

Reversed latitudinal gradient in species richness of sawflies (Hymenoptera, Symphyta)

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In several taxa regional species richness typically decreases towards the poles. However, the species richness of Old World sawflies (Hymenoptera, Symphyta) shows the opposite latitudinal trend, so that species richness is highest in the north. Among the forest-dwelling insect groups, aphids also make a similar exception to the general pattern. We examine the hypothesis put forward by Dixon et al. (1987) on the reversed gradient of aphids. Both sawflies and aphids are highly host-specific, which is in accordance with the hypothesis. However, other life history traits of sawflies do not fit Dixon et al.'s hypothesis. We propose that the increase in sawfly species richness is due to the increase in the diverse community of their principal host plant group, the *Salix* species. In general, the groups with high species richness in a particular area should deserve special attention in an analysis of diversity and ecosystem properties and functioning. It is possible that sawflies form such a group in northern boreal forests.

1. Introduction

Latitudinal trends in species richness have received a lot of attention from ecologists since the first observations made by Wallace (Wallace 1878). He stated that generally species richness — or the luxuriance of life — is highest in the tropics and decreases towards the poles. Since

then this observation has been verified separately for several invertebrate, vertebrate and plant groups, like snakes, birds, ants (Dobzhansky 1950, Fischer 1960, Kusnezov 1957), lizards (Pianka 1983), vascular plants (Lahti et al. 1988) and tree species (Currie & Paquin 1987). Causes of this general latitudinal variation have been discussed several times (e.g. (Begon et al. 1986, Currie & Fritz 1993, Pianka 1966, Turner et al. 1987), but a general explanation of the phenomenon is still quite obscure.

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Recently, Rohde (1992) made an attempt at offering a primary cause or general explanation for the latitudinal variation in species richness. After reviewing the hypothesis and supporting evidence Rohde found that most of the explanations and reasoning in this area are open to criticism. He found, however, that only differences in the amount of solar energy seem to be consistently linked with species richness. This applied not only to the latitudinal variation but also to altitudinal variation and variation along a depth gradient in aquatic systems. The possible mechanisms that relate solar energy to species richness are as yet unknown, but Rohde (1992) proposed that solar energy may affect generation times, mutation rates and selection so that these will be higher at higher temperatures.

Although these patterns in species richness provide us with empirical data to show the generality of the phenomenon, the exceptions to the general rule may provide some insight into the underlying mechanisms. It is interesting to note that exceptions to the general rule have so far received very little attention (Järvinen & Sammalisto 1976, Järvinen et al. 1987).

In this paper we analyze latitudinal species richness of sawflies (Hymenoptera, Symphyta), and in particular we compare the observed to that found among aphids (Dixon et al. 1987) and peatland birds (Järvinen et al. 1987). Basically, Dixon et al. (1987) proposed that certain peculiarities in the life-histories of aphids make them less numerous in the tropics. For another group, Finnish peatland birds, Järvinen et al. (1987) claimed that the preponderance of exceptionally favourable breeding habitat is connected to reversed species richness. We will compare sawfly species richness to these two established exceptions from the general pattern.

We also have another aim. In the context of conservation biology and especially in view of the recent emphasis on biodiversity, we ought to know what species or species groups are globally characteristic to different regions, and what may be the causes of these patterns. Especially in terms of community organization and ecosystem functioning the groups whose density or species richness are high in a particular area deserve special attention.

2. Material and methods

To analyze geographical variation in the species richness of sawflies we used published data from the Old World. To analyze the relationship of sawfly species and host plant species we gathered data on plant species as well. This restricted our analysis to eight areas or countries from the tropics to around 67°N. Thus, the area coverage was quite adequate. The sources of data are listed in Table 1. All the species in the group Symphyta were included in our analysis.

Since species richness is correlated typically with the area, we corrected the number of species in each country so that they are more comparable. We used the equation

$$S_{\text{corr}} = S_{\text{orig}} / A^z$$

where S_{corr} is the corrected number of species per 1000 km², S_{orig} is the number of species reported from the country, and A is the area of the country; z is constant in the typical exponential species-area relationship. It was assumed to be 0.25 for both plants and sawflies. This is based on the general finding that $z = 0.25$ in several taxa (Dixon et al. 1987, MacArthur & Wilson 1967).

Table 1. Countries or regions, their areas (1000 km²), numbers of plant species (flowering plants and gymnosperms) and numbers of sawfly species.

Country	Area	Plants	Sawflies
Britain	245	1550	ca. 500
Finland	338	1040	710
Latvia	64	1205	404
Central Germany	100	2000	432
Balkan Peninsula	271	4900	237
Asiatic Turkey	780	8472	370
Cyprus	9	1650	33
Africa (Ethiopian region)	18000	21 000	156

Sources of data: Plants: Hämet-Ahti et al. 1986, World Conservation Monitoring Centre 1992. Sawflies: Britain (Quinlan & Gauld 1981), Finland (Viitasaari & Vikberg 1985), Latvia (Cinovskij 1953), Central Germany (Weiffenbach 1985), Balkan Peninsula (Hellén 1967), Asiatic Turkey (Benson 1968), Cyprus (Schedl & Kraus 1988), Africa (Malaise 1945).

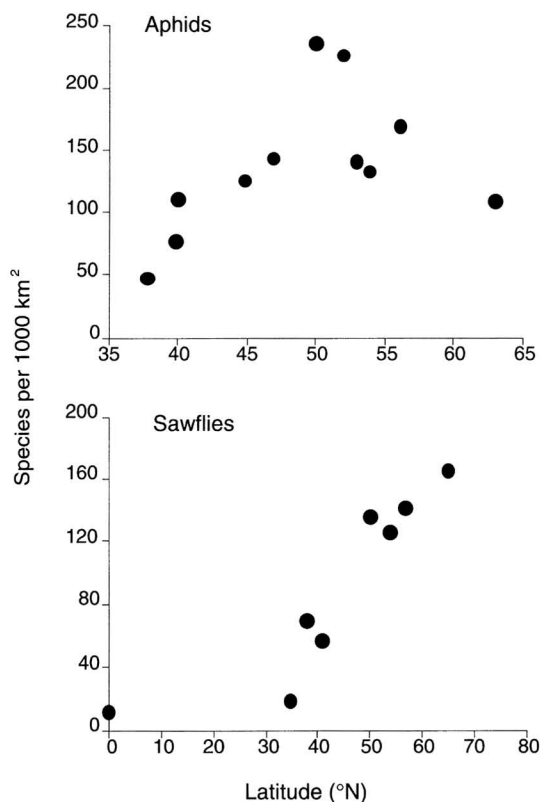


Fig. 1. Latitudinal variation in species richness (calculated per 1000 km²) of aphids and sawflies. Data for aphids is from (Dixon et al. 1987)

3. Results and discussion

We found that sawfly and aphid species richness clearly increases from tropical to polar regions (Fig. 1). We also found that the ratio of sawflies to number of plant species is similar to that among aphids (Fig. 2), i.e. there is a negative exponential relationship between the number of plant species and ratio of sawfly species to plant species richness. Hence, the latitudinal gradient of sawflies is a clear exception to that generally found among other terrestrial organisms.

Since Dixon et al. (1987) found a seemingly similar pattern among aphids, we will next review the mechanism proposed by Dixon et al. and examine whether a similar mechanism is likely to be involved in the explanation of sawfly richness variation. Basically, Dixon et al. argued

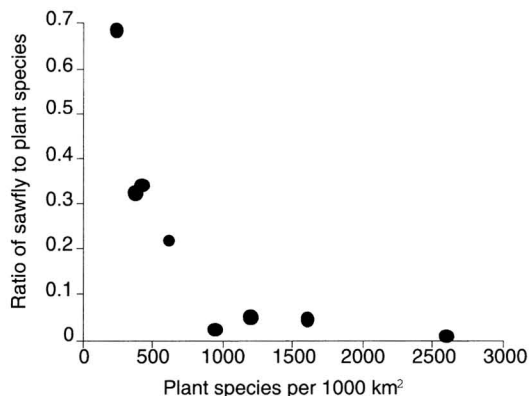


Fig. 2. Ratio of no. of sawfly species to number of plant species per 1000 km².

that three specific characteristics of aphids and their host plants affect the reversed latitudinal decrease in species richness. First, the high degree of host specificity of aphids is crucial. Second, aphids have low efficiency in locating their host plants. Third, aphids cannot survive long periods separated from their host plants, since their particular life-history and fast growth rate requires a continuous supply of resources. Aphids are exceptional animals in the sense that they commit simultaneously to growth and reproduction. From these observations it follows that only common species are likely hosts for aphids. This is simply because the areal range of rare species is usually so limited that aphids cannot locate and utilize them. Thus, we should find fewer aphid species when most of the plants are regionally rare, and this is what we might expect in the tropics (Dixon et al. 1987).

There is one notable similarity among sawflies and aphids: both groups are highly host-specific (for sawflies see Neuvonen & Niemelä 1983), and this is in clear contrast to, for example, macrolepidopteran species (Neuvonen & Niemelä 1983, Niemelä 1983). Life-styles of sawflies and aphids, however, differ in several ways. Since sawflies do not commit simultaneously to growth and reproduction, it is not necessary for them to locate host plants as rapidly as aphids should. Host locating efficiency in sawflies is generally unknown but, for example, *Pristiphora erichsonii*

seems to be able to locate even the most isolated larch (*Larix*) hosts in Finland (P. Niemelä, pers. observ.). This suggests that the sawflies' ability to locate hosts may be better than among aphids. Thus we find Dixon et al.'s (1987) explanation to be unlikely for geographical variation in species richness among sawflies.

Because there are generally more potential host plant species near the tropics we are left with the question of why there are more sawflies in the north and whether this host specificity is linked to a reversed richness gradient. To explain the reverse gradient we should look at the available resource base and — since sawflies are typically monophagous — especially resource diversity. Sawflies generally feed on woody plants (Haack & Mattson 1993). Numerically the most widely used plant group are willows (*Salix* spp.) (Haack & Mattson 1993, Neuvonen & Niemelä 1983), but *Betula* species also harbour several sawflies.

The geographical ranges of several *Salix*-species usually extend high up in the north (Haack & Mattson 1993, Jalas & Suominen 1976) thus permitting the occurrence of several sawflies at these latitudes. But in addition to this several *Salix* species occur only at northern latitudes, thus permitting the occurrence of several host-specific sawflies. We thus propose that the reversed latitudinal gradient of sawflies could be due to an exceptional increase in both the abundance and diversity of their most important host plant, the genus *Salix* at northern latitudes (see also Haack & Mattson 1993).

However, this is not a genuine solution to the reversed gradient since it effectively transfers the problem only one level down: why, then, are there so many *Salix* species in the north? It is very common for several *Salix* species to hybridize with each other at northern latitudes (Jalas 1965, Kallio et al. 1975, Price & Roininen 1993). There are probably two ecological reasons for this. First, different *Salix* species tend to occur in the same habitats in the north whereas in the south their habitats may be distinct. Second, the flowering period is shorter in the north, and consequently several *Salix* species flower simultaneously. This permits cross-pollination of different species and makes hybridization more common. We therefore suggest that speciation in *Salix* may be exceptionally common in the north and

this makes the speciation of monophagous *Salix* living sawflies more likely.

Rohde (1992) suggested that, due to high temperature, generation times may be shorter and mutation rates may be higher close to the equator. Even though this may be likely among several groups, the short growing season in the north may also cause increased rate of speciation by compressing flowering time and increasing the probability of interspecific hybridization. The effects of this are most likely manifested also in the upper trophic level but only when herbivores are exceptionally monophagous.

Why sawflies are extremely host-specific (Neuvonen & Niemelä 1983) and why they are host-specific to the *Salix* group in particular, however, still remains open to discussion. The great diversity of northern sawflies is especially due to the diversity of the group Nematinae. In this subfamily there are several parthenogenetic species groups that seem to be extremely host-specific. It is possible that some of these groups are currently undergoing fast speciation. As an example, we can quote the *Amauronematus fallax* (Lepelletier) species group that is taxonomically easily distinguished as a group. This group includes numerous specialized taxa. The different taxa feed mainly on *Salix*, but at least one species group feeds on *Betula*, one on *Potentilla fruticosa* and another on *Vaccinium* (A. Zinojev & M. Viitasaari, unpubl. observ.). Why the *A. fallax* group — among others — has not radiated more extensively to other plant genera remains obscure.

Our explanation is that the second most important host genus, *Betula*, also has a similar pattern of speciation, albeit perhaps to a lesser degree. Unfortunately, *Betula* hosts far fewer sawflies (Neuvonen & Niemelä 1983), thus making testing of this prediction less than satisfying. However, it is interesting to note that plant taxonomists separate only three different birch species. Yet sawflies discriminate even between different sub-species. For example, *Dineura virididorsata* (Symphyta, Tenthredinidae) is specialized only on mountain birch *B. pubescens* ssp. *tortuosa* in Lapland. It is also known that birch species commonly hybridize (Kallio & Mäkinen 1978, Kallio et al. 1983).

One reason for the recent concern about the biodiversity crisis (Wilson 1988, Wilson 1992)

stems from the largely unknown relationship between diversity and ecosystem functioning (Lawton & Brown 1993, Solbrig 1991, Solbrig 1992). It is hypothesized that diversity and ecological redundancy in ecological systems may be essential for the proper functioning of ecosystems (Haila & Kouki 1994). From the ecosystem function point of view, groups that are common or moderately common may be the most important ones, since they comprise the highest proportion of community biomass and, thus, the majority of energy and matter fluxes may flow through these species. Both aphids and sawflies are probably very important components of the boreal forests, but for different reasons: aphids often have mutualistic relationships with ants, and ants on the other hand may affect species richness and basic ecological processes in several other groups. Sawflies are probably essential resources for several vertebrate and invertebrate predators. In terms of biodiversity conservation and ecosystem functioning these groups deserve special attention.

In conclusion, the northward increase in sawfly species richness is most likely explained by an increase in the resource richness of this particular group, and our explanation is thus similar to that proposed for the reversed latitudinal gradient of Finnish peatland birds (Järvinen et al. 1987). The increase in resource diversity, for example in species richness in *Salix* species, on the other hand, is most likely due to peculiar characteristics of the host plant genus and seasonal effects of the environment. We further point out that due to their high diversity at northern latitudes sawflies may be an especially important group in terms of ecosystem functioning.

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