

PROJECT UPDATE: ARTHROPODS OF THE BOREAL ZONE

A review of the insects of the boreal zone has been completed, and some salient conclusions from that review¹ are summarized below. They provide potential points of departure for studies of the boreal fauna of Canada. The final section of this update considers possibilities for the Biological Survey's boreal project.

The boreal zone

The boreal zone, comprising in its restricted sense the closed coniferous forest of the same name which covers 2.6×10^6 km² in Canada, has short summers and long, very cold winters. It supports simple coniferous forests with some deciduous tree associates and an understory of mainly ericaceous, lichen and moss species. Such a forest of similar appearance occurs over vast areas, but includes an unexpected diversity of terrestrial habitats produced by terrain differences and disturbance, interspersed with abundant aquatic habitats of many kinds. Although the forest trees contain much structural material, productivity of the zone is only low to moderate. The forest changes from south to north by a decrease in broadleaf and increase in coniferous trees and a decrease in tree height and canopy density.

The insect fauna

The insect fauna of the boreal zone is richer in the south than in the north. Even in the southern part, however, faunal diversity of these cool temperate systems is relatively limited. Nonetheless, the zone as a whole is estimated to contain about 22,000 insect species. Its taxonomic structure is determined by the prevalence of northern groups, because many taxa of southern affinities are absent.

Many boreal species are very widely distributed. About half have transcontinental ranges, and may occur also in forested habitats in the western mountains south of the boreal zone. Nearly one-tenth of boreal species appear to be holarctic. However, the most noteworthy feature of the boreal fauna as a whole is that a large number of the species found in the zone are not characteristically boreal. Few species that occur there are strictly confined to it. Many of the forms not confined to that zone are generalist species from widespread habitats; others reach their limit of distribution in the boreal zone, even though centred elsewhere. The distributional limits are imposed in several different ways, suggesting that most boreal insects respond individually to conditions through the zone, each species exploiting the resources for which it is best suited. There is no collective response of some type of "boreal community". Such a pattern can also be detected for plants, many of which enter part but not all of the boreal forest in south-north or east-west directions. The conclusion that distributions chiefly reflect the different responses of individual species parallels ideas on the Pleistocene history and development of past and present North American coniferous forests, in which displacements of component organisms appear to have been largely independent of one another.

Although the distributions of many species only partly coincide with the boreal zone, many particular species are predictably encountered when boreal habitats are sampled. The

¹ Danks, H.V. and R.G. Footitt. 1989. Insects of the boreal zone of Canada. *Can. Ent.* 121(8): 625-690.

majority live in distinctive boreal habitats such as peatlands, or (like spruce- or pine-feeding bugs, moths and beetles) are associated with transcontinental boreal food plants.

The boreal fauna originated chiefly from species that survived Pleistocene glaciations in habitats to the south, notably the northern United States. Insufficient evidence is available for most species to show whether current ecological conditions or lack of time since deglaciation contribute more to the present ranges of species in this fauna, but the scanty evidence available suggests that ecological influences are at least as significant as historical ones.

Ecosystem features

Characteristics of the boreal zone, notably the long cold winters and the reduced diversity of resources, favour certain adaptations. For example, the short growing season is reflected by the prevalence of univoltine species. Insects survive the winters by cold hardiness and dormancies. Species from disturbed habitats disperse widely. The limited diversity of resources is confirmed by the fact that the food range of some groups of herbivores is wider than in their southern relatives.

Boreal ecosystem relationships are complex, especially relative to the arctic. Numerous associations among insects, and between insects and other organisms, have been demonstrated. However, some evidence suggests that the structure of northern biotic communities might depend more on the tolerance of individual species than on interactions among the species.

Two ecological elements of the zone are especially striking: the great extent and wide distribution of similar habitats, which is reflected in wide distributions; and the remarkable spatial and temporal heterogeneity of these habitats, maintained by microtopographic, edaphic and environmental diversity and by disturbance and other factors. Fire and seasonal flooding are especially influential.

In view of such spatial and temporal complexity, the diversity of interactions with abiotic and biotic factors, and the prevalence of data that correlate with rather than explain population changes, our current failure fully to understand the population dynamics of boreal insects such as the spruce budworm is not surprising, because many factors probably combine to determine the population of a given species at a given time and place. Moreover, frequency of disturbance, coupled with cold climates, may explain why "ruderal" and "stress-tolerating" species appear from preliminary information on life history adaptations to be at least as prevalent as "competitive" species in boreal faunas, although "competitive" species might normally be expected to dominate forests of long-lived plants.

Future research needs

Information on insects of the boreal and subarctic zones, which together occupy nearly half of the area of Canada, is limited and piecemeal. In particular, biological information on most boreal species, even those of economic importance, has been reported in detail only from southern transition zones, and needs to be compared with data collected in the mid-boreal itself, where climates are more severe and biotic diversity is lower.

The ecological dynamism of the boreal zone suggests that the zone can best be understood through long-term and wide-scale investigations. Most previous work has not been done in this way. Studies of the effects of climatic change on the fauna would be instructive from this long-term perspective, but in most areas even a basic description of the insect faunas of given sample sites is not available.

Resources for study are not unlimited. Therefore, finite coordinated projects that aim toward a published synthesis are most useful. Such projects can be organized from taxonomic, habitat, ecosystem or regional perspectives.

General taxonomic work is required to assess diversity and allow identification in large and important but very inadequately known groups such as mites and parasitic Hymenoptera. Many species in aquatic groups such as chironomids cannot be identified especially in the immature stages normally encountered. Useful detailed taxonomic and morphometric work would assess transcontinental and other patterns of intraspecific variation (especially in relation to host-plant use, for example), and analyze selected species complexes that might give further insight into the evolution of differences among species. It is already apparent that the differentiation of taxa in western montane habitats, isolated by topographic and other differences, and with a different Pleistocene history, is much greater than in most transcontinental boreal forms.

The faunas of soils and of peatlands, two of the most extensive boreal habitats, have not been studied in detail. The boreal soil fauna differs from that of more southern areas by the absence or reduction of several groups of insects as well as other invertebrates, so that oribatid mites and fly larvae are especially important to the fertility of northern forest soils. Basic taxonomic work and basic ecological information are lacking for most of these species. Larval descriptions and adult associations have not been made for most of the fly species, although species of several dozen families of Diptera are associated with trees.

The heterogeneity of boreal habitats and the key role of disturbance in shaping them suggests that a focus upon adaptations such as long distance dispersal, adaptations to spring spates and flooding of terrestrial habitats, attraction to fires, and group effects that favour rapid colonization (as in bark beetles) would be useful.

Current understanding of boreal ecosystem processes, such as trophic structure, stability, and population dynamics, are based chiefly on holistic theoretical ideas, on extensive rather than intensive field observations, and on analogies from species studied elsewhere. Few analyses stem from detailed information on large numbers of co-occurring species, or from properly replicated field experiments. Even when considerable amounts of data are available, few of the conclusions are unassailable because so many of them depend merely on correlations (e.g. of population outbreaks with a particular ecological factor).

The structure of boreal systems could be assessed by focussing on guilds of species (herbivores, predators, parasitoids, etc) associated with particular widely distributed boreal plant species such as jack pine, white spruce or black spruce. Very little is known about the biology of "non-outbreak" species and their natural enemies on these trees, nor about the true specificity or polyphagy of many of the herbivores and most of the natural enemy species. A meaningful analysis, as opposed to an over-generalized model, of the nature and possible control of community structure requires specific biological information. Such information could be consolidated by a concentrated approach to the structure of selected guilds. This approach would be feasible because it has a clear focus and because synopses of the frequent herbivores on the dominant boreal trees are already available.

Studies of certain regions of the boreal zone might be especially instructive. For example, information from Newfoundland, isolated by a sea passage from the main continental landmass, have indicated how current ecological factors largely appear to determine the current fauna

except in groups with limited dispersal abilities, where historical factors may be more important. Such indications could be pursued by wider comparisons of mainland and Newfoundland representatives.

In summary, the differences among groups, together with the huge scale of the zone and its dynamism and complexity, suggest that the nature of the boreal fauna can be assessed only by studying a wide taxonomic and ecological range of species. Hence results will not be satisfactory if efforts are superficial or fragmented. By the same token, sufficiently substantial and coordinated study of the insects of the boreal zone will provide very interesting information to a wide range of entomologists.

The Survey's boreal project

The themes that emerge from this review of the boreal zone show that a project on the arthropods of that zone should be long-term and wide-scale in scope. The Biological Survey has been supporting the idea of a project that would concentrate on a particular guild of arthropods, such as phytophagous insects and mites and their natural enemies on a host-plant typical of the boreal zone. Jack pine (*Pinus banksiana*) and white spruce (*Picea glauca*) are the most typical and widespread conifers in the zone and also are of particular interest for forestry. In addition, these conifer species have been studied extensively by systematists and population geneticists, providing information on biology, morphology, genetic variation, and chemistry. Consequently, there is a good base of knowledge on taxonomic variation in these plants. Detailed studies of associated insects could therefore be used very profitably in the analysis of patterns of diversity, host utilization and variation on a broad geographical or regional basis. For example, there is considerable interest in the study of variation and diversity of phytophagous insects in regions of hybridization among pine species, such as the zones of hybridization between *P. banksiana* and *P. contorta* in Canada.

Interest in the insects of the boreal zone is growing, but considerably more input will be needed to develop an appropriate boreal project, requiring not only the interest of individual systematists and ecologists, but also the determination of those interested in Canadian forestry to profit from more broadly based cooperative studies. The Survey is coordinating interest in the themes already identified, and we invite your expressions of interest and your ideas on the form that a specific project should take. Points to consider are the scientific basis for the project, your particular participation, and the form (e.g. symposium, publication) in which results will be synthesized.