STRUCTURE, SPECIFICITY, AND EVOLUTION OF INSECT GUILDS RELATED TO CONES OF CONIFERS IN WESTERN EUROPE

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INTRODUCTION

Patchy and ephemeral resources, such as the cones of conifers, can be very useful in the study of plant-insect relationships. Studies of such relationships in forest entomology are typically complicated by the spatial and temporal characteristics of the host plants, which occur over vast areas and have lifespans of decades or even centuries. The reproductive structures of conifers, on the other hand, are much more easily studied because they mature within 1 to a few years and occur as discrete, easily sampled units. They also play a unique role in forest ecosystems.

Seed cones, which correspond to female flowers in most gymnosperms (Pinaceae, Taxodiaceae, Araucariaceae, most Cupressaceae), develop both as singular units and as integral parts of cone-bearing trees. Though development varies with tree species, general trends appear similar, corresponding to the progressive development of the female flower into a lignified cone that can release mature seeds. These overall similarities in cone development among most conifers facilitate a comparison of the fauna inhabiting cones (Roques 1988a).

Cone maturation is always extremely rapid compared to tree lifespan. The morphological, physiological, and biochemical changes which occur during the lifetime of the reproductive structures are thus condensed into a much more limited time and space (cone size varies from 0.6 cm in *Juniperus sabina* to 15 cm in *Abies alba*, and time from flowering to seed release ranges from 6-1/2 months in *Larix decidua* to 2-1/2 years in *Pinus silvestris*, for instance). Very distinct environmental conditions are thus offered to insects during successive and temporally restricted periods. Moreover, in most conifers spatial distribution of cones is heterogeneous among trees as well as within trees (Mattson 1979) and cone crop appears to vary over time, generally being neither annual nor cyclic (masting phenomena, according to Fenner 1985).

Individual cones may therefore be viewed as temporary subunits of the forest biocenosis which form discrete habitats with a limited carrying capacity for possible inhabitants. Niche characteristics, especially size limitations, would predict a highly specific entomofauna adapted to host discontinuity in space and time.

Though a large body of literature has dealt with the functioning of insect guilds of similar structures of angiosperms (among many others, Janzen 1969, 1970, Zwölfer 1979, 1982, 1987, 1988), very few studies have provided a synthesis of the relationships between cones and associated insect guilds, with the exception of some notable work done in eastern Europe (Stadnitskii 1971, Stadnitskii et al. 1978, Skrzypczynska 1977, 1981, 1982, among others). In this contribution, which is part of a

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wider study of cone-insect relationships (Roques 1988a), I synthesized the European literature with the following goals: 1) analysis of the structure of ecological groups in cones of native and introduced conifer species in western Europe, 2) specificity of the host of individual cone-insect relationships, and 3) exploration of the consequences for the structure and evolution of insect guilds.

ECOLOGICAL GROUPS RELATED TO CONES: DIVERSITY AND LIMITATION

Insects inhabiting cones in western Europe can be divided into three ecological groups in relation to trophic habits: a) phytophagous insects with their parasite and predator complexes, b) mycophagous and detritivore species developing in the detritus food chain deriving from the previous group, with their own natural enemies, and c) insects using the galleries made by phytophages as hibernating shelter sites. This structure of entomological communities is, naturally, based upon the phytophagous group, whose previous damage creates conditions that support development of the other groups.

Insects Using Cones as Hibernating Sites

These species are uncommon. Only a few species with no accurately defined tropic relation, are regularly encountered overwintering within cones: adults of *Rhizobius chrysomeloides* Hbst. (Coleoptera: Coccinellidae) and some stages of *Leptothorax affinis* L. (Hymenoptera: Formicidae) in *P. silvestris* (Roques 1977); some stages of *Crematogaster* spp. (Hymenoptera: Formicidae) in Mediterranean pines; adults and nymphs of *Gastrodes abietum* Bergroth and *G. grossipes* De Geer (Hemiptera: Lygaeidae) in spruce (Roques 1983). These insects will be excluded from the following discussion.

Mycophagous and Detritivore Species

Larvae of several species commonly develop on fungi and detritus in cone galleries made by phytophages. Dipterous larvae are exclusively observed in western Europe: Chloropidae, one species, and Cecidomyiidae, one species. These larvae do not directly attack cone structures but may, as does *Camptomyia pinicolana* Mam. (Cecidomyiidae), seed browning that leads to seed abortion (Roques 1983). The detritivore subguild is more important in other European regions. In addition, 15 other species, mainly Diptera but also Coleoptera (Cryptophagidae, Anobiidae, Lathridiidae) have been noted in Poland and in the European part of the Soviet Union (Skrzypczynska 1977, 1981, 1982, Stadnitskii et al. 1978).

Phytophagous Species

By contrast, diversity in families and orders is a dominant feature of the phytophagous group. Larvae of weevils, microlepidoptera, gall-midges, and seed-chalcids, among others belonging to 13 families and four orders of insects are known to feed on cones of the various conifers growing in western Europe (Fig. 1a, from data in Roques 1983). In addition, mites of the family Eryiophiidae have been reported, e.g. *Trisetacus* spp. (Roques 1983, Roques et al. 1984).

This diversity, however, is only superficial. The number of species and, more importantly, the number of genera observed in the cones are limited. Fifty-nine species from only 30 genera are currently recorded in western Europe (Fig. 1b, from Roques 1983, Roques et al. 1984, Roques and Raimbault 1986). The subsequent total of recorded phytophages and detritivores is 61 species and 32 genera. The same values total only 72 and 33, respectively, when all of Europe, including the European part of the Soviet Union, is considered (calculations from data in Annila 1976, Wiersma 1978, Skrzypczynska 1977, 1981, 1982, Stadnitskii et al. 1974, 1978). This shows both relative stability

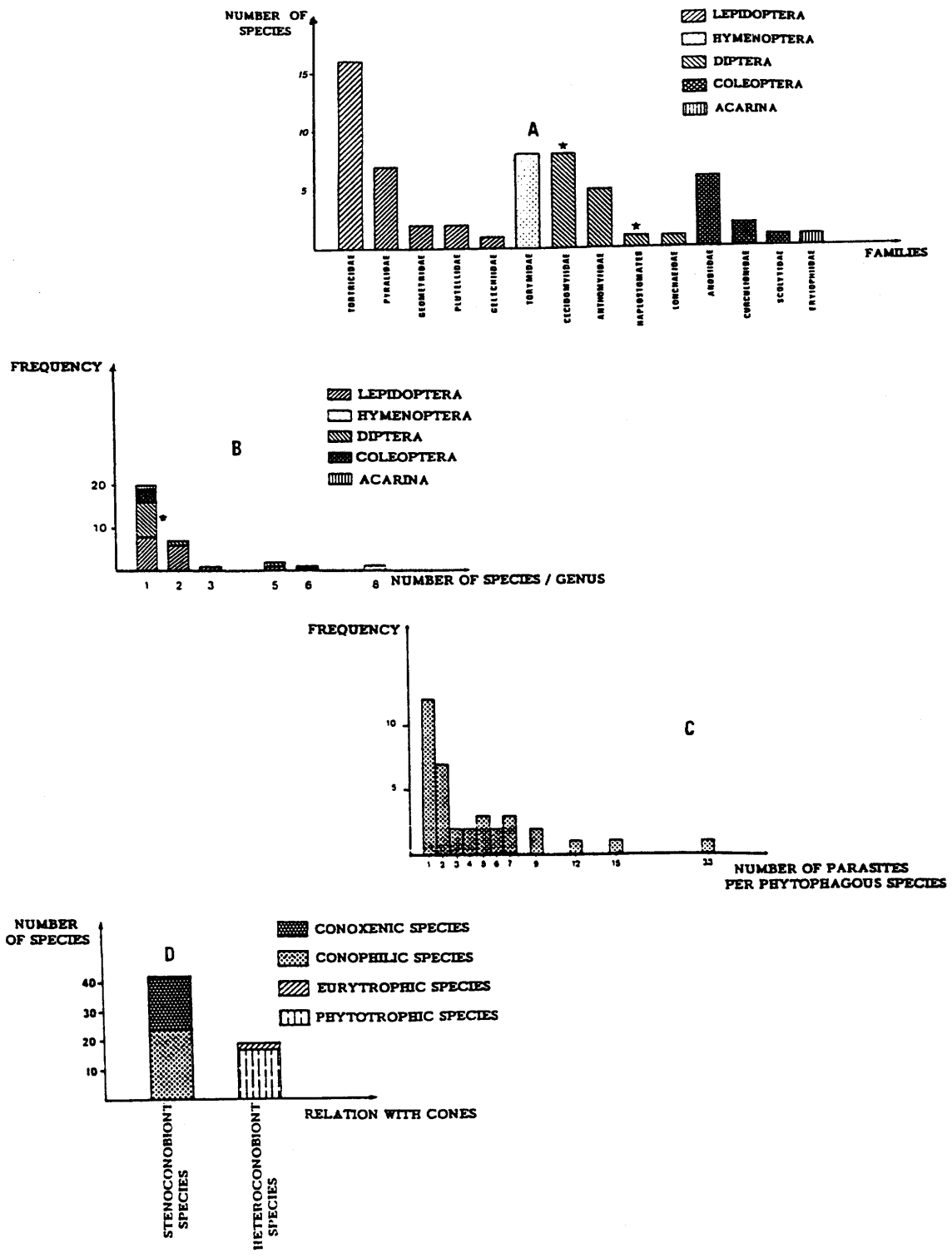


Figure 1. Faunal characteristics of insect guilds related to cones in western Europe: a) families and orders involved in phytophagous and detritivore species (* 1 detritivore species), b) extent of speciation within phytophagous genera (* 2 genera with 1 detritivore species), c) frequency of entomophagous species per phytophagous species, and d) specificity to cones and developmental features shown by the phytophagous and detritivore species.

in cone-insect relationships at the continental level and the present limitation of speciation processes within cones to a reduced number of genera, whose species are specializing in the exploitation of these distinct substrates (especially Anthomyiids of the genus *Strobilomyia*, Chalcids of the genus *Megastigmus*, Pyralids of the genus *Dioryctria*, and Anobiids of the genus *Ernobius*).

The guilds of phytophagous insects associated with cones include three trophic strategies by which the resource is partitioned. A first group, representing 40 percent of the insects (27/59), feeds on cone tissues as well as on seeds: conoseminiphagous insects, e.g. members of the Anthomyiid genus *Strobilomyia*, members of the tortricid genera *Barbara*, *Petrova*, *Cydia*, and *Pammene*, and the weevil *Pissodes validirostris*, among others. The second group, less important (19/59), develops only on cone tissues: conophagous insects, e.g. some members of the Pyralid genus *Dioryctria* and Argyresthiidae of the genus *Blastotere*). The third group (15/59) is specialized in seed exploitation: seminiphagous insects, e.g. members of the chalcid genera *Megastigmus* and *Torymus* and members of the Cecidomyiid genera *Plemeliella* and *Resseliella*, among others. It must be noted that all the insect species from a single genus exploit the same cone level, independently of tree species. These characteristics of the phytophagous group--diversity of families and limited speciation process related to a similar specialization in resource exploitation by species of the same genus--may be viewed as the result of an evolutionary process leading to complete utilization of the niche.

Parasite and Predator Complexes

Only 38 of the 61 phytophagous and detritivore species are presently known to have parasites and predators within cones in western Europe (data compiled by Roques in Yates 1988). One hundred twenty-two species, mainly Hymenoptera, have been identified in this group (Table 1).

The number of parasite species per host species is limited, generally fewer than 10 (Fig. 1c). It has been assumed that the cryptic nature of most cone insects underlies this phenomenon (Yates 1986). Thus the number of natural enemies observed in phytophagous insects that can feed on structures other than cones is strongly affected by the type of tissue occupied, e.g. three parasites in cones versus 20 in shoots for the pine shoot moth, *Rhyacionia buoliana* Schiff., in the same French localities (Roques 1977).

DEGREE OF SPECIFICITY OF THE VARIOUS INSECT GROUPS

High Host Specificity for Most Phytophagous Insects

Seventy-one percent of these species, defined as stenoconobiont species (after Stadnitskii 1971), need to complete their larval development, at least in part, within cones (Fig. 1d, from Roques 1988a). More than half--the conophilic show an extreme adaptation in spending their entire larval and pupal development within cones species as opposed to the conoxenic species, which exit the cone to pupate--(Fig. 1d). All seminiphagous species exhibit this former type of development. Close adaptation to seed substrate thus appears as the result of an extreme niche specialization.

Conversely, less than one third of common phytophages, the heteroconobiont species, are able to develop in other tree structures, such as buds and shoots. Most of them (14/19) damage the cones only occasionally, when insect population density is out of proportion to the resources offered by the normal host, e.g. as in outbreaks of the larch bud moth, *Zeiraphera diniana* Guenée (Roques 1988b), and as with pine shoot moths, *Rhyacionia pinicolana* Dbld. and *Rh. buoliana* Schiff., in young stands (Roques 1977). A minority of heteroconobiont species do prefer the cones and feed occasionally on other vegetal structures. *Dioryctria mutatella* Fuchs may develop in pine shoots in case of cone crop

Table 1. Parasites and predators associated with phytophagous cone insects in western Europe

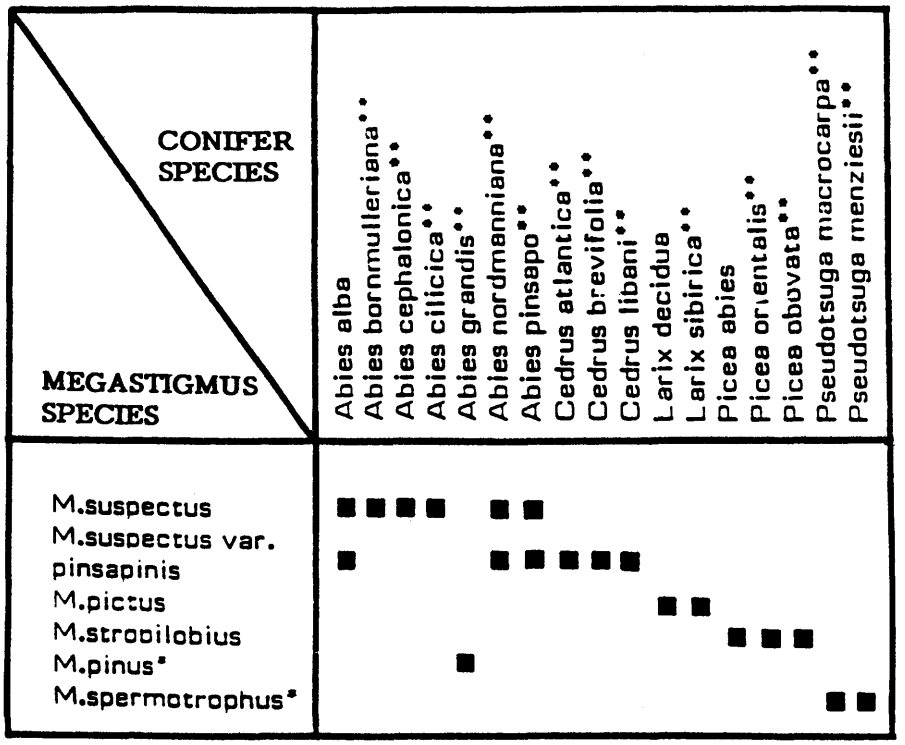
Order	Family	Number of species
Hymenoptera	Ichneumonidae	43
	Braconidae	28
	Pteromalidae	22
	Torymidae	5
	Eulophidae	4
	Eupelmidae	3
	Tetrastichidae	2
	Platygasteridae	1
	Eurytomidae	1
	Encyrtidae	1
	Trichogrammatidae	1
	Cynipidae	1
Diptera	Tachinidae	5
	Lonchaeidae (predator)	2
Neuroptera	Chrysopidae (predator)	1
	Rhaphidiidae (predator)	2

failure (Charles and Roques 1977). This certainly confers an adaptive advantage upon these latter species, allowing their populations to minimize the consequences of irregular cone crops.

Despite appearances, however, no European cone and seed insect species is entirely host-specific. The apparent specificity observed in western Europe results from the present range of conifers in this geographical region, where in several cases only one species per genus survived after Quaternary glaciations, e.g. *Larix*, *Picea*, and *Abies*.

The example of the *Megastigmus* species is significant. The speciation process is highly developed in this genus as compared with other cone insects, resulting in seven native species, to which, subsequently, four species introduced from North America have been added (Roques 1983). Larvae of these chalcids developing entirely in seeds are completely at the mercy of host selection pressure, with no possibility of escape (Labeyrie 1977). Therefore, conifer taxa may be assumed to serve as platforms for adaptive radiation of *Megastigmus*, insect species ultimately mirroring conifer speciation. Such a process is observed, but with a substantial evolutionary lag. Native conifer species in western Europe are each attacked by a single *Megastigmus* species, with the exception of *Pinus* spp., in relation to which disappearance with glaciations probably explains the absence of chalcids (Roques 1988a). However, where sympatric stands of congeneric host species exist, e.g. *Juniperus* spp. in central and mediterranean France, they are colonized by the same chalcid species (Roques et al. 1984). In addition, records in arboreta where exotic and native tree species are mixed show that each *Megastigmus* species is still capable of attacking allopatric Eurasian congeners of the natural host (Table 2), whereas these allopatric species are colonized by other chalcid species in their native areas. Similar results have been obtained with most other cone insects, e.g. *Strobilomyia* spp. and *Cydia* spp. (Roques 1983). Host specificity thus remains at a superspecific level, though local adaptive differences in insect populations probably exist.

Table 2. Host range of *Megastigmus* species observed within seeds of native and exotic species growing at the Arboretum des Barres (France)



* Insect species introduced along with host species
** Introduced host species

High Phenological Synchrony with Cones

There is close phenological coincidence of attack period in phytophagous insects with the appearance of unique, ephemeral stages in cone development. This is observed in all conifer species (Roques 1983, Roques et al. 1984). Most phytophagous insects are univoltine species, apart from some *Dioryctria* spp. (Roques 1983), and close synchrony in attack period is probably an adaptation to structural changes occurring within the cone which differentiate it from other tree structures, especially buds and shoots.

Fig. 2, based on the homology in cone development observed in western conifers, presents a synthesis of colonization of successive cone development phases by the 59 European phytophages. The stenoconobiont core of cone entomofauna is essentially recruited during cone growth and onset of seed development, when physical and chemical changes are both more substantial and more rapid. By contrast, previous and subsequent development phases, during which cones may be less distinct from surrounding tree structures, are dominated by heteroconobiont species.

Fig. 2 also shows the decrease in conoxenic species, due to successive departures from the cone, after the completion of cone growth. This may be considered an "evasion" strategy (sensu Zwölfer 1982), minimizing intra- and interspecific competition for limited cone resources.

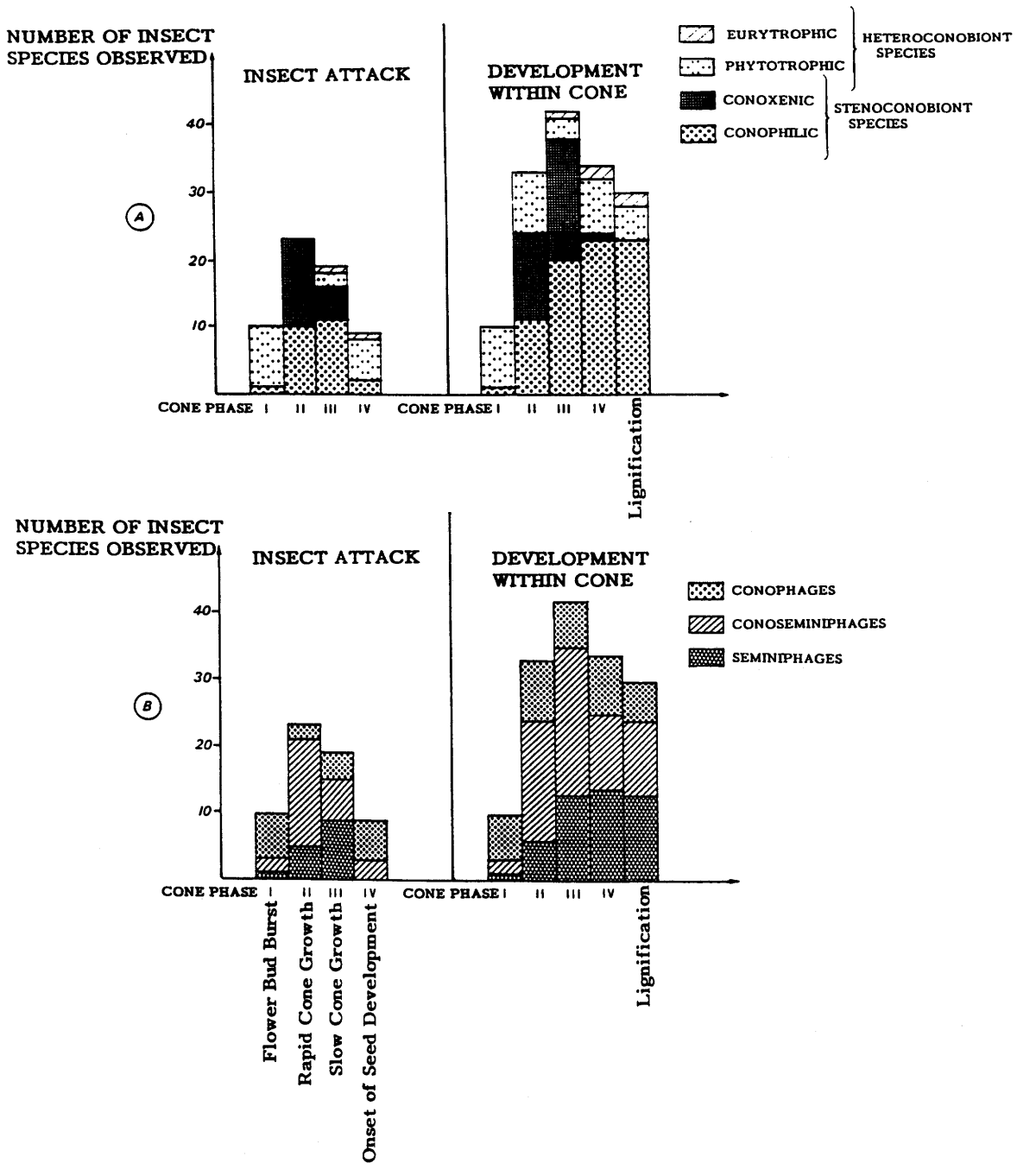


Figure 2. Patterns of cone colonization by the phytophagous and detritivore guilds during cone development as a function of a) host specificity and b) trophic level. Calculations based on the 61 species commonly observed in cones in western Europe.

Comparative Polyphagy of Etomophages and Phytophages

In *P. silvestris*, for instance, 14 of the 15 entomophages, whose cone insect host is identified, also prey on insects from other structures of scots pines (trunk, shoots, buds) or insects developing in the cones of other tree species (Roques 1988a). Similar relationships have been established in larch (Roques 1988b) and spruce (Stadnitskii 1971). More generally, at least 80 of the 122 entomophages (i.e. 66 percent) recorded in cones in western Europe show alternate hosts that do not develop in cones. Only a few chalcids of the genera *Mesopolobus*, *Anogmus*, *Amblymerus* (Pteromalidae), *Eupelmus* (Eupelmidae), and *Torymus* (Torymidae) seem specialized for the attack of seminiphagous insects. Polyphagy of entomophages effectively decreases from conophagous to seed insects, in relation to the increasing specialization of hosts (Roques 1988a).

The parasite speciation process in adaptation to phytophagous hosts thus appears to be more delayed than phytophage adaptation to conifers. Several factors may be involved. Differences in parasite complexes in regard to the plant substrate have previously been noted in heteroconobiont species. A substantial similarity is also observed in some phytophagous species of the same genus colonizing various tree structures, e.g. *Pissodes* spp. (Mills and Fisher 1986). It can be assumed that the parasite complex evolved from preadapted entomophages of these other insects. The slow progress of this process can be inferred from the variations in parasitism rate observed when a phytophagous cone insect colonizes a new introduced host. *P. validirostris* Gyll. immediately adapted to cones of *Pinus contorta* when this tree species was introduced into Europe. However, *Pissodes* parasites apparently faced barriers in locating their normal host in an introduced conifer. Parasitism levels remain low in *P. contorta* (2 percent versus 40 percent in *P. silvestris*) in Finland (Annila 1976) as well as in France (Delplanque et al. 1988). Parasite colonization thus apparently requires adaptation to both phytophagous host and cone host.

CONSEQUENCES FOR GUILD STRUCTURE AND EVOLUTION

Analogies in Cone Phytophage Succession in Native Tree Species

Similar specializations in cone resources are shown by congeneric insect species with respect to the synchrony of insect attack period with cone development; this results in a relative similarity of faunal structure within each native conifer species. Three main groups, within which fauna are homologous, are clearly distinguishable (Fig. 3).

Pinaceae with annual seed-cone development (i.e. *Picea abies*, *L. decidua*, *A. alba*) show quite homothetic fauna where distinct insect species from the same families (and often from the same genus) colonize the same cone development stages in four successive attack periods.

Although tree species fauna also appear homologous, insect families and genera colonizing Juniperaceae are quite different from the previous ones. In addition, sympatric *Juniperus* spp. (*J. communis* and *J. nana* in northern areas versus *J. oxycedrus* and *J. phoenicea* in mediterranean areas) have common fauna. The peculiar case of *J. thurifera* will be considered further on.

Pinaceae with superannual seed-cone development (i.e. *Pinus* spp.) have comparatively fewer cone phytophages and their fauna are more dissimilar. Three subgroups can be delimited: pine species of the *silvestris* group (*P. silvestris*, *P. nigra*, *P. uncinata*, *P. mugo*), mediterranean pines (*P. pinea*, *P. pinaster*, *P. halepensis*), and *P. cembra* (subgenus *strobus*). The single common component among these species is the occurrence of *Dioryctria* spp. (Pyralidae) and, in the two former groups, the weevil, *Pissodes validirostris*. The latter tree species is colonized only by three nonspecialized insects.

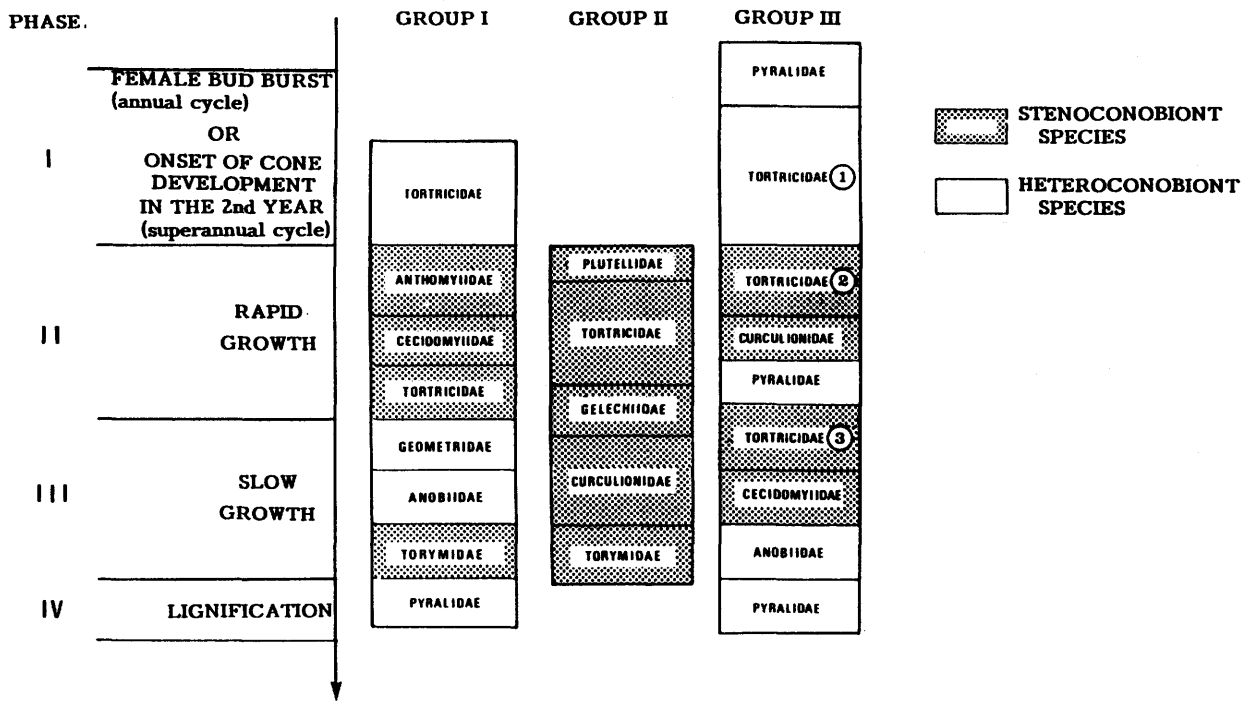


Figure 3. Classification of conifer species native in western Europe as a function of homologies seen in successive attacks of insect and mite families during cone development. Group I: Pinaceae with annual seed-cone development; Group II: Juniperaceae; Group III: Pinaceae with superannual seed-cone development.

The magnitude of the differences between groups with respect to the structural regularity within each group suggests a common origin for the fauna occupying cones of conifer species from groups with similar reproductive cycles. The insect fauna occurring at present may be the result of a further parallel diversification within each group.

Variation in Phytophage Guild with Tree Species and Stands

The total number of phytophagous species recorded in western Europe (species richness) varies with tree species, irrespective of cone size (Fig. 4a). However, an analysis of the respective contributions of stenoconobiont and heteroconobiont insects to species richness leads me to group tree species in a way similar to that above (Fig. 4b).

This confirms the existence of similarities or links in the colonization process within each of these groups. Pinaceae other than *Pinus* spp. show the largest diversity in cone insects, including a majority of stenoconobiont species. Juniperaceae have fewer species, but all are specialized in cones. Mediterranean pines and pines of the *silvestris* section are clearly separated, specific characteristics of the former being close to Juniperaceae. Fauna of the latter subgroup, though more diverse, is less closely adapted (50 percent of heteroconobiont species). Last of all, *Pinus cembra* appears similar to most introduced species: it is characterized by very low colonization, mainly by heteroconobiont species.

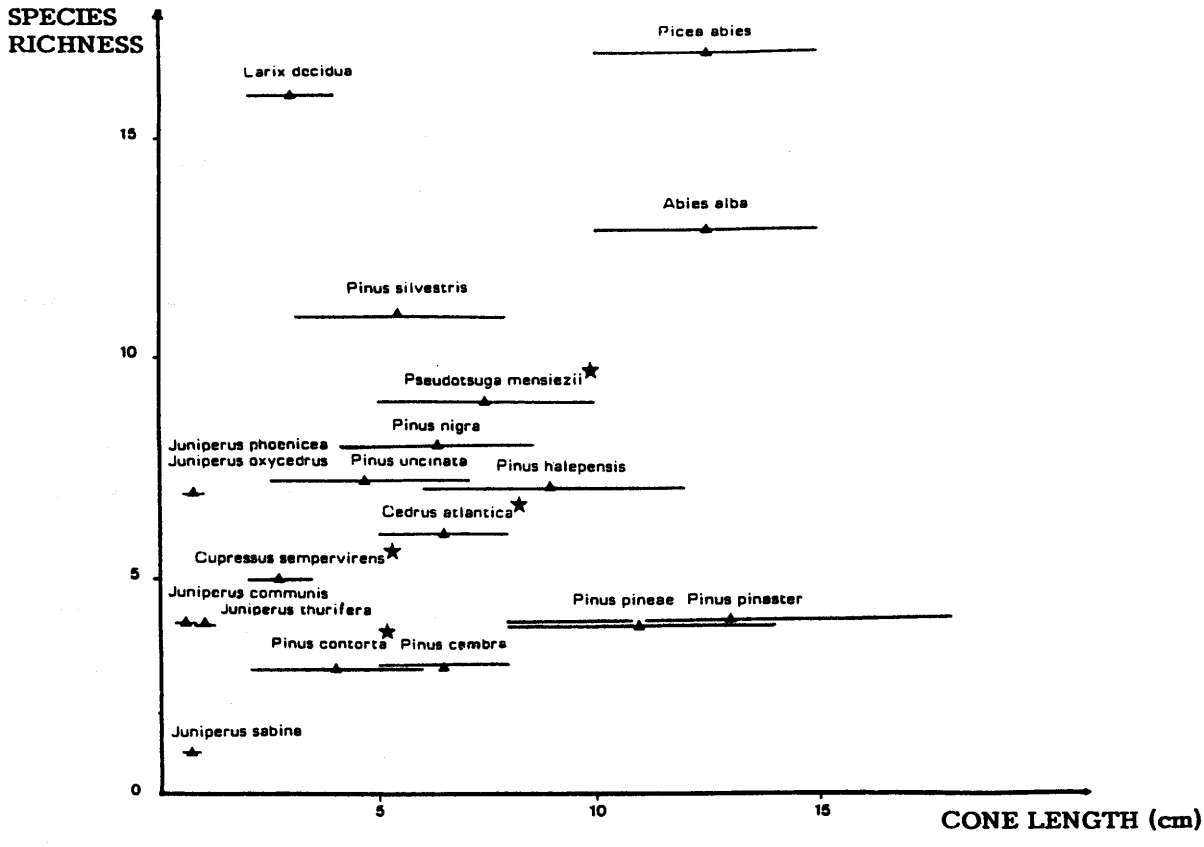


Figure 4. Species richness in phytophagous guilds related to cones in western Europe: a) relation with cone length and b) respective contribution of stenoconobiont vs. heteroconobiont species. *Introduced conifer species.

However, species richness provides a biased view of relationships between tree species and insect guilds by hiding possible variation with geographical range. When species packing (i.e. the number of species recorded in a given stand under standard sample collections) is the measure used, such variation appears in most conifers (Fig. 5).

Interspecific variation within a given area does not seem significantly related to the date of first reappearance of tree species after Quaternary glaciations, at least in French regions where sufficient paleobotanical data are available (Roques 1988a).

Conversely, intraspecific variation within tree ranges appears related to species reappearance in a species like *Picea abies*, which has a continuous distribution (Fig. 6). Species packing varies along a gradient following the postglaciation development of spruce from eastern Europe. The relative importance of closely adapted insects decreases from the location of the secondary evolution center of *P. abies*; Zwölfer (1987) noticed a similar pattern in thistle-head phytophagous guilds. The asymptotic curve indicates that insect evolutionary delay is limited in regard to host range expansion. When this progress is continuous, the faunal composition, including very specialized seed insects, can occur in less than 2,000 years. This development lasts longer in isolated stands of human creation, such as in the Pyrénées (Fig. 6). First colonization is, nevertheless, carried out by a certain number of insect species that are cone-specialized without being tree-specific. Faunal recruitment consequently results from

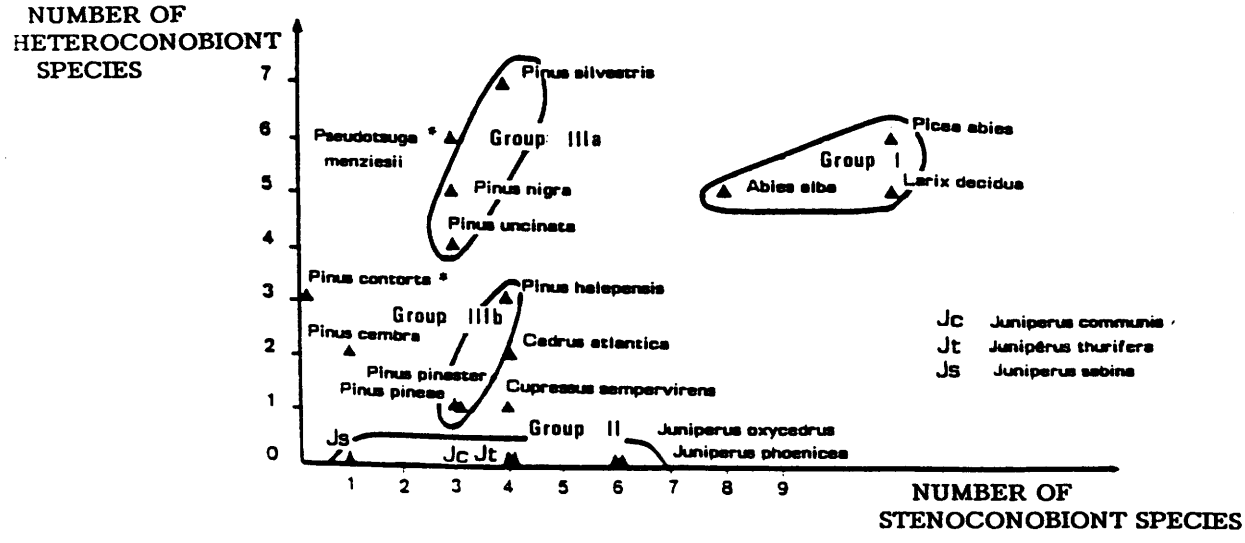


Figure 5. Variations in species packing of phytophagous guilds observed within cones through the natural range of four conifer species. Species packing is indicated by numbers within circles, host range by either hatching or points.

development of preadapted insects in cones of native conifer species. Early occurrence of insect species more adapted to tree species may be explained by insect flight capacity relative to stand isolation, ornamental trees being "relays" for the spread of insects, as shown for Douglas-fir (Roques 1986) and mediterranean cypress (Roques and Raimbault 1986).

Observations in species showing a relictual natural range following Quaternary glaciations confirm these results. In *J. thurifera* and *P. cembra*, cone fauna probably disappeared partially or completely during that period. Fig. 7 presents their respective recolonization patterns (from data in Roques 1983, Roques et al. 1984). In *J. thurifera*, differences among species result from local recruitment of insects occupying similar cone structures in either northern or mediterranean junipers, depending on stand location. In *P. cembra*, the recolonization progresses from insects observed on other sympatric conifers of genera *Pinus* and *Picea*, one of them, *Cecidomyia pini*, feeding on other structures than cone (i.e. foliage) in the usual host. Nevertheless, this last process has barely begun, no conoseminiphagous or seminiphagous (i.e. specialized) insects having been observed.

In introduced tree species, relative taxonomic isolation--number of congeneric species in the area of introduction (Zwölfer 1982)--also plays a decisive role in the rapidity of insect colonization. Exotic species without native European congeners (e.g. *Pseudotsuga*, *Tsuga*, *Sequoia*, *Cryptomeria*, *Chamaecyparis*, and others), or even without taxonomically close species in the same genus in some cases (pines of the *strobus* section), generally show a majority of conophagous insects (Roques 1983, 1988a). The conoseminiphagous minority is observed to include heteroconobiont or ubiquitous stenoconobiont species related to the insect genera commonly found in cones in the tree's native area. No seminiphagous insects are noted, except when *Megastigmus* chalcids have been introduced along with the host. Conversely, the phytophagous guild is much more complete in *Pinus contorta* or Asian spruce species: specialized insects passing to these new hosts from taxonomically close European pines of the *silvestris* section and from Norway spruce, respectively (Roques 1983 1988a).

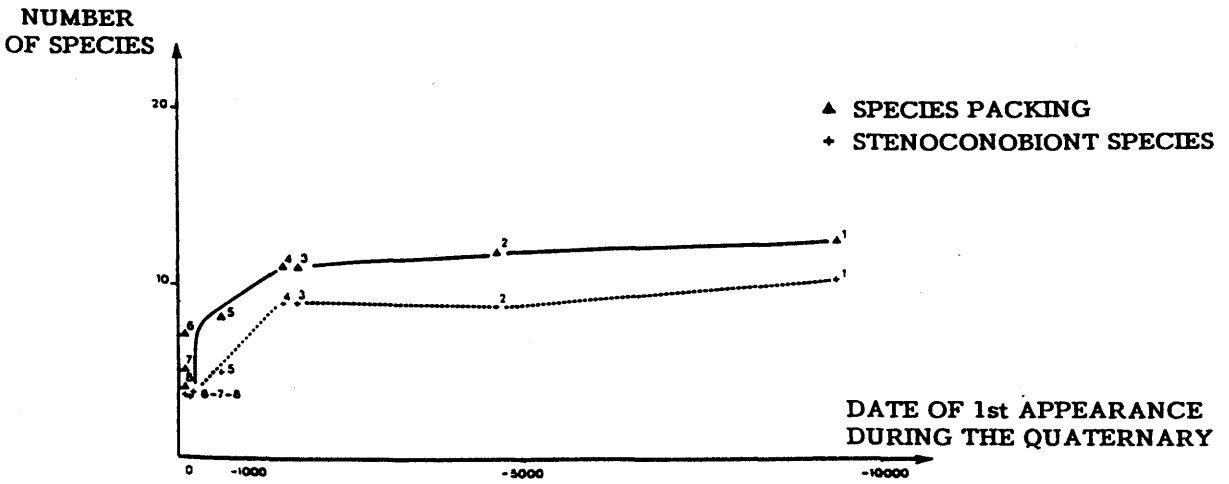


Figure 6. Relationships of species packing and host specificity in the phytophage guild of cones of *Picea abies* with the date of reappearance of this tree species during the Quaternary era in several regions of Europe: 1) Polish Carpathians (from Skrzypczynska 1982), 2) Upper Adige (from Del Favero and Masutti 1974), 3) Maurienne Valley, 4) Briançonnais, 5) Vosges; 6) southwestern France, 7) western Pyrénées, and 8) Fontainebleau Forest (from Roques 1983).

CONCLUDING REMARKS

The structure and composition of the phytophagous cone and seed insect guilds, the most characteristic among cone insects in western Europe, thus appear to result from an adaptive process which began largely before the Quaternary era. I have previously discussed the assumption of a common original fauna colonizing the new cone niche based on its presumed appearance during the lower Carboniferous period in conifer ancestors, the Cordaitales, from nonspecialized insects feeding on other tree structures (Roques 1988a). Though this idea remains highly questionable, the present results clearly suggest a common colonization during the Tertiary era, at least in Pinaceae and Juniperaceae. From these fauna three distinct patterns of phytophagous guilds would have evolved through adaptation to the different length of vegetative reproductive cycle, followed by parallel diversification in regard to increasing cone specialization. It must be noted, however, that the current situation may be substantially distorted because it results from an evolutionary process that involved many conifer species and genera that are now extinct in Europe--10,000 gymnosperm species existing in the Cretaceous period as opposed to the 600 existing today, according to Wieland (in Gaussen 1955).

From this point of view, the present heteroconobiont species may be considered precursors of future new stenoconobiont species, but the large dominance of this latter group in phytophagous guilds also indicates that the niche may be full in native tree species. The current range of host acceptance in stenoconobiont species shows, however, the probable direction of the actual evolution of phytophages related to cones: new species diversification through adaptation to a single host in response to relative geographic isolation in many conifers in western Europe.

Evident similarities in structure and functioning are noticeable when one compares cone insect guilds to those of other habitats characterized by limitation in space and time, especially the thistle-heads, as described by Zwölfer (1979, 1982, 1987, 1988). In the two cases, insect specialization

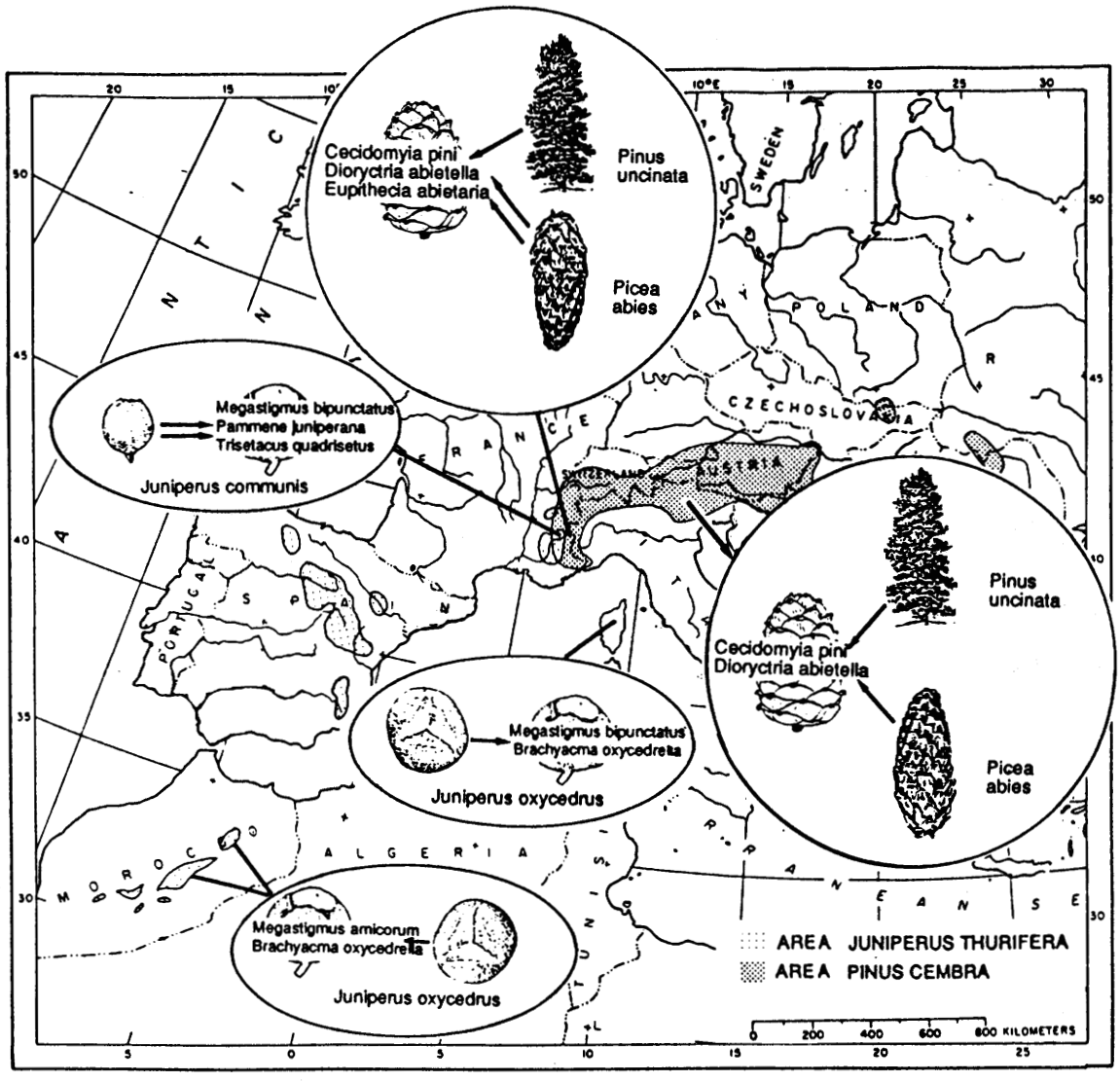


Figure 7. Recruitment of new cone phytophages in certain parts of the range of *Pinus cembra* and *Juniperus thurifera* from preadapted fauna of related sympatric conifer species.

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is directly associated with the occurrence of evasion strategies minimizing competition for limited food resources. Thus cone-insect systems are similarly observed to include partitioning of cone space, both by insect specialization in specific cone structures and by limitation in the number of competitors for the same structure, and sharing of time by adaptive differentiation of both arrival and exit of insect species (Rappaport and Volney 1986). However, this system faces an additional limit in food resources imposed by annual crop fluctuations, which do not occur to this extent in other systems. The latter evasion strategies are ineffectual when cones do not exist over large areas.

Other adaptive mechanisms, especially prolonged diapause, have been shown to allow the survival of insect species depending on cone occurrence (Bakke 1963). It is particularly interesting to note that prolonged diapause is not only limited to stenoconobiont species (at least 55 percent show it,

to our present knowledge), but this phenomenon is also more effective in insect species attacking conifers with an annual seed-cone development (Roques 1989). This confirms the existence of previous differences in faunal evolution pattern. Prolonged diapause is also a general characteristic of seminiphagous insects, emphasizing the occurrence of seed-insects as "indicators" of the current status of phytophage guild specialization in each tree species.

Particular relationships between the cones and the remaining forest biocenosis are initiated by the consequences of the following factors: insect evolutionary delay in regard to conifer speciation and occurrence of heteroconobiont species and dominant polyphagy in entomophages. Cones, then, constitute a nutritional reservoir for insects damaging other tree structures as well as corresponding to a potential reservoir of alternate hosts for parasites and predators commonly found in the biocenosis. Cones also develop in competition with other vegetal structures for the consumption of photosynthesis products (Kozlowski 1971). These interrelations imply that no intrinsic regulation can exist at quantitative levels in cone-insect systems considered separately from the biocenosis, though the qualitative composition of cone entomofauna depends mainly on cone development. The definition of merocenosis, as used by Balogh (1958), has previously been proposed to qualify such a functioning in the case of *Pinus silvestris* (Roques 1977). Concordant data recorded in other species (Roques 1988a) suggest that the notion of merocenosis can be generalized to insect guilds related to cones in each native conifer.

SUMMARY

Cones can be regarded as dynamic plant microunits, with both limited lifespan and size and highly variable spatial and temporal distribution. Fifty-nine phytophages, two detritivores, and 122 entomophages have been regularly observed to develop within cones in western Europe. Entomofauna structure in native conifer species is characterized essentially by phytophagous guilds highly specialized in cone utilization, the other insect groups being mainly polyphagous. However, specialization shown by most phytophages appears delayed in regard to the evolution of conifers, each insect species being still capable of attacking cones of congeneric tree species. Possible origin, evolution, and direction of future diversification of fauna in further adaptation to hosts are discussed. Finally, entomofauna related to each conifer species is defined as a merocenosis, whose regulation is under the control of forest biocenosis.

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