Adaptive radiation into ecological niches with eruptive dynamics: a comparison of tenthredinid and diprionid sawflies

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Summary

1. We tested the hypothesis that the bottom-up influence of coniferous plant resources promotes the probability of outbreak or eruptive dynamics in sawflies. The literature was examined for three geographical regions – North America north of Mexico, Europe and Japan.

2. In each region tenthredinid sawflies (Hymenoptera: Tenthredinidae) were significantly more likely to be eruptive on conifers than on angiosperms.

3. The diprionid sawflies (Hymenoptera: Diprionidae) that attack conifers exclusively showed a significantly higher probability of eruptive dynamics than the tenthredinid sawflies on angiosperms in two regions, North America and Europe, and in Japan the trend was in the same direction.

4. The probability of species showing eruptive dynamics on coniferous hosts was not significantly different among tenthredinids and diprionids on conifers in North America, Europe and Japan.

5. The weight of evidence supports the hypothesis of conifers supporting a higher percentage of eruptive species than angiosperms.

6. In the adaptive radiation of tenthredinid sawflies from flowering plants onto conifers, larches (*Larix*) appear to be particularly favourable for colonization, but pines (*Pinus*) have not been colonized in any region, a pattern likely to be explained by the growth characteristics of the host plants.

7. Among tenthredinid species in Europe, where sawfly/host relationships are best known, there is a significant trend for an increasing proportion of outbreaking species from herbs, to shrubs, to trees.

8. The results indicate for the first time the strong bottom-up effects of plant resources on the population dynamics of sawflies, involving general features of host plant taxa and growth characteristics.

Key-words: Diprionidae, Hymenoptera, insect herbivore population dynamics, plant resources, Tenthredinidae.

Introduction

During the process of adaptive radiation some species appear to enter into ecological niches that result in eruptive population dynamics, while others are more latent in their dynamics. Even within the same insect family and genus, some species may be outbreak species while others remain uncommon or rare in their communities (cf. Hunter 1991, 1995a). For example, no family of forest moths (Macrolepidoptera) includes 100% of outbreaking species, or 100% of non-outbreaking species. And, while species that are well defended against natural enemies and/or are gregarious, are well represented in the outbreaking species, these

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traits are not present in all the outbreaking species (Hunter 1991, 1995a). Other characters associated frequently with eruptive dynamics are spring feeding, high fecundity, polyphagy, clustering of eggs and reduced dispersal ability (Wallner 1987; Haack & Mattson 1993; Larsson, Björkman & Kidd 1993; Hunter 1995a,b). Therefore, valuable insights may be gleaned from an examination of additional factors that might contribute to patterns of dynamics in herbivorous insects. In particular, the resources utilized by herbivores have not been emphasized in the search for patterns in eruptive species population dynamics.

The sawflies (Hymenoptera: Symphyta) show similar mixing of outbreak and latent dynamics within families and genera as in the Macrolepidoptera (Hanski & Otronen 1985; Hanski 1987; Haack & Mattson 1993; Larsson *et al.* 1993; Hunter 1995a); but a clear phylogenetic difference exists between the tenthredinid sawflies (Tenthredinidae), with a relatively small percentage of outbreak species, and the diprionid sawflies (Diprionidae), with a high number of outbreak species (Haack & Mattson 1993; Price 2003). In North America, for example, about 3% of tenthredinids on angiosperms were estimated to be eruptive species, while 40% of diprionids on conifers were calculated as outbreak species (Price 2003). The adaptive radiation of the tenthredinid sawflies has centred on the angiosperms and that of diprionid sawflies has been on conifers. Does this major distinction in resources utilized play a role in different frequencies of eruptive population dynamics?

The tenthredinids and diprionids are regarded by some as sister families (e.g. Gauld & Bolton 1996; Schulmeister 2003), or perhaps the diprionids constitute a subfamily of the Tenthredinidae (Rasnitsyn 1980), or are at least nested within the tenthredinids (Schulmeister, Wheeler & Carpenter 2002). Vilhelmsen's (2001) hypothesis showed that tenthredinids were more basal in the phylogeny than diprionids, from which we can conclude that angiosperm feeding evolved before conifer feeding. Indeed, the superfamily Tenthredinoidea, including both tenthredinid and diprionid sawflies, is thought to have radiated in the late Cretaceous, co-incident with the radiation of the angiosperms (Gauld & Bolton 1996). Therefore, during the radiation of the tenthredinoid group, expansion was perhaps first on angiosperms, followed by colonization of a new adaptive zone on conifers. However, because conifers were present long before angiosperms radiated, the lineages of tenthredinid and diprionid sawflies may not differ much in age, suggesting equal opportunity for radiation. Gauld & Bolton (1996, p. 95) suggest that the tenthredinoids 'may have been the dominant exophytic leaf-eating group of insects' during the Palaeocene and Eocene, as the Macrolepidoptera did not radiate until the Oligocene. Hence, radiation could proceed apparently unimpeded by significant competition.

The tenthredinid and diprionid sawflies share a common phylogenetic heritage, with similar morphology of the ovipositor for laying eggs into plant tissue, and precise placement of eggs into the plant substrate. Therefore, according to the Phylogenetic Constraints Hypothesis (Price *et al.* 1990; Price 2003) we may expect the same kinds of population dynamics, but this is clearly not the general case.

We test the hypothesis that it is the host plant type that results in different population dynamics, with angiosperm hosts resulting in more latent dynamics, and conifer hosts producing a higher probability of eruptive population dynamics. We test this hypothesis by examining the dynamics of tenthredinid sawflies that have colonized conifers. If plant resources are the basis for bottom-up dynamics in diprionid sawflies, they should play a similar role in the dynamics of tenthredinid sawflies on conifers. Unfortunately, the reciprocal test is not available because no pine sawflies have colonized angiosperms (Smith 1979; Haack & Mattson 1993; Larsson *et al.* 1993). Therefore, in this paper we ask the question: in the adaptive radiation of the tenthredinid sawflies, has the new adaptive zone of conifer feeding resulted in a higher probability of eruptive population dynamics than on the angiosperms? In the discussion we consider a mechanistic hypothesis to explain the shift in dynamics. We were also interested in the kinds of conifer species utilized by tenthredinids when compared to diprionids, which may reveal limits on the scope of their radiation onto conifers.

Methods

The tenthredinid and diprionid sawflies have radiated mainly in the northern hemisphere, especially in cool temperate climates. Therefore, we chose for study three geographical regions with relatively well-known sawfly faunas, host plant records and characteristics of population behaviour: North America north of Mexico, Europe and Japan. For each region we searched the literature to find the number of sawfly species in the common and pine sawflies, the numbers recorded as outbreak or pest species and, for the tenthredinids, the number of species on herbs, grasses and ferns, shrubs, angiosperm trees and gymnosperm (= coniferous) trees.

We accepted designations as outbreak or pest species provided in the literature. Outbreak species are commonly recognized in the forestry literature, which was employed by Haack & Mattson (1993) and Larsson *et al.* (1993) to summarize outbreak history for sawflies in North America and Europe. In addition, we used sources that noted garden, agricultural and orchard pests, which contributed to the list of sawflies on herbs and grasses, shrubs and other woody growth (e.g. for North America: Westcott 1973; Hill 1987; Arnett 1993; Metcalf & Metcalf 1993). The term 'pest species' has been used commonly in the literature on small-plot agriculture and gardens, in situations where angiosperm herbs and shrubs are commonly grown. We have accepted the designation in the literature as a pest species as a criterion for including with outbreak species in order to capture the full range of noticeably abundant

Table 1. Numbers of tenthredinid and diprionid species recorded in North America north of Mexico, and the numbers that are outbreak, or pest species on herbs, grasses and ferns, shrubs and trees.[1] See Appendices I and II for outbreak species and host plant genera

| Family | Total species | Species on angiosperms and pteridophytes | | Species on gymnosperms |
		Herbs, grasses and ferns	Woody plants (shrubs/trees)[2]	Trees
Tenthredinidae	789			
With known hosts, total	363	85	263 (49/214)	15
Native species	330	76	240 (44/196)	14
Introduced species	33	9	23 (5/18)	1
Unknown hosts	426			
Outbreak species, total	55 (15%)	7 (8%)[3]	41 (8/33) (16%)	7 (47%)
Native species	35 (11%)	6 (8%)	23 (6/17) (10%)	6 (43%)
Introduced species	20 (61%)	1 (11%)	18 (2/16) (78%)	1 (100%)
Diprionidae	48			
With known hosts, total	45	0	0	45
Native species	40	0	0	40
Introduced species	5	0	0	5
Outbreak species, total	23 (51%)	0	0	23 (51%)
Native species	19 (48%)	0	0	19 (48%)
Introduced species	4 (80%)	0	0	4 (80%)

[1]Sources: Arnett (1993), Baker (1972), Ball (1988), Davidson (1966), Furniss & Carolin (1977), Haack & Mattson (1993), Hill (1987), Larsson *et al.* (1993), Mattson *et al.* (1994), Metcalf & Metcalf (1993), Potter (1998), Price (1970), Smith (1979), Wallace & Cunningham (1995), Westcott (1973).

[2]Woody plants are subdivided into shrubs and trees, with numbers of species provided for each category in parentheses.

[3]Values in parentheses show the percentage of species that are outbreak/pest species within a category. For example, with 85 species of tenthredinids 'with known hosts, total' in the 'herbs and grasses' column, and seven species in the 'outbreak species, total' row, the percentage of outbreak/pest species is approximately 8%.

and therefore damaging sawflies. This may result in an underestimate of species on herbs and grasses that qualify as abundant and damaging, for many may occur on wild plants which go unnoticed and unrecorded. However, given the incredibly rich flora under domestication, we have had a major opportunity to observe pest species in managed environments. The richness of cultivated plants is documented in Bailey & Bailey (1976), which includes 20 397 species in North America North of Mexico.

Many introduced species of sawfly occur in North America (Haack & Mattson 1993; Mattson *et al.* 1994), so we kept separate records for native and introduced species as well as providing an estimate of total species in each host plant category. In Europe, many species were listed as polyphagous by Liston (1995), and could not be categorized as attacking herbaceous or woody plant species because both types were utilized. Therefore, these species were treated separately.

Statistical testing of differences in pairwise comparisons used the χ^2 test for goodness of fit between observed and expected numbers of species per category (Sokal & Rohlf 1995). Expected numbers of species assume a random distribution of probabilities of outbreak and non-outbreak species among taxonomic comparisons. A 2 × 2 matrix was employed for, as an example, the numbers of outbreaking and non-outbreaking species in tenthredinids on angiosperm woody plants vs. diprionids on conifers. In all cases the d.f. (degrees of freedom) was 1.

Results

In North America there are 789 recorded species of tenthredinid sawflies, of which 363 species have known hosts (Table 1). Of these, 55 species are considered to be outbreaking or pest species in the literature (Appendix I), or 15% of species with known hosts. However, assuming that all abundant sawflies have their host-plant species identified, then the percentage of outbreak species in all the tenthredinids is reduced to 7%. For native tenthredinid sawflies, the percentage of outbreak species is 4% of all species recorded. However, of the 15 tenthredinid species known to attack conifers, almost half are listed as outbreak species, or 47% of species. There is a dramatic and significant difference between the frequency of outbreaking or pest species in tenthredinids on angiosperms and conifers ($\chi^2 = 15.28$, $P < 0.001$).

In the diprionid sawflies, with all species confined to coniferous trees, of the 45 recorded species in North America north of Mexico, 23 (51%) are regarded as outbreak species in the literature (Table 1, Appendix II); this is if we accept that biotypes with subspecies names warrant species status, as accepted in Larsson *et al.* (1993). Among the native pine sawfly species 48% are regarded as outbreaking species.

Comparing tenthredinids on angiosperm woody plants and diprionids on conifers, the frequency of outbreaking native species is significantly higher in the diprionids ($\chi^2 = 38.66$, $P < 0.001$).

Table 2. Numbers of tenthredinid and diprionid species recorded in Europe, and the numbers that are outbreak, or pest species on herbs, grasses, ferns and mosses, and shrubs and trees.[1] See Appendices III and IV for outbreak species and host plant genera

Family	Total species	Species on angiosperms, pteridophytes and bryophytes		Species on gymnosperms	
		Herbs, grasses ferns, mosses	Woody plants (shrubs/trees)	Trees	Polyphagous species
Tenthredinidae	1011				
With known hosts, total	637	218[2]	350 (201/149)	33	36
Native species	636	218	349 (200/149)	33	36
Introduced species	1	0	1 (1/0)	0	0
Unknown hosts	374				
Outbreak species, total	103 (16%)[3]	9 (4%)	75 (32/43) (21%)	13 (39%)	6 (17%)
Native species	102 (16%)	9 (4%)	74 (31/43) (21%)	13 (39%)	6 (17%)
Introduced species	1	0 (0%)	1 (1/0) (100%)	0	0
Diprionidae	23				
With known hosts, total	19	0	0	19	
Native species	19	0	0	19	
Introduced species	0	0	0	0	
Outbreak species, total	9 (47%)	0	0	9 (47%)	
Native species	9 (47%)	0	0	9 (47%)	
Introduced species	0	0	0	0	

[1]Sources: Gauld & Bolton (1996), Hill (1987), Larsson *et al.* (1993), Pschorn-Walcher (1982), Vappula (1965), Viitasaari (2002), Wallace & Cunningham (1995).
[2]Includes 30 spp. on Pteridophytes and two spp. on mosses.
[3]As in Table 1.

In contrast, we see strong convergence in the tenthredinids on conifers toward the outbreak dynamics of diprionids, with 43% and 48% of native species in each family, respectively. In fact, the numbers of species in each family that are outbreak species are not significantly different from expected ($\chi^2 = 0.09$, NS). This result is consistent with the hypothesis that the coniferous resource base results in a higher probability of outbreak dynamics than angiosperm host plants. Entering into the conifer-feeding adaptive zone results in a dramatic shift in population characteristics for almost half the sawfly species involved.

As to be expected, eruptive species are well represented in those species that are immigrants to North America. Eruptive species are likely to be common, widespread and abundant, and therefore likely to be transported. Also, the potential for rapid increase is likely to contribute to colonizing ability, although many other factors are probably involved (Niemelä & Mattson 1996). In tenthredinids, 61% of introduced species are eruptive and in the diprionids, 80% (Table 1). As Niemelä & Mattson (1996) note, and as a comparison of Appendices I and II with Appendices III–VI show, the vast majority of introduced species have been into North America.

The 15 species of tenthredinids on conifers in North America are represented by six species on larch (*Larix*), four on juniper (*Juniperus*), three on spruce (*Picea*) and two on cypress (*Cupressus*) (Smith 1979; Haack & Mattson 1993). Four genera of sawflies are represented; *Anoplonyx*, *Pikonema*, *Pristiphora* and *Susana*, suggesting at least four independent colonizations

from angiosperms to gymnosperms in the Tenthredinidae. It is noticeable that a high proportion of species (40%) on conifers utilize larch while none have colonized pines (*Pinus*), the largest genus of conifers. Tommi Nyman (personal communication) has estimated that there have been at least five independent colonizations by tenthredinid sawflies onto *Larix* worldwide.

Results similar to those from North America were evident in Europe and Japan (Tables 2 and 3). Comparisons of tenthredinid sawflies on woody angiosperms and conifers in Europe showed 21% outbreaking native species on the angiosperms and 39% on conifers, a significant difference ($\chi^2 = 5.71$, $P < 0.02$). In Japan, the same comparison yielded a significant 28% vs. 75% difference ($\chi^2 = 7.27$, $P < 0.01$). When tenthredinids on woody angiosperms were compared with diprionids on conifers, outbreaking species were significantly higher than expected in the diprionids in Europe (21% vs. 47%, $\chi^2 = 7.00$, $P < 0.01$), but in Japan the difference was not significant, although in the hypothesized direction (28% vs. 55%, $\chi^2 = 3.27$, NS). Comparing tenthredinids on conifers with diprionids on conifers, among native sawfly species, there were no significant differences in Europe (39% vs. 47%, $\chi^2 = 0.31$, NS) or in Japan (75% vs. 55%, $\chi^2 = 0.76$, NS). The results were generally consistent with those predicted by the hypothesis that conifers, in some way, promote the development of eruptive population dynamics in sawflies.

Host genus utilization by tenthredinids on conifers in Europe and Japan were also similar to that in North

Table 3. Numbers of tenthredinid and diprionid species recorded in Japan, and the numbers that are outbreak, or pest species on herbs, grasses and ferns, and shrubs and trees.[1] All are regarded as native species. See Appendices V and VI for outbreak species and host plant genera

| Family | Total species | Species on angiosperms and pteridophytes | | Species on gymnosperms |
		Herbs, grasses and ferns (ferns)	Woody plants (shrubs/trees)	Trees
Tenthredinidae	454			
With known hosts, total	157	70 (19)	79 (41/38)	8
Unknown hosts	297			
Outbreak species, total	40 (25%)[2]	12 (17%)	22 (4/18) (28%)	6 (75%)
Diprionidae	19			
With known hosts, total	11	0	0	11
Native species	11	0	0	11
Introduced species	0	0	0	0
Outbreak species, total	6 (55%)	0	0	6 (55%)

[1]Sources: Asahina *et al.* (1965), Kobayashi & Taketani (1994), Okutani (1967a,b), Umeya & Okuda (2003), Japanese Society of Applied Entomology & Zoology (1987), Wallace & Cunningham (1995).
[2]As in footnote 3 in Table 1.

America. The host genera were *Larix* and *Picea* in Europe, and Japan (Appendices III and V). In Europe 62% of outbreaking tenthredinid species utilized *Larix* and 38% used *Picea*. In Japan, five of six outbreaking tenthredinid sawflies on conifers used *Larix*, and one exploited *Picea*. As in North America, no tenthredinids in Europe and Japan used *Pinus* as a host.

In all geographical localities tenthredinid species on herbaceous plants contributed a lower percentage of outbreak or pest species than on woody plants (in North America, 8% vs. 16%; Europe, 4% vs. 21%; Japan, 17% vs. 28%). Only in Europe was the difference significant ($\chi^2 = 31\cdot28$, $P < 0\cdot001$). However, when shrubs and trees were treated separately, in Europe herbs had a significantly lower percentage of outbreak species than shrubs (4% vs. 16%, $\chi^2 = 15\cdot69$, $P < 0\cdot001$), and trees (4% vs. 29%, $\chi^2 = 44\cdot56$, $P < 0\cdot001$) and shrubs supported significantly fewer outbreak species than trees (16% vs. 29%, $\chi^2 = 9\cdot11$, $P < 0\cdot01$). In Japan, the patterns were similar for herbs and trees (17% vs. 47%, $\chi^2 = 11\cdot07$, $P < 0\cdot001$) and shrubs and trees (10% vs. 47%, $\chi^2 = 13\cdot82$, $P < 0\cdot001$), but not for herbs and shrubs (17% vs. 10%, NS). In North America no significant differences were evident in the percentage of outbreak species on host plant types (8% vs. 14% vs. 9%). There is a suggestion that the probability of outbreaking species increases as plant architecture increases (complexity of growth form increases), particularly evident in Europe where the sawfly fauna and flora are better known (63% of sawfly species with known hosts in the Tenthredinidae, vs. 46% in North America and 35% in Japan).

The polyphagous tenthredinid species in Europe showed a relatively high percentage of outbreak species, comparable to those occurring only on woody plants (17% vs. 21%). However, woody plants are included in the records of all six species listed in Appendix

III (e.g. *Rosa*, *Rubus*, *Salix*, *Betula* and others), so a non-significant difference is not surprising.

Discussion

We are not aware of any literature that has noted the convergence of outbreak dynamics in tenthredinids and diprionids on conifers, except Price (2003). In their broad analysis of sawflies on woody plants, Haack & Mattson (1993) did not treat this subject, although they noted several traits found commonly in species that are outbreak-prone, and in their discussion of diprionids Larsson *et al.* (1993) did not note the importance of the conifer plant substrate as an influence on dynamics. Phytochemical attributes of pines were considered by Hanski & Otronen (1985), but Hanski (1987) concluded later that a case for phytochemical involvement in sawfly dynamics could not be supported (but see Larsson, Ekbom & Björkman 2000). The new perspective that we suggest, focusing on strong bottom-up effects from host plants, will help to broaden the scope of discussions on the mechanisms resulting in eruptive population dynamics and the patterns that are produced.

The most viable hypothesis to account for differences in dynamics of sawflies on angiosperms and conifers was called the Determinate Growth of Conifers Hypothesis (Price 2003). The major hosts of diprionid sawflies, *Pinus*, *Picea* and *Abies*, all have determinate growth on all shoots, defined by tissues already present in the overwintering bud (Kozlowski 1971; Kozlowski & Pallardy 1997). This permits rapid growth in the short growing season available in northern latitudes to which the conifers are adapted. For diprionid females utilizing young needles there is little time for oviposition into new, soft needles, emergence times will be brief, females are likely to be proovigenic, and lay all their eggs rapidly [During

the radiation of diprionids, oviposition into young needles appears to have been the primitive condition (Catherine Linnen, personal communication)]. Egg clusters usually contain many eggs, and the likelihood for gregarious feeding is high. There may be no ovipositional preference and larval performance linkage because females heavily laden with eggs cannot fly well (Gauld & Bolton 1996, personal observations), and do not select high quality resources for larvae (median flight duration was 8 s at 25 °C for a *Neodiprion* species (Björkman, Larsson & Bommarco 1997). The result is eruptive or outbreak dynamics because larvae evolve to eat a wide range of leaf quality. The consequence is a high carrying capacity in a forest – in fact, almost all needles in a coniferous forest can be consumed, causing death of trees after a few years (e.g. Baker 1972; Furniss & Carolin 1977). The diprionids appear to conform to the capital breeder syndrome described by Tammaru & Haukioja (1996), in which females depend for reproduction entirely on energy derived from larval feeding.

Contrasting with the conifers, angiosperms show indeterminate growth, with a longer growing period, providing more time for oviposition by sawflies. Females can evolve to be more resource selective, with synovigenic egg production, and a strong ovipositional preference for shoot qualities favourable to larval performance (e.g. Craig *et al.* 1989). Such high-quality resources are likely to be at low density, setting a low carrying capacity in the environment, and constraining populations to latent dynamics with low fluctuations in density (Price *et al.* 1990; Price 2003).

Larch appears to be particularly favourable for tenthredinid sawflies, when shifting from angiosperms. The tree is an unusual conifer, being both deciduous and having indeterminate growth of leading shoots (Kozlowski 1964; Haack & Mattson 1993). Thus, it resembles angiosperms more than other conifers, and has been colonized relatively frequently.

The lack of tenthredinid sawflies on pines may be associated with growth in *Pinus* being extremely different from that in woody angiosperms (Price 2003). Young pine needles are available for a brief period in any location because new stem growth precedes leaf elongation, after which needles develop rapidly. Also, pine needles are tough and highly resinous. In comparative studies of length of growing season, pines have been noted repeatedly as having the shortest, or among the shortest growth periods, when compared to other conifers and angiosperm trees (Kozlowski 1964), and the availability of young needles will be even shorter.

We have answered the question posed in the introduction of this paper on whether conifer feeding in sawflies is associated with a higher than expected frequency of eruptive species. In all regions examined, outbreaking tenthredinid species on conifers were significantly more frequent than expected when compared to species on angiosperm woody plants. In two of three regions, tenthredinids on angiosperms were less frequently eruptive than expected compared to

diprionids on conifers. Japan was the exception, although the trend was in the same direction as in North America and Europe. Also, in all three regions the frequency of outbreaking species of tenthredinids and diprionids on conifers was not significantly different.

The trend of a lower frequency of outbreak tenthredinid species on herbaceous plants compared to woody plants in all three regions may also be explained by host plant characteristics. Herbaceous plants are usually distributed patchily compared to woody species, and less persistent through time. Therefore, sawfly numbers are likely to remain low, and are less likely to be observed in outbreak numbers. The trend of increasing percentages of outbreak species from herbs to shrubs to trees, well illustrated in Europe, may well have a mechanistic basis in plant architecture and distribution. In North Temperate regions trees are frequently the dominant vegetation type with the highest density of primary production, providing a relatively high carrying capacity for herbivores. Tree and forest persistence also probably contribute to habitat stability and the probability of outbreaks.

As in all evolutionary scenarios, such as the Phylogenetic Constraints Hypothesis (Price 2003), what is predicted as evolutionary trends can be overridden by ecological factors in nature. Therefore, an evolutionary prediction can only hope to explain some of the outcomes. In the adaptive radiation of tenthredinid sawflies, predictions from the Phylogenetic Constraints Hypothesis are generally consistent with the data, that population dynamics of species are likely to be latent for species on angiosperms. However, the results reported here suggest how different population dynamics can become when host plant resources change dramatically. This difference should promote more careful consideration of host plant architecture and phenology when examining the adaptive radiation of insect taxa.

Acknowledgements

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Appendix I. Tenthredinid species in North America regarded as pests or outbreak species in the literature[1]

Species name	Host plant genus	Native or introduced
On herbs and grasses		
Ametastegia glabrata (Fallen)	*Rumex*	Native
Ametastegia pallipes (Spinola)	*Viola*	Native
Dolerus unicolor (= *arvensis*) (Beauvois)	Grasses	Native
Dolerus collaris Say	Grasses	Native
Empria maculata (Norton)	*Fragaria, Potentilla, Rubus*	Native
Monostegia abdominalis (Fabricius)	*Lysimachia*	Introduced
Pachynematus extensicornis (Norton)	Grasses	Native
On angiosperm shrubs		
Allantus cinctus (L.)	*Rosa*	Introduced
Cladius difformis (Panzer)	*Rosa*	Native
Endelomyia aethiops (Fabricius)	*Rosa*	Native
Erythraspides vitis (Harris)	*Vitis*	Native
Monophadnoides geniculatus (Hartig)	*Rubus*	Native
Nematus ribesii (Scopoli)	*Ribes*	Introduced
Priophorus morio (= *rubivorus*) Lepeletier	*Rubus*	Native
Pristiphora rufipes (= *pallipes*) Lepeletier	*Ribes*	Native
On angiosperm trees		
Caliroa cerasi (L.)	*Malus, Sorbus*, etc.	Introduced
Caliroa fasciata (Norton)	*Quercus*	Native
Caliroa quercuscoccineae (Dyar)	*Quercus*	Native
Caulocampus acericaulis (MacGillivray)	*Acer*	Introduced
Croesus castaneae Rohwer	*Castanea*	Native
Croesus latitarsus Norton	*Betula*	Native
Dimorphopteryx melanognathu Rohwer	*Betula*	Native
Dimorphopteryx pinguis (Norton)	*Alnus, Betula*	Native
Eriocampa ovata (L.)	*Alnus*	Introduced
Eupareophora parka (Cresson)	*Fraxinus*	Native
Fenusa dohrnii (Tischbein)	*Alnus*	Introduced
Fenusa pusilla (Lepeletier)	*Betula*	Introduced
Fenusa ulmi Sundervall	*Ulmus*	Introduced
Hemichroa crocea (Geoffroy)	*Alnus*	Introduced
Heterarthrus nemoratus (Fallen)	*Betula*	Introduced
Hoplocampa brevis (Klug)	*Pyrus*	Introduced
Hoplocampa cookie (Clarke)	*Prunus*	Native
Hoplocampa testudinea (Klug)	*Malus, Pyrus*, Crataegus, etc.	Introduced
Messa nana (Klug)	*Betula*	Introduced
Messa populifoliella (Townsend)	*Populus*	Native
Nematus limbatus Cresson	*Salix*	Native
Nematus salicisodoratus Dyar	*Salix*	Introduced
Nematus ventralis Say	*Populus, Salix*	Native
Nematus sp.	*Populus, Salix*	Native
Phyllocolpa bozemani (Cooley)	*Populus*	Native
Pontania proxima (Lepeletier)	*Salix*	Introduced
Pristiphora abbreviata (Hartig)	*Pyrus*	Introduced
Pristiphora geniculata (Hartig)	*Sorbus*	Introduced
Profenusa lucifex (Ross)	*Quercus*	Native
Profenusa thomsoni (Konow)	*Betula*	Native
Tethida cordigera (Beauvois)	*Fraxinus*	Native
Tomostethus multicinctus (Rohwer)	*Fraxinus*	Native
Trichiocampus viminalis (Fallen)	*Populus, Salix*	Introduced
On gymnosperm trees		
Anoplonyx occidens Ross	*Larix*	Native
Anoplonyx laricivorus Rohwer and Middleton	*Larix*	Native
Pikonema alaskensis (Rohwer)	*Picea*	Native
Pikonema dimmockii (Cresson)	*Picea*	Native
Pristiphora erichsonii (Hartig)	*Larix*	Introduced
Pristiphora lena Kincaid	*Picea*	Native
Susana cupressi Rohwer and Middleton	*Cupressus*	Native

[1]Sources: as in Table 1.

Appendix II. Diprionid species in North America, all on tree host plants, regarded as pests or outbreak species in the literature[1]

Species name	Host plant group	Native or introduced
Diprion similis (Hartig)	*Pinus*	Introduced
Gilpinia frutetorum (Fabricius)	*Pinus*	Introduced
Gilpinia hercyniae (Hartig)	*Picea*	Introduced
Monoctenus suffusus (Cresson)	Cupressaceae	Native
Neodiprion abietis (Harris)	Pinaceae	Native
Neodiprion autumnalis Smith	*Pinus*	Native
Neodiprion dubiosus Schedl	*Pinus*	Native
Neodiprion edulicolis Ross	*Pinus*	Native
Neodiprion excitans (Rohwer)	*Pinus*	Native
Neodiprion fulviceps (Cresson)	*Pinus*	Native
Neodiprion lecontei (Fitch)	Pinaceae	Native
Neodiprion nanulus contortae Ross	*Pinus*	Native
Neodiprion nanulus nanulus Schedl	*Pinus*	Native
Neodiprion pinetum (Norton)	*Pinus*	Native
Neodiprion pratti banksianae Rohwer	*Pinus*	Native
Neodiprion pratti paradoxicus Ross	*Pinus*	Native
Neodiprion pratti pratti (Dyar)	*Pinus*	Native
Neodiprion rugifrons Middleton	*Pinus*	Native
Neodiprion sertifer (Geoffroy)	*Pinus*	Introduced
Neodiprion swainei Middleton	*Pinus*	Native
Neodiprion taedae linearis Ross	*Pinus*	Native
Neodiprion taedae taedae Ross	*Pinus*	Native
Neodiprion tsugae Middleton	Pinaceae	Native

[1]Sources: Larsson *et al.* (1993), Mattson *et al.* (1994), Smith (1979).

Appendix III. Tenthredinid species in Europe regarded as pests or outbreak species in the literature,[1] including polyphagous species

Species name	Host plant genus
On herbs, grasses and ferns	
Ametastegia pallipes (Spinola)	*Viola*
Ametastegia equiseti (Fallén)	*Rumex*, *Plantago*, *Polygonum*
Athalia rosae (L.)	*Brassica*, *Raphanus*, etc.
Cladius difformis (Panzer)	*Fragaria*, *Filipendula*, *Rosa*
Dolerus niger (L.)	Grasses
Heptamelus ochroleucus (Stephens)	Ferns
Phymatocera aterrima (Klug)	*Polygonatum*
Pristiphora aquilegiae (Vollenhoven)	*Aquilegia*
Rhadinoceraea micans (Klug)	*Iris pseudacorus*
On angiosperm shrubs	
Apethymus apicalis (Klug)	*Rosa*
Ardis brunniventris (Hartig)	*Rosa*
Bacconematus pumilio (Konow)	*Ribes*
Blennocampa phyllocolpa Viitasaari & Vikberg	*Rosa*
Endelomyia aethiops (Fabricius)	*Rosa*
Eriocampa dorpatica Konow	*Ribes*
Eurhadinoceraea ventralis (Panzer)	*Clematis*
Euura testaceipes (Brischke)	*Salix*
Metallus albipes (Cameron)	*Rubus idaeus*
Metallus pumilus (Klug)	*Rubus idaeus*
Monardis plana (Klug)	*Rosa*
Nematus bohemani (Thomson)	*Salix*
Nematus caprea (L.)	*Salix*
Nematus coeