rather than deciduous tree genera, there was no single explanation for this phenomenon. The differing phenologies and structures of the leaves will clearly influence colonisation by invertebrates but this is likely to be confounded by other attributes such as coniferousness, leaf size, etc. A further complication in use of such a measure is the difficulty of allowing for the abundance of host trees, especially when there have been extensive plantings, as is the case for commercially grown conifers. In relation to niche provision, however, it is likely that continuous availability of foliage is likely to provide increased micro-habitat availability compared with deciduous trees. This will be discussed further in considering the characteristics and significance of within-tree niches.

CONIFER CHARACTERISTICS

Comparisons between invertebrate diversity on conifers and on broadleaved tree species appear to indicate that, in many cases, the latter harbour more species than the former. Such is the case for British trees where the greatest diversity is recorded from the principal broadleaved genera, such as *Salix*, *Quercus*, *Betula*, *Crataegus* and *Populus*. The only conifer genus to approach the species richness of even the least colonised of the above broadleaved tree group is *Pinus*, which has other attributes, such as abundance and time in Britain as important determinants of invertebrate richness. Among the intrinsic characteristics of conifers are the presence of needles, rather than planar leaves, and the well developed resins, high in monoterpenes, that have considerable defensive qualities in relation to invertebrate colonisation (Haukioja and Honkanen, 1996).

SPECIFIC NICHE PROVISION

The combinations of ecological characteristics above illustrate the complexity inherent in attempting to develop robust relationships between invertebrate diversity and one or more measures of the biotic and abiotic forest factors that influence them. The factors commence at the whole tree level but are mainly at wider temporal and spatial scales that are more concerned with presence or absence of available resource in a given location. The actual interface between invertebrates and their hosts is, of course, at the tree level where invertebrate detection of the whole tree as a potential habitat and the precise suitability of niches for feeding and/or reproduction is determined by within tree characteristics. At this structural level, the roles of niche availability can be examined both in terms of total invertebrate abundance and, through the characteristics of the niches themselves, in relation to the ability of the tree to support invertebrates with specialist feeding or reproduction habits.

Tree size

It is, perhaps, stating the obvious that trees are the largest of the plants available for colonisation by invertebrates. However, this is one of the key factors that underlies the

range of other characteristics that have been discussed earlier. Size carries with it several attributes, of which apparency is one of the most important. The concept of apparency suggests that trees, by being prominent features of the landscape (combined with their long life span), are more easily «found» by both actively and passively dispersing invertebrates. Apparency includes both features directly linked with size, i.e. bigger plants are more easily located than smaller plants (Strong *et al.* 1984) and they also contain more niches for exploitation by a wider range of invertebrates adapted to exploit those niches (see below). Strong *et al.* (1984) investigated this explicitly in assessing the numbers of insect species associated with different categories of plants. They showed that the ratios of numbers of insect species associated with trees in relation to shrubs and herbs were 27:1 and 21:1 respectively, thus implying that trees could carry over 500 times more herbivore species than herbs.

Size is, therefore, an important attribute of trees whose longevity will clearly influence the range of sizes within given genera or species. Longer lived, old-growth forests will contain bigger trees, both in terms of absolute height and, more significantly, in overall biomass and structural complexity, than younger forests. For Scots pine, the complexity of the canopy and the provision of specific niches, particularly availability of deadwood, is certainly greater in old-growth forests. For example, the species composition of xylophagous Coleoptera in Finnish forests is significantly different in primaeval compared with managed Scots pine and Norway spruce (*Picea abies*) forests, even though the total numbers of xylophagous species was greater in managed forests (Vaisanen *et al.*, 1993). The authors showed that the main differences were in availability of much larger quantities of deadwood and the larger trunk diameters (i.e. size) in the primaeval forests. They also pointed out that the larger trees offered more heterogeneous habitats for Coleoptera, particularly those with specialist requirements. Thus, the fauna of primaeval forests differed almost completely from those of managed forests, but both carried high biodiversity.

Tree architecture

Plant architecture usefully defines both the size of a plant and the availability of niches on that plant (Lawton, 1983). Trees have considerable structural diversity and a complex plant architecture, arising both from their size *per se* and from the range of plant parts available. This is implicit in the observed carrying capacities of different plant groups mentioned earlier. Plant architecture carries with it both availability of feeding/breeding sites but also the potential to offer shelter from attack by natural enemies, leading to the concept of «enemy-free» space, a term coined by Jeffries and Lawton (1984). Herbivores feeding in protected situations, such as in buds or within, rather than on, leaves will tend to be more likely to avoid attack by natural enemies than open canopy feeders. Feeding strategy by invertebrates will, therefore, be a trade-off between feeding site, which may offer superior nutrition, and the degree of exposure of that site to natural enemy pressure. The effects of feeding site are most likely to manifest themselves in the amount of time that the herbivore takes to complete its development and is, thus, exposed to potential natural enemies. This concept of «slow growth-high mortality» has been shown to apply for some host plants such as various species of willow. The leaf beetle *Galerucella lineola* (Coleoptera: Chrysomelidae) developed much more slowly on *Salix dasyclados* than it did on *S. viminalis* and suffered significantly greater predation on the

former willow species (Haggstrom and Larsson, 1995). Although such results would be expected to apply to all situations where herbivores have extended feeding periods, this is certainly not universally the case. Comparing larval performance and levels of predation of pine beauty moth on different provenances of lodgepole pine, Leather and Walsh (1993) showed that larvae with the fastest growth rates on favoured provenances actually suffered greater predation than on less suitable provenances. This result indicates that there may be other factors, such as attraction of natural enemies to particular combinations of host plant odours, that can outweigh the risks to herbivores from feeding more slowly on less intrinsically suitable hosts.

Specific niches

Trees can be divided into many niches potentially capable of supporting invertebrate colonisers with specific feeding or reproductive requirements. The degree of sub-division of the tree will depend on invertebrate requirements rather than on strict physical partitioning of the tree itself. For example, bark feeding insects can be separated into groups on the basis of bark thickness, on structural or chemical composition of bark or on degree of degradation of bark (deadwood specialists). Thus, although it is convenient to split the tree into easily described physical niches, there is a considerable degree of complexity associated with each category.

