

Ecological biogeography: its history in Finland and recent trends

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Ecological biogeographers study biogeographical patterns in relation to ecological processes causing these patterns. While introducing the special issue “Trends in Ecological Biogeography” of *Annales Zoologici Fennici*, the history of Finnish ecological biogeography is also briefly reviewed. Instead of exhausting the pool of potential references the discussion is delimited to studies that serve as relevant landmarks even at present. Issues in ecological zoogeography related to concepts such as environmental heterogeneity, dispersal and interspecific interactions are discussed more thoroughly. Another typical feature of Finnish biogeography is an emphasis on quantitative data.

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1. Ecological biogeography as a non-discipline

Biogeography has been regarded as a strange discipline (Nelson 1978), as it usually has neither chairs nor departments, not even many specialized journals. Yet the subject is fundamental: the causal explanation of species distribution patterns on Earth. One of the reasons for this non-status of biogeography may be that it is an interface of many other disciplines, such as traditional zoology and botany, evolutionary studies, ecology, taxonomy and systematics, and geography (Udvardy 1969).

One of the thrusts in recent biogeography has been the development in the interface of ecology and biogeography, i.e., the interface of ecology and a discipline that is an interface in itself. We believe that it would be justified to regard ecological biogeography as a non-discipline on this basis alone. It is a very living non-discipline though.

One of the stepping stones towards modern ecological biogeography was undoubtedly MacArthur's and Wilson's (1967) theory of island biogeography. This monograph has affected much of recent ecology and biogeography. In the preface to their book MacArthur and Wilson stated that during the course of their work they had come to realize that ecology and biogeography merge so that they were “unable to see any distinction between biogeography and ecolog-

gy”. One of the spin-off effects of their monograph was to stimulate studies in new fields such as conservation biology and ecology of populations living in patchy environments.

In this special issue of *Annales Zoologici Fennici* we use the term “ecological biogeography” to denote the study of biogeographical patterns in relation to ecological processes causing these patterns. In this sense *The Theory of Island Biogeography* (MacArthur & Wilson 1967) was very much ecological biogeography: the basic patterns studied were species-area relationships and species distributions on islands, but the causal processes involved were ecological, such as stochastic demography, interspecific interactions, dispersal and the ecology of colonization.

One of the problems in ecological biogeography is that it assumes that biogeographical patterns can be reduced to ecological processes. Because in some instances history and in others the spatial and temporal scales of the study are important and lead to differences in emphasis (Hengeveld 1982 and this issue, Wiens et al. 1986), a true reduction is not always possible.

The origin of this issue traces back to a Nordic event that had a non-macarthur-wilsonian (not necessarily anti-) tenet: a *Nordic Council for Ecology* course for graduate students on ‘non-island biogeography’. As the organizers of the course, we wished to

call attention to aspects of ecological biogeography that had often been neglected in the recent decades of (island) biogeography. Our original idea about emphasizing mainland areas has now matured towards emphasizing the totality where islands also play a role, but even in island biogeography there are many concepts and ideas that deserve emphasis besides the equilibrium theory and its associates (see the last article in this issue; see also Haila et al. 1982, Haila 1983, Niemelä et al. 1985, 1987). We believe that the balance of this issue, as regards the whole non-discipline of ecological biogeography, is now better than the scope of our "non-course" was. Perhaps we learnt, and thanks go to the Nordic Council for Ecology and the Academy of Finland for economical support.

2. Finnish ecological biogeography

Patriots as we are, the question why a course on ecological zoogeography in Finland should lead to an international collection of papers on the topic in a Finnish zoological journal has little personal interest to us: it just seems so obvious. Less obvious reasons for non-believers will be examined below.

Fennoscandia is one of the places on Earth where biological history is almost trivial: the little we have is interesting — as one example we mention paleobotanical studies that have led to such fascinating syntheses as Huntley's and Birks's (1983) work on the colonization of Fennoscandia by trees, with deep implications to ecological theory and the nature of ecological communities — but 10000 years is pathetically little to capitalize on in a world where animals are about five orders of magnitude older and first plants even older. Excluding a few sporadic preglacial finds, the history of Finnish biota is *tabula rasa*: what there was, was erased by the latest glaciation. In Finland even historical biogeography thus tends to be ecological: dispersal of species to deglaciated areas (this is nothing but primary succession on a grand scale), and pulses of expansion and recession in the distribution of species, traceable to postglacial climatic fluctuations.

In the following, we review some Finnish biogeography. We exclude descriptive biogeography (for example, the many zonations of Finnish vegetation), even though good descriptions are vital to good interpretations, particularly in a field that often has to remain non-experimental (Brown & Gibson 1983:6).

We will also exclude geographical studies of intraspecific variation, as the emphasis there is often more taxonomic or evolutionary than ecological. Note, however, the remarkable coincidence of variation patterns within some species with important biogeographic boundaries in Finland (Voipio 1956; for other references, see Järvinen & Väisänen 1980), which would suggest climatic differences as the underlying causes.

Below, we will examine a number of issues in ecological biogeography that Finnish pioneers have studied in a way that is still relevant and enlightening. However, we will not provide a complete history, but rather review a few studies in greater detail (for a history of Finnish biogeography, see Voipio 1984).

2.1. Environmental heterogeneity

Much of the classic theory in ecology is based on processes operating in homogeneous environments. Among early Finnish ecological biogeographers, A. Palmgren (1948) emphasized the usefulness of the study of well-limited habitat patches. Particularly botanists have studied Finnish islands, not only because of their well-defined limits but also for their land uplift: land-uplift islands are natural experiments in primary succession that seems to follow generalizable patterns (for references, see Järvinen & Ranta, this issue).

In recent years Hanski (e.g., 1982a) has analysed spatial heterogeneity theoretically and proposed the concept of *core* and *satellite* species. Core species are widely distributed, common and abundant species, whereas satellite species are rare and sporadic. Hanski suggests that communities are composed of core and satellite species, and that interspecific competition is presumably most important among the core species. This idea emphasizes a point that is also prominent in the paper by Brown & Kurzius in this issue: species living in the same habitat and having overlapping ranges may yet rarely coexist in the same species assemblages.

Spatial heterogeneity is a major theme in this issue. Järvinen & Ranta focus on patterns found in studies of Fennoscandian islands. These islands experience pronounced seasonal variation as compared with more oceanic and more southern islands that have been mostly studied when applying the theory of island biogeography. Moreover, the biota on Fennoscandian islands are young (many of the is-

lands have emerged from the sea thousands of years after the deglaciation), so problems of endemism do not generally arise.

Spatial heterogeneity also plays an essential role in the analysis by Haila et al. These authors compare the bird species assemblages breeding in the contiguous taiga of the western Palearctic with the assemblages found in isolated European coniferous forests south of the taiga. Another large-scale forest system is examined by Salo (see also Salo et al. 1986): the Amazonian rainforest. Salo examines critically the evidence for the proposed Pleistocene refugia, and he finds the support quite unsatisfactory. He proposes (see particularly Salo et al. 1986) that an abiotic process — namely, river dynamics — causes considerable spatial heterogeneity in western Amazonia at least. Thus, a major cause of rainforest diversity there would be caused by processes operating in the ecological time scale.

Finally, spatial heterogeneity is one of the key issues in Hengeveld's paper analysing the problem of scale — both spatial and temporal — in ecology. One of the fundamental trends in recent ecological biogeography is undoubtedly a focus on patterns typical of heterogeneous environments. This is clearly a realistic emphasis.

2.2. Dispersal

Classifying dispersal as an ecological factor in biogeography is not straightforward. Here we do not mean sweepstake dispersal, nor dispersal of organisms from one tectonic plate to another. Rather, we mean short distances, fair chances and dispersal from one species assemblage to another, fairly similar one, over an ecological time scale (see, e.g., Haila 1983). Of course, such dispersal is implied in the idea of heterogeneous environments: a patchy environment without interpatch dispersal would be a collection of homogeneous isolates.

One of the truly original ideas in Finnish ecological biogeography is due to A. Palmgren (1915–17, 1922). He observed in his studies of the vascular plants of wooded meadows on the Åland Islands that the area of the wooded meadows helps to predict the number of plant species present (Järvinen 1982a gives more details), but the exact species composition varies from one area to another. One of the reasons for this variation is the role that chance plays in dispersal: on a first-come, first-served basis, priority ef-

fect is important — the late arrivals are not able to compete effectively with the species already established.

Means of dispersal also account for the distribution of many species in Finland, as shown by Palmén (1944) in his monograph on the anemohydrochorous dispersal of insects. Anthropochorous dispersal of plants explains the distribution of many plants (Linkola 1931; see also Hanski 1982b). The debate on the dispersal history of glacial immigrant crustaceans (Segerstråle 1956) is now settled, and the key role of ice-dammed, or proglacial, waters as dispersal paths are now generally recognized (Segerstråle 1957, 1982, Holmquist 1966).

It would be incorrect to label the study of dispersal as a recent trend in ecological biogeography, except in the sense that dispersal is one of the perennial problems in ecological biogeography and will always be a modern topic to consider. So it is no wonder that many papers of this issue discuss dispersal. Interspecific or intraspecific differences in dispersal ability form an ingredient in the papers by (Hengeveld and Järvinen & Ranta), and problems of dispersal are an important component in the patterns revealed by Brown & Kurzius in their study of desert rodents. In a metaphorical sense, dispersal is an important element in the review by Tahvanainen & Niemelä, for it seems that, for herbivores, taxonomic relatedness among the host plants affects the utilization probability of new hosts in the same sense as distance affects the colonization probability of new areas.

2.3. Interspecific interactions

Many of our above remarks have touched the role of interspecific interactions in ecological biogeography. Particularly interspecific competition of plants has been attributed a major role in many papers in Finnish ecological biogeography. Pioneers in primary succession are poorer competitors than species establishing later (e.g., A. Palmgren 1912; see also the review of successional patterns in the Baltic archipelagoes by Järvinen & Ranta in this issue).

A. Palmgren (1915–17), as mentioned above, regarded priority effect as important in the structuring of the plant communities he studied. His conclusions were remarkable: because of the priority effect, late arrivals are excluded, and therefore species number is stabilized. This is a theory about equilibrium species numbers in isolated habitats 50 years prior to

MacArthur & Wilson (1967), but the equilibrium Palmgren envisioned was not dynamic, but rather static. If species turnover is often due to very small populations contributing relatively little to the total numbers of individuals of all species (for a Fennoscandian example, see Järvinen & Ulfstrand 1980), A. Palmgren's view may offer interesting insights. Palmgren also pointed out that the explanation he offered leads to distributions where species are lacking from suitable habitats because they did not happen to reach the site early enough. He was thus very early in emphasizing the role of chance elements in biogeography (A. Palmgren 1929).

Another remarkable achievement by A. Palmgren, related to interspecific interactions, was that he was the first to observe that the species-to-genus ratio (or, as it was then used, its inverse) is not a valid indicator of the intensity of interspecific competition, but decisively affected by sample size (A. Palmgren 1925; for a history of the repeated discovery of this fact, see Järvinen 1982b).

In zoogeography, interspecific competition was seen as an important process in the range fluctuations of some northern and southern species. For example, Merikallio (1951) regarded the fluctuation of two *Fringilla* finches in terms of interspecific competition; the fluctuating boundary of the two species was determined by climatic changes (but see Järvinen & Väisänen 1979). The main tendency in Finland, however, has been to examine ecological biogeography from an autecological standpoint, often in terms of abiotic factors, such as temperature, snow cover, etc. An environment where this is particularly evident is the Baltic Sea, which is very species poor along the Finnish coasts. Here the distribution limits of species have been connected with salinity gradients quite convincingly (Segerstråle 1951, 1965; for plants, see Luther 1951). The adversity of the climate has also been often invoked. For example, Luther (1961) attributed a great deal of species turnover of vascular plants on Baltic islands to frequent summer droughts. An economically important aspect of ecological biogeography in Finland is the ecological limitation of the northern tree line. Here climate again seems of paramount importance (Hustich 1961). Climatic adversity in the north was also invoked by Järvinen (1979), who found that several parameters characterizing bird species assemblages show particularly large values in Northern Europe.

In this issue interspecific interactions have a prominent place, for one whole section is devoted to them. Connor & Bowers review the literature on the

spatial consequences of interspecific competition. Competition is a major topic also in the paper by Brown & Kurzius. These authors include coevolutionary aspects, as do also Tahvanainen & Niemelä in their review of the biogeography of herbivore-plant interactions.

We regard this section as a good example of recent trends in ecological biogeography, even if the biogeographic potential of interspecific interactions has been recognized very early. However, the present criteria for establishing the role of interspecific interactions, both in the ecological time scale and in terms of coevolution, have developed greatly during the last decade and are now much more rigorous than before (Futuyma & Slatkin 1983, Simberloff 1983, Boucher 1985; for other references, see Connor & Bowers, this issue). The development is reflected both in the analysis techniques and in conceptual issues related to methodology (hypothesis testing, etc.).

2.4. Range fluctuations

Range fluctuations are a speciality of Finnish ecological biogeography (see Mayr 1970:301). Early work (e.g., Siivonen & Kalela 1937, Kalela 1949, Hustich 1952, Kaisila 1962) stressed the role of the recent climatic amelioration in the causation of range fluctuations, but more recently the role of human-caused habitat changes has been the prevailing paradigm (Hustich 1978; for examples and references to the literature, see von Haartman 1973, Helle & Järvinen 1986). One of the impressive examples in this vein is the monograph by Stjernberg (1979) on a cardueline finch, *Carpodacus erythrinus*. Stjernberg showed, based on a long-term study of population ecology, that the dramatic range expansion of *Carpodacus* in recent decades can be traced to the increased reproductive success of the species in the new, human-made breeding habitat (see also Stjernberg 1985).

We regret that this collection of papers has little to offer in this field, even if the importance of range fluctuations cannot be questioned. On the other hand, Finnish authors have published on this theme abundantly in recent years and also reviewed much of the literature, so we did not feel that a new review would now be necessary (for additional references, see Järvinen 1981, Väisänen et al. 1986; the latter paper and Helle & Järvinen 1986 also consider the implications that scale problems have in interpreting long-term range and population changes).

2.5. Quantitative approach

A final aspect that we will discuss is the quantitative approach to ecological biogeography. Biogeography becomes easily a science based on interpreting mapped distributions of organisms, but, in ecological biogeography at least, the causative ecological processes are related to population numbers. Quantitative studies have been typical of Finnish ecology for a long time (P. Palmgren 1930, Krogerus 1932, Renkonen 1938, Platonoff 1943, Levander & Purasjoki 1947, Lindberg 1948, Kontkanen 1950, Meriläinen 1967 are just a few noteworthy examples). One frequently quoted classic is Renkonen (1938, 1944, see also Kontkanen 1957), who proposed the percentage similarity index that is still widely used in ecological and biogeographical comparisons. Voipio (1984) also emphasized the importance of quantitative studies in his history of Finnish biogeography.

Finnish quantitative ecology, however, has had a distinctly biogeographical flavour for a relatively short time only. The earlier approach was rather community ecological, or if there was a biogeographical problem, the work tended to be descriptive rather than focusing on the causative ecological processes. Exceptions in this field are several early papers on range fluctuations (above).

We definitely regard the quantitative approach as very important among recent trends in ecological biogeography (see also Pielou 1979). The review by Birks on methodology is useful for all those approaching biogeographical problems quantitatively. In order to emphasize the importance of the topic we have started the whole issue with his paper. Many

papers in this issue employ quantitative analysis techniques that would have been unthinkable in the pre-computer era, but are irreplaceable in the analysis of large and complicated data sets, typical in biogeography.

Another aspect of quantitateness is also abundantly present in this issue: counts of individuals as opposed to interpretations of distribution maps. The major theme in the paper by Haila et al. is the often dramatic contrast between presence-absence and census data in interpreting biogeographical patterns. Also, the major conclusions by Brown & Kurzius depend on quantitative sampling of rodent populations in the field; their conclusions would be entirely different if based on maps only. Quantitative sampling is also essential in the analyses by Hengeveld.

We have offered these glimpses into the history of Finnish ecological biogeography in order to give the reader an idea of some of the important ideas of the past in relation to trends that are now topical in the field. In many aspects there is a continuity from the past to the present, but, of course, there has been much development. Perhaps the review also shows that not all current ideas were unknown in the past, but a careful study of the classics may provide useful insights.

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