In addition, the concept of feeding guilds can also be considered in relation to the diversity of invertebrates that actually colonise the tree. Many authors recognise the major guild categories proposed by Moran and Southwood (1982), in which they categorised chewers, sap-suckers, epiphyte fauna, scavengers, insect predators, other predators, parasitoids, ants and tourists. The following section is broadly based on these categories:

- Herbivores or Phytophages: this guild is rather a general description of all the invertebrates that feed on the host tree and may not always reflect reproduction on that tree. A number of sub-guilds can also be recognised and are specifically described in relation to their possible interactions with Scots pine as a host tree.
 - Chewers: these exploit the leaves and small twigs of the trees and have chewing mouthparts that directly remove host plant tissue, including both outer and inner leaf tissues. They are most commonly represented by larval Lepidoptera, larval sawflies (Hymenoptera: Symphyta) and both adult and larval Coleoptera. On Scots pine, most have been studied because of the extensive defoliation that they occasionally cause. Notable among these are the regular outbreaks of *Panolis flammea*, *Bupalus piniaria*, *Dendrolimus pini* and *Lymantria monacha* throughout most of the forests of mainland Europe (Klimetzek, 1979).
 - Suckers: nutrition is extracted by direct penetration of the phloem cells by sucking mouthparts. Nutritional requirements are quite specialised and this group tends to respond primarily to nitrogen availability. They are represented mainly by aphids, leaf hoppers (all Homoptera), true bugs (Heteroptera) and mites (Acari). Schwenke (1978) lists five damaging species of Homoptera on pine, the most common being *Pineus pini*, *Schizolachnus pineti* and *Cinara pini*.
 - Xylophages: a guild that feeds on components of the wood itself, usually involving those with chewing mouthparts, but can also include others with less well de-

veloped mouthparts, such as suckers and various Diptera that have rudimentary mouthparts. The guild can be split further into sub-guilds.

- * Bark feeders: a wide range of invertebrates exploit the bark of both living and dead trees (see saproxylic invertebrates below). Most require entry by the adult stage, after which the larvae remain under bark, usually exploiting the cambial layer. Others, such as the pine bark bug, *Aradus cinnamomeus*, on Scots pine feed by inserting long stylets into the cambial tissue, while remaining protected under pine bark scales (Eidmann, 1985). The beetle family Scolytidae contains the great majority of bark feeders and are generally regarded as pest insects; they can exploit both living trees and, more usually, stressed and recently dead trees. In Scots pine, they form an important component of the total biodiversity but, because of their pest status, are not usually regarded as positive contributors to the forest fauna. However, by being the first group to exploit bark after tree mortality, they are important in initiating the sequence of events that can lead to a rich saproxylic fauna (Speight, 1989).
 - * Wood feeders: a number of functional groups feed directly within the wood of trees, usually after a period of feeding in the cambial layer. Notable among these are the Cerambycidae (Coleoptera) that include both pests and representatives of conservation value. Although some are capable of exploiting living trees, the majority of wood feeders are deadwood feeders. It is interesting to note that, prior to intensive forest practice, which is a process that produces an abundance of suitable breeding material in the form of stumps and logs on site, many Cerambycidae, especially *Monochamus* spp., were regarded as uncommon (Hellrigl, 1971).
 - * Saproxylic invertebrates: this is a grouping to describe all invertebrates that live in dead and decaying wood. The grouping includes Coleoptera, Hymenoptera, Diptera and a range of saprophagous feeders, such as Collembola, Thysanoptera, etc. In relation to biodiversity, saproxylic invertebrates have considerable value in both species richness and in their potential to act as indicators of other parameters such as species mixtures typical of old-growth forests, etc. Depending on the quantity and nature of the deadwood, there may be a number of specialist invertebrates present, some of which have limited dispersal capacity and, thus, will only be found in old-growth forests with a long history of continuous presence in a given area. Aspects of the biology and conservation characteristics of saproxylic invertebrates have been comprehensively reviewed by Speight (1989). A general overview of the value of deadwood in conservation has been provided by Albrecht (1991) who noted that «natural» forests in Germany can contain 50-200 m³ of deadwood per ha, compared with only 1-5 m³/ha in managed forests. Both the volume of deadwood and its condition serve as indicators of the status of a given forest and of its conservation value, which in Germany may include approximately 1300 species of beetles.
- Epiphyte feeders: a group that is linked with the epiphyte flora associated with trees, rather than with the tree itself. However, these offer quite precise niches that can provide considerable variation over the surface of a tree. Prinzing (1997) showed clearly, in studies of the Collembolan *Entomobrya nivalis*, on a number of

broadleaved trees, that horizontal and vertical bark crevices and both fruticose and crust-like lichens were important micro-habitat determinants of abundance. The presence of lichens will vary considerably depending on factors such as light penetration, trunk surface area and atmospheric pollution and, thus, will be important determinants of epiphyte specialists in pine forests.

- Scavengers: a broad description to include those invertebrates that exploit non-living components of the tree. This group is taken by some authors to include saproxylic invertebrates, but here it is taken to mean those that exploit transient food sources that may only be loosely associated with a particular tree species. For example, in pine forests, Collembola are typical scavengers usually associated with needle detritus in the lower canopies and leaf litter. In Scots pine pole stage forests they increase rapidly from the forest edge through to closed canopy interiors, reflecting the greater retention of cast needles in the inner zone (Ozanne *et al.*, 1997).
- Predators: a broad group that exploits other invertebrate fauna associated with trees. Both invertebrate and vertebrate predators use this resource, but relatively few are specific to one or more prey species and, thus, they are often regarded as opportunistic and may not feature in samples taken from a given tree. An exception is *Rhizophagus grandis* (Coleoptera: Rhizophagidae) the specific predator of great spruce bark beetle, *Dendroctonus micans*; both predator and prey are occasionally recorded on Scots pine (Evans and Fielding, 1996). Carabids (Coleoptera) are also generalist predators, some of which are strongly associated with pine plantations and can have a considerable influence on other trophic groups both on the ground (particularly) and in the canopies of trees and shrubs.
- Parasitoids: these live within and, occasionally on, the bodies of their hosts, eventually leading to host mortality. In terms of total invertebrate biodiversity they are extremely common, making up around 10 % of all insect species (Eggleton and Belshaw, 1992). In contrast to predators, parasitoids tend to show high degrees of host specificity and, consequently, have well developed powers of host location, even when their hosts are deep within the wood of trees. An excellent example is *Rhyssa persuasoria* the ichneumonid (Hymenoptera) parasitoid of the woodwasp *Urocetus gigas* (Hymenoptera: Siricidae). This species can, using both olfactory and acoustic cues, locate larvae of the woodwasp in the wood itself and has a long ovipositor (up to 30 mm long) to drill through the wood to lay its eggs close to the host larva.
- Ants: ants combine predatory and scavenger roles and are important modifiers of invertebrate abundance in many Scots pine stands. Wood ants, notably *Formica rufa* and *Lasius niger*, combine territorial behaviour and aggressive foraging and defensive traits to induce considerable mortality to both ground and canopy dwelling invertebrates in pure pine and in mixed stands (Whittaker and Warrington, 1985). They are, therefore, indirectly associated with niches within individual pine trees, but can be strongly associated with the general environment in which pine grows.
- Tourists: this category refers to those invertebrates that do not have direct association with pine or any components of the pine ecosystem. They may be in transit or may be using the forest ecosystem for aggregation during dispersal or for mating, etc. Some may also opportunistically feed on pine or associated flora or fauna but are not specifically linked to any particular component of the pine ecosystem.

Tree structure and the provision of niches

In common with other conifers, Scots pine offers a range of niches that varies with tree age and state of health. Vertical structure, and the potential presence of exploitable niches, is presented schematically in Table 1. Each of the niches will provide both nutrition and shelter to the various guilds outlined above. However, the precise suitability of given niches will depend on both physical and biochemical composition and may be modified according to components such as seed origin of the tree, the site on which it is growing and on other biotic and abiotic factors. The physical limits of each niche will clearly depend on tree size which is, in turn, a correlate of tree age and other site factors. Precise measures of niche size, such as volume or surface area, can be made and potentially related to more easily measured parameters such as tree height or dbh. The percentage volume figures in Table 1 are based on average data from several studies. Recent emphasis has been on development of models of tree growth, ostensibly for use in prediction of yield over the life of a tree crop, that would also allow prediction of niche availability to be made (Perttunen *et al.*, 1996). Such models concentrate on crown structure and its relationship to dbh and height and, thus, do not always provide predictions of the quantity of specialist niches for a given tree species. For example, the LIGNUM model of Perttunen *et al.* (1996) is based on division of the tree into various segments, branching points and buds, each pair being separated by a branching point. New production is dependent on numbers of buds that, in turn, give rise to new tree segments, branching points and buds. The tree segments themselves comprise wood, bark and foliage and, thus, correspond to some of the potential niches exploited by the guilds described earlier. The LIGNUM model is driven by physiological processes, especially photosynthesis, and is strongly dependent on availability of light that is, in turn, a function of canopy structure and shading. More detailed breakdown, especially to cones and seeds, is not included in this or other models.

TABLE 1
SCHEMATIC CLASSIFICATION OF THE MAJOR NICHE PROVISIONS IN A SCOTS PINE TREE, INCLUDING ESTIMATED PROPORTIONATE VOLUME IN EACH NICHE

Clasificación de las principales provisiones de los nichos en un árbol de Pino silvestre, incluyendo la proporción estimada del volumen en cada nicho

NICHE	COMPONENTS	PROPORTION (%)
Crown foliage	Buds	6
	Needles	
	Cones/seeds	
Branchwood		12
Stem	Bark	10
	Wood	60
Stump and root		12
	Litter and detritus	
	Soil	

Data from J. Methley and J. Christie, Forest Research, unpublished.

Invertebrate diversity in relation to niche availability

There have been relatively few studies of the faunal composition of invertebrates on Scots pine in relation to niche availability in this tree species. However, using the information available, it is possible to assess the relative contributions of different niches to the total invertebrate fauna on Scots pine. In this sense, assessment will concentrate on the herbivores because they link directly with tree suitability at the niche and, ultimately, at the whole tree level.

One of the earliest studies of whole tree faunas in relation to tree parameters was that of Kennedy and Southwood (1984) which has already been alluded to in relation to wider ecological explanations for the diversity of insects on British trees. Among the parameters considered by the authors was the breakdown of insect diversity into guild categories. Although not providing the level of detail required to consider some of the specialised niches, the guild structure acts as a surrogate for niche availability. In the Kennedy and Southwood approach, it also enabled Scots pine to be considered in relation to other conifer genera and to broadleaved trees, thus providing a contrast between two extremes of leaf structure and availability. Fig. 1 provides a summary analysis of the relative contributions of guilds to the overall species richness on selected conifer and broadleaved genera. Fig. 1a shows the total numbers of species in each guild and illustrates the much greater diversity of insects on the two broadleaved genera and the fact that they are dominated by the herbivore class. This includes both leaf and bark feeders, making it difficult to compare between tree genera. In fact, the structure of herbivore classes in conifers tends to be dominated by bark and wood feeders in contrast to broadleaved trees where the foliage harbours the greatest numbers of chewers. Taking the proportions, rather than absolute numbers, in each guild class removes much of the variation between tree genera for the chewer guild (Fig. 1b). Although there is considerable variation, the proportion of invertebrate species is relatively constant for the two principal conifer genera, pine and spruce, compared with oak and willow. Unfortunately, the numbers of species and, hence, the proportions in each category make it difficult to interpret the relative contributions of guilds within the least common conifers. However, it is interesting to note that, even with a relatively impoverished invertebrate fauna, yew carries as many gall formers as any of the other conifers, but none approaches the numbers on broadleaves. Sap feeders also show a relatively constant proportionate presence across tree genera, with the exception of spruce where there is a higher proportion than for the other trees. Considering that spruce is a relatively new genus to Britain, although it was actually present in the interglacial period, it has accumulated more sap feeders than might be expected. It is not clear why this would be, but in relation to international transport of invertebrates it is conceivable that sap feeders are more likely to remain undetected, particularly if whole plants are imported.

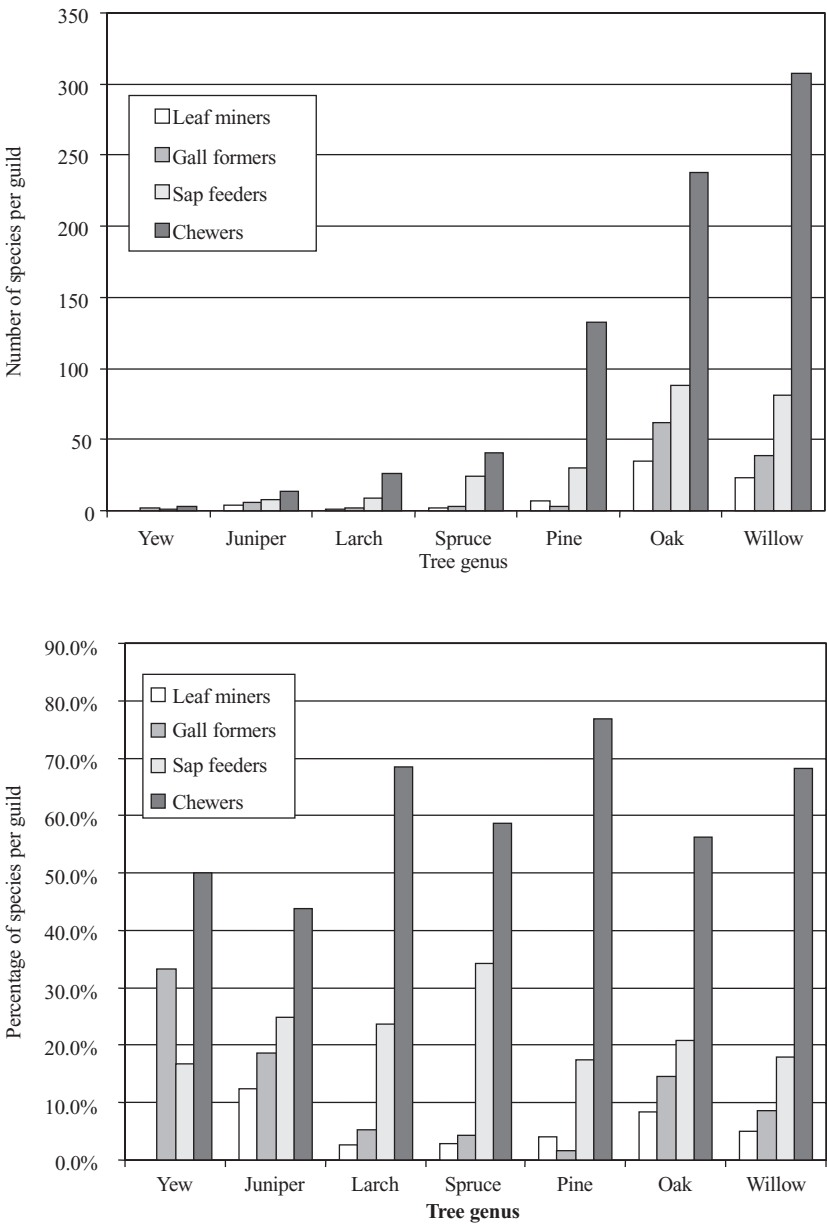


Fig. 1.—The numbers (a) and proportions (b) of various guilds on selected British trees (based on Kennedy and Southwood, 1984)

Número (a) y proporción (b) de varios grupos de insectos en árboles británicos (basado en Kennedy y Southwood, 1984)

Cone and seed niches

This niche is both age and tree size dependent, the production of cones varying between years in relation to both tree growth and environmental conditions. In addition, there may be differences in suitability of cones for colonisation depending on the seed origin or clonal selection within a given tree species. For example, there was significant clonal variability in susceptibility to attack by coneworms (*Dioryctria* spp.) in loblolly pine (*Pinus taeda*) seed orchards in the USA (Askew *et al.*, 1985). With regard to Scots pine, Annala and Hiltunen (1977) demonstrated significant clonal variation in susceptibility of cones to attack by the weevil *Pissodes validirostris*. They attributed this to variation in quantities and types of monoterpenes, especially α -pinene, although more damage was noted when other monoterpenes, such as myrcene, 3-carene, β -phellandrene and p-cymene were present. Comprehensive studies of the insect fauna of Scots pine cones have been made by Roques (1977). He described the occurrence and biology of 36 species of insects, some directly feeding on cones and others associated with them (e.g. natural enemies). The focus of these studies has been on the pest status of the insect species recorded and, thus, there is relatively little information on the biodiversity value of this niche. The proportion of Coleoptera within this niche provides only a minor contribution to the total Scots pine fauna recorded by Hunter (1977).

The canopy niche

Although concentrating on the very well known British insect fauna, the Kennedy and Southwood analysis suggests that chewers are likely to be the dominant guild in any temperate forest ecosystem, particularly in their rather broad use of the term chewers. In relation to Scots pine specifically, a more recent study of canopy arthropods by Simandl (1993) included numerical assessment of numbers within guilds and limited assessment of species richness. However, the relative contributions within guilds provided an interesting breakdown by feeding category (Fig. 2). The results indicated that, on Scots pine, the defoliators (chewers) and detritivores were dominant, but were also accompanied by a complex of natural enemies responding to the high numerical abundance of prey items in the canopy. Wood feeders (xylophages) were relatively uncommon in the canopy. Contrasts between young and old stands of Scots pine were included in Simandl's study. The greatest numbers of individuals were recorded from medium aged (41-50 years old) stands, which the author attributed to the greater volume of foliage in such stands.

Analysis of crown invertebrates in *Vaccinium*-Scots pine forests in Poland revealed that Homoptera (suckers) and Hymenoptera (ants - predators) were dominant (Fig. 3) (Ziogas and Gedminas, 1994). The presence of high numbers of foraging ants in the canopy reflected the abundance of prey items. However, the overall species richness in the crowns was relatively low and did not differ significantly between age classes of Scots pine (Fig. 4), although numerical abundance of Lepidoptera and Homoptera increased with increasing age. Although the age classes in this study were similar to those studied by Simandl (1993), there were some contrasts in species dominance. Both studies indicated that presence of suckers (Homoptera) was notable in younger trees, but in the older tree age classes chewers were more dominant in Simandl's study, reflecting the presence of a number of sawfly (Hymenoptera: Diprionidae) species in the Czech study. The cano-

py niche, therefore, is an important component of the Scots pine ecosystem but most studies in Europe have been concerned with the importance of chewers in relation to impacts on the trees. It is interesting to note that, in studies of conifer forests in North America, the general finding that suckers dominate the early successional stages was repeated (Schowalter *et al.*, 1988) but, in old-growth forests, the canopy niche was dominated by fewer herbivore species with lower total biomass (Schowalter, 1989). Within the overall canopy niche, some invertebrates specialise on buds (both leaf and flower). This habitat is high in resins and, thus, the invertebrates are well adapted to cope with the copious resin flow that tends to occur once the buds are attacked. Notable among the recorded species on Scots pine are pine shoot moth, *Rhyacionia buoliana*, its northern equivalent, *R. logaea* and the pine resin gall moth *Petrova resinella* (all Lepidoptera: Tortricidae) (Bevan, 1987). A requirement for synchrony with bud burst may also distinguish specialist bud and young needle feeders from other herbivores that are general crown feeders, as is the case for eastern pine shoot borer, *Eucosma (Epinotia) gloriola* on Scots pine in the USA (Steiner, 1974).

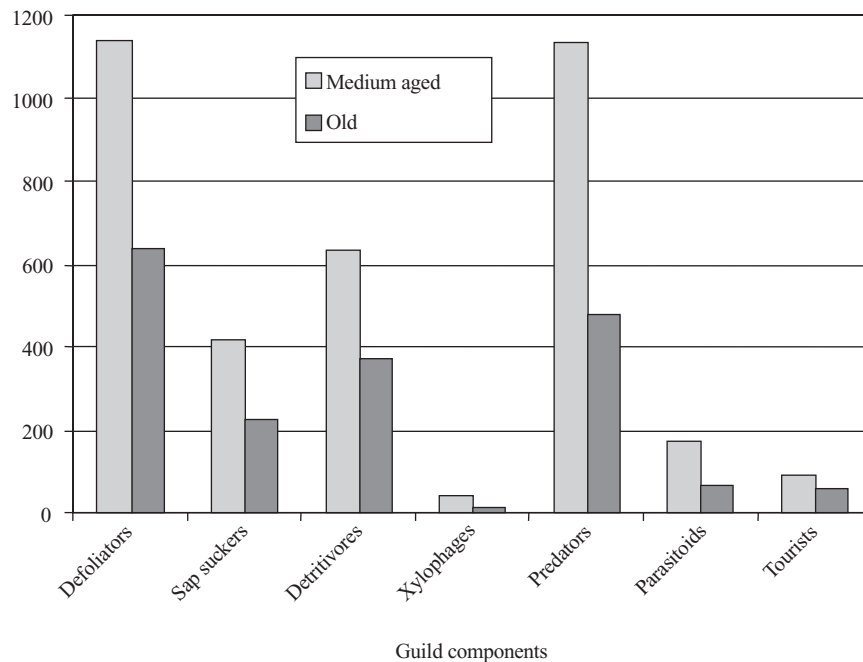


Fig. 2.—The numbers of individuals in various guilds in the canopies of medium aged and old Scots pine stands using knock-down sampling (from Simandl, 1993)

Número de individuos en varios grupos de insectos en doseles de rodales de Pino silvestre de media edad y viejos, utilizando un muestreo por apeo (de Simandl, 1993)

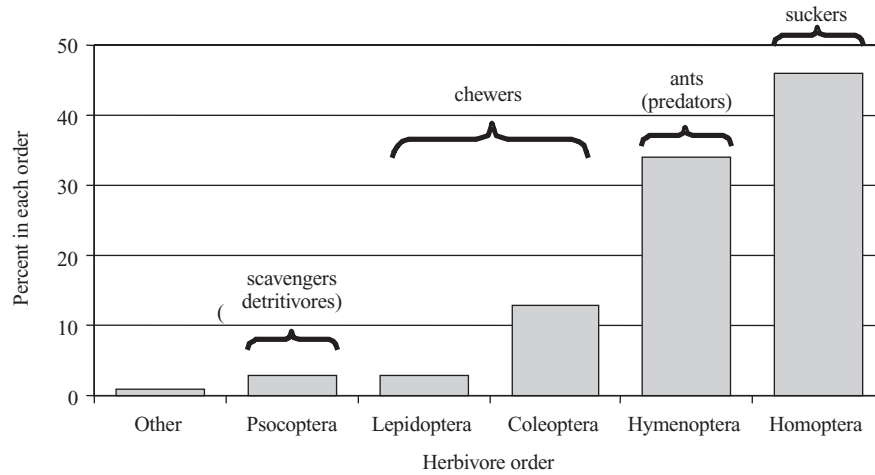


Fig. 3.—The percentage of the major invertebrate orders in selected guilds on Scots pine in Poland (based on Ziogas and Gedminas, 1994)

Porcentaje de los principales órdenes de invertebrados, según grupos selectos, en Pino silvestre en Polonia (basado en Ziogas y Gedminas, 1994)

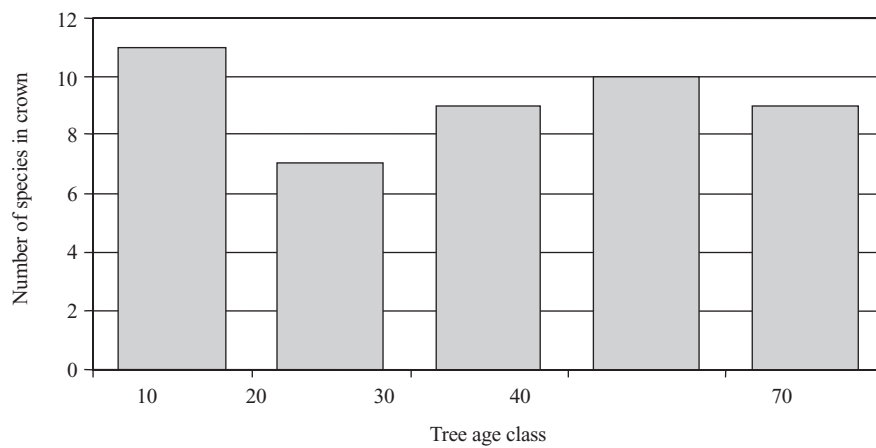


Fig. 4.—The numbers of species of herbivores in the crowns of Scots pine in Poland in relation to tree age (based on Ziogas and Gedminas, 1994)

Número de especies de herbívoros en la copa de Pino silvestre en Polonia, en función de la edad del árbol (basado en Ziogas y Gedminas, 1994)

Bark and wood niches

Although bark and wood can be regarded as separate niches, it is convenient to consider them together because most insects that ultimately exploit the wood will do so after spending part of the life cycle in the bark. Both live and dead wood can be included in this category, again reflecting the succession from exploiters of live bark through to the ultimate saproxylic fauna in decaying wood. In relation to available biomass, bark and wood provide the principal niches in Scots pine and other trees. This is well illustrated by a detailed study of Scots pine Coleoptera by Hunter (1977) who examined the distribution of Coleoptera species in a number of niches within the pine ecosystem. A summary of the proportions of species found within the different niches is provided in Fig. 5, where the dominant roles of bark and wood are clear. Most of the Coleoptera in this study are found exclusively or mainly on Scots and other pines and, thus, provide a measure of tree genus specialism, which in Britain includes those associated with relict Scots pine woodlands. A total of 83 species of beetle was recorded from the bark/wood category (63 % of the total). Hunter attributed this to a number of factors including the size of the trunk, branch or twig, moisture content, especially in relation to fallen deadwood in the early stages of decay, nutritional requirements of the beetles and linkages to other factors such as fungal associates. It is also significant that the distributions of many of the beetles recorded in this study coincide quite precisely to the distributions of relict Scots pine in Britain, thus illustrating the value of old-growth forests but also highlighting the problems of colonisation of new pine stands by invertebrate species with limited dispersal capacity. It was also evident that succession of habitat suitability, particularly through to the late stages of wood decay are important attributes in retaining rare species of Coleoptera.

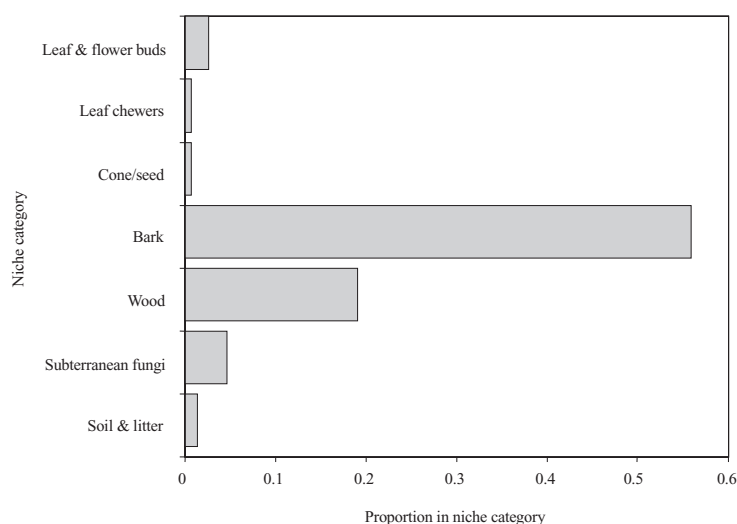


Fig. 5.—The proportion of species of Coleoptera in Scots pine in Britain in relation to niche category (based on Hunter, 1977)

Proporción de especies de coleópteros en Pino silvestre en Gran Bretaña, por categoría de nicho (basado en Hunter, 1977)

Studies of saproxylic bark and wood-dwelling Coleoptera in both managed stands and in primaeval Scots pine and Norway spruce forests in Finland provided some interesting contrasts in relation to both species richness and in the «rarity value» of the beetle species present (Vaisanen *et al.*, 1993). Species richness and abundance was greater in the managed stands (78 species, 1302 individuals) than in the primaeval forests (55 species, 512 individuals). However, as might be predicted from the history of the stand and the average age of the trees (>250 years), the proportion of rare species was much higher in the primaeval forest (65 % compared with 33 %). A concern that is often expressed concerning conservation of invertebrates is whether the trees (live or dead) in the forests provide resources that could result in invertebrates developing into pests before providing any conservation value. In this context, it was interesting to note in the above study that the proportion of bark beetles (Scolytidae) in the primaeval stands was much less than in the managed stands (<5 % compared with >50 % in managed stands), despite the fact that availability of deadwood, especially large diameter fallen trunks, was considerably greater in the primaeval forests. This finding is likely to reflect the high availability of freshly felled material in a managed forest, thus providing greater continuity for the more damaging bark beetles that rely on dying or recently dead bark for reproduction (Kulhavy and Miller, 1989).

Root, litter and soil niches

The litter and below ground areas within pine forests can provide rich habitats for invertebrates and will reflect the characteristics of the canopies above, particularly in relation to accumulation of dead needles and in the extent of light penetration and potential for development of a field and shrub layer. In the study of Hunter noted above (Fig. 5), soil and litter dwelling Coleoptera were relatively poorly represented, but subterranean fungi provided valuable niches for beetle colonisation. In general, the litter layer is dominated in terms of abundance of individuals by scavengers (detritivores), especially Collembola and Psocoptera. Stumps remaining after felling the Scots pine crop also make a significant contribution to below ground invertebrate niche availability spanning live wood, through various successional stages to fully decayed biomass. Although being principally concerned with colonisation by ants, Franch and Espadaler (1988), carried out a comprehensive study of the total invertebrate fauna in Scots pine stumps in San Juan de la Peña Forest in Spain and provided some interesting insights to sequences of colonisation of this niche over time. Colonisation of the stumps was studied over a 16 year period after the trees were felled. During this period, a total of 187 species of invertebrates was recorded, the patterns of colonisation initially reflecting variation in suitability of bark over time and, later, the increasing presence of decaying wood. The numbers of species in the major orders of invertebrates recorded over the 16 year period are summarised in Fig. 6. The Coleoptera were clearly dominant and also served to illustrate how succession within the order varied with bark and wood suitability. Scolytidae, reflecting their links to relatively fresh and intact bark dominated initial colonisation. The weevil, *Hylobius abietis*, also exploited the bark over a 2-3 year period after the tree was felled. Later succession was dominated by Cerambycidae, firstly *Rhagium inquisitor* and later the two other species in Fig. 6. Finally, the elaterid beetle *Malanotus rufipes* was recorded as decay of the stump accelerated. During this period the numbers of saproxylic species increased, being dominated by those orders on the left side of the horizontal scale

in Fig. 6. Wood ants dominated the Hymenoptera, again reflecting the increasing availability of resources for nest building as the stumps decayed. This study provided an excellent illustration of the dynamic nature of deadwood in the form of stumps and roots as a niche and emphasises that retention and continuity of the resource is important to maximise its successional biodiversity value.

CONCLUSIONS

Invertebrate-host interactions at the tree level reflect the precise habitat and nutritional requirements of the potential invertebrate colonisers. However, as has been discussed in the paper, the biodiversity value of the tree will be dependent on many ecological factors at a range of spatial and temporal scales. Ultimately, the availability of quite precise resources will determine reproductive success by invertebrates and, thus, one of the features that must be considered in assessing the biodiversity of invertebrates in a given forest system is the availability of those resources. In this paper, we have considered the potential for describing resource availability in relation to niches within the tree. Although there are many studies of the biology and habitat requirements of individual or groups of invertebrate species, there is relatively limited information on interactions at the level of whole tree faunas, particularly for European conifer species, including Scots pine. Even when useful compilations of species have been analysed in relation to wider ecological principles [for example the studies by Kennedy and Southwood (1984) and Vaisanen *et al.* (1993)], the emphasis has been on relationships at the tree, rather than the niche level. However, the few studies, such as that of Hunter (1977), that have considered species richness in relation to niche availability indicate that both local and regional information on biodiversity can be considered at the micro scale of the niche itself. This is particularly true for those species that have precise habitat requirements that may be represented only within the tree ecosystem itself.

Preferences for niches are not a simple function of the total availability of a particular niche on a tree. Surprisingly, there is little information on the quantitative relationships between invertebrate colonisers and niche availability at the tree level. However, some approximation to test the null hypothesis that presence of both diversity and abundance of species is a direct function of the relative presence of niches in the tree as a whole can be made. For example, the data gathered by Hunter (1977) on proportion of Coleoptera in given niches can be plotted against the proportion of total tree volume in those niches. This has been done in Fig. 7 for four niche categories. If niche colonisation is simply a function of volume then the plotted line in Fig. 7 would apply. It is immediately apparent that bark feeders, in particular, have a much higher proportionate presence than expected on the basis of available volume. To a lesser extent, wood feeders occupy a lower proportion of the expected volume. This result is not surprising in relation to the cues that invertebrates use to detect and colonise trees. Both physical and chemical cues will contribute to whether a given niche is exploited, while the nutritional content will determine how many individuals can be supported within a given niche (Slansky, 1990). Thus, wood, with its high cellulose and low nitrogen contents, is the least nutritious of the available resources within a tree and would, therefore, be predicted to carry lower species diversity than expected on the basis of volume. Conversely, the reasons for relatively high exploitation of the bark resource, considering that it quite transient once the tree has died, needs to be investigated.

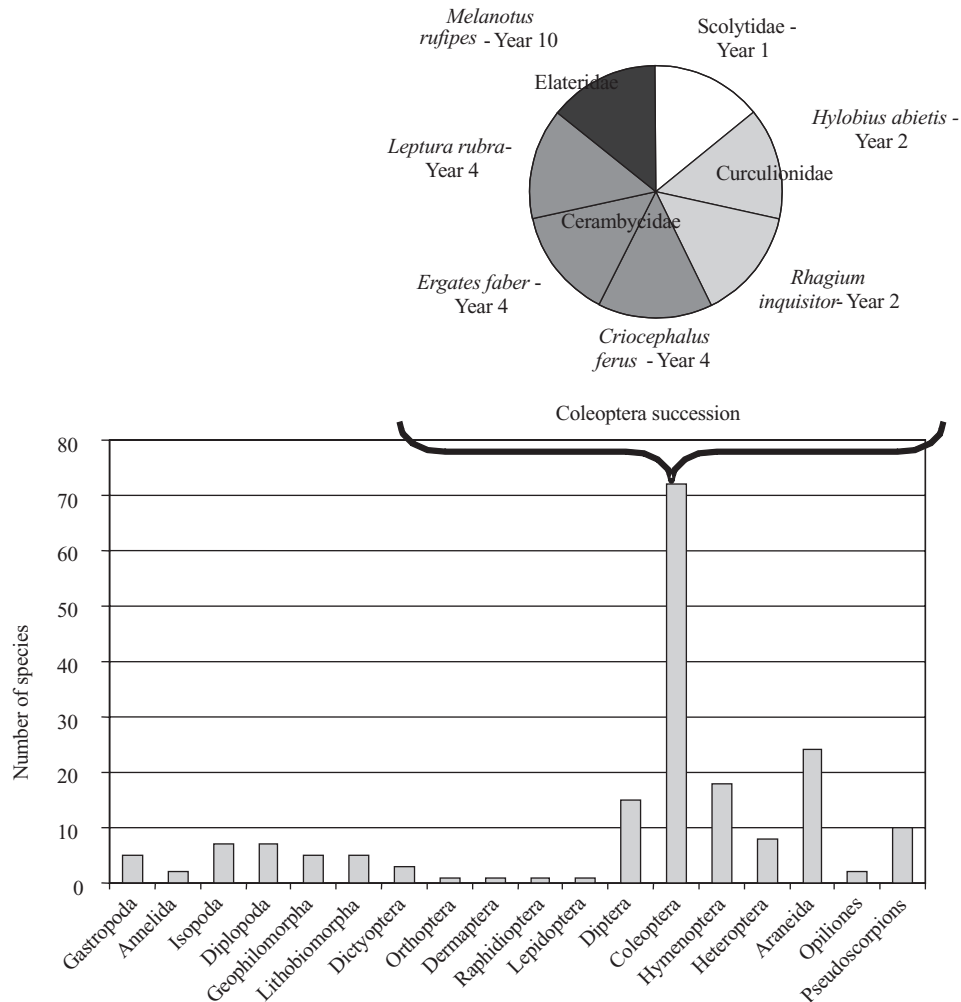


Fig. 6.—The numbers of species in invertebrate orders in Scots pine stumps in Spain during a 15 year period after tree felling. A more detailed chart of the succession of Coleoptera over a 10 year period is also shown (based on Franch and Espadaler, 1988)

Número de especies en los órdenes de invertebrados en los tocones de Pino silvestre en España durante un período de 15 años tras la corta. También se muestra un gráfico más detallado de la sucesión de coleópteros durante un período de 10 años (basado en Franch y Espadaler, 1988)

The whole question of relative niche exploitation, especially for those guilds other than foliage feeders could usefully be explored with a view to retaining or enhancing biodiversity, both in generality and specifically for rare invertebrates with precise niche requirements. Although it is clear that considerably more research is needed to understand

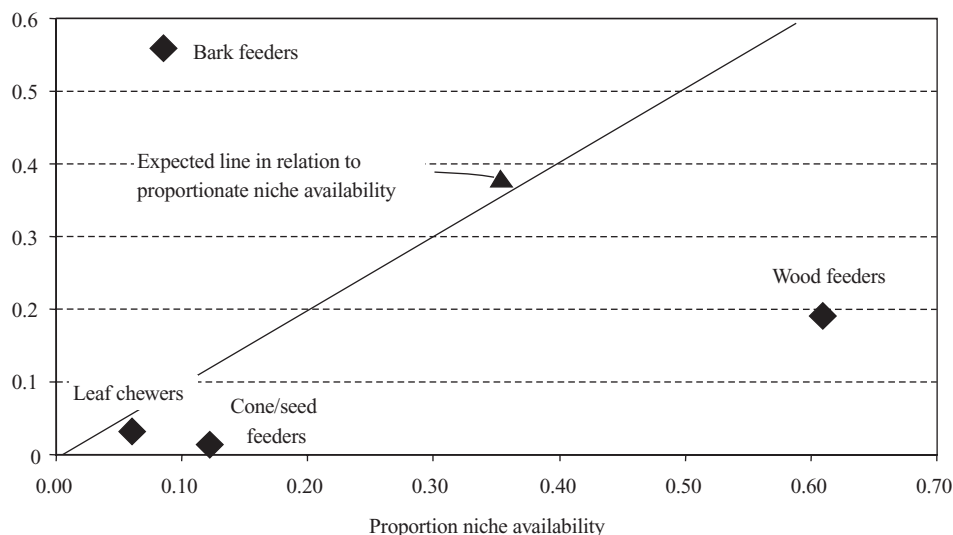


Fig. 7.—The projected relationship between proportion of total Coleoptera in each niche category (based on Hunter, 1977) and the proportion of tree volume occupied by that niche (Forestry Commission data). Bark feeders and wood feeders have a greater and lower presence than expected on the basis of direct linkage between volume available and species present

Relación proyectada entre la proporción de coleópteros totales en cada categoría de nicho (basado en Hunter, 1977) y la proporción del volumen de árbol ocupado por ese nicho (Datos de la Forestry Commission). Los insectos que se alimentan de corteza y madera tienen una presencia mayor y menor, respectivamente, de la esperada basándose en la relación entre volumen disponible y especies presentes

and extend the concepts of niches, the principles involved can be incorporated at a basic level into management of forest resources to enhance biodiversity. From the information presented in this paper, it would be prudent to consider how niche availability changes over time within the lifetime of the crop. It is likely that the relative proportions, by volume, shown in Table 1 will dominate during the stages up to normal commercial maturity of a forest. Thus, proportionate foliage availability will increase rapidly during the early stages of growth and will then reach relative stability after canopy closure — the canopy then moving upwards as the trees mature and lower, shaded branches die back. Only around 6 % of the available volume on the tree will be retained in this niche but this will be important for many Lepidoptera and Homoptera, some of which will have high conservation value.

The anomalous position of bark as a resource in relation to volume has already been discussed. Encouragingly for managers considering retention of trees to develop uneven aged stand structures and to increase the availability of «old-growth» forests, the numbers of damaging bark beetle species actually appears to fall as the forests shift from intensively managed to a more stable system with constant availability of mature trees (Vaisanen *et al.*, 1993). However, it is still debatable how biodiversity should be measured as a whole and the results of Vaisanen *et al.* (1993) indicate that total species rich-

ness and abundance is actually greater in managed stands, but at the expense of rarity value. Managers have to compromise between the two aims of increasing total biodiversity and of encouraging relatively rare species with potentially highly specialised requirements; knowledge of niche availability, especially the «quality» of niches may eventually allow choices to be made on a rational ecological basis, particularly at quite local scales.

Management in the final stages of stand development must, inevitably, concentrate on availability of deadwood. Here it is a safe assumption to state that «more is better». The data from Germany alluded to earlier (Albrecht, 1991), indicate that at least 10-50 times the volume of deadwood per ha can be available in natural forests, compared to intensively managed forests. Albrecht suggested that at least 10 m³/ha should be left in managed forests and this would certainly be a minimal figure in encouraging significant saproxylic invertebrate biodiversity. Other factors, especially the distance of managed forests from sources of old-growth forests, will be significant, indicating that while niche availability will be important in selection of resources and retention of invertebrates at those resources, other factors at stand and landscape scales must also be considered. Clearly a wider ecological appreciation of the multiplicity of factors affecting biodiversity will add greatly to the knowledge base that can be used to manage forests effectively in the future.

ACKNOWLEDGEMENTS

We are indebted to Dr Paulius Zolubas, of the Lithuanian Forest Institute for translation and additional data in relation to the paper by Ziogas and Gedminas.

RESUMEN

El papel de la disponibilidad del nicho como un factor determinante de la diversidad y abundancia de invertebrados en Pino silvestre (*Pinus sylvestris* L.)

Se revisan distintos aspectos de la biodiversidad de invertebrados relevantes en la gestión de los bosques de Pino silvestre. A un nivel de paisaje, el área ocupada por la especie del árbol anfitrión, el tiempo que la especie ha estado presente, y la relación taxonómica del anfitrión con los otros árboles, influyen en la biodiversidad invertebrada. A un nivel de rodal, el tamaño del árbol y la arquitectura aérea afectan el número de nichos disponibles. Debe prestarse atención a los diversos grupos alimenticios de invertebrados, puesto que ellos explotan diferentes componentes de esos nichos. Aunque ha habido pocos estudios publicados sobre el número de invertebrados en relación con la disponibilidad del nicho en Pino silvestre, parece que el hábitat de la madera muerta está infrarrepresentada en los bosques de Pino silvestre y que el aumento de la disponibilidad de este nicho mejoraría la diversidad biológica de invertebrados. Un aspecto para los gestores es la necesidad de distinguir entre el aumento de la biodiversidad total y favorecer las especies raras con requisitos particulares del nicho que también pueden depender de la continuidad de ese nicho dentro de un paisaje.

PALABRAS CLAVE: Invertebrados
Nichos
Grupos de Alimentación
Pino silvestre

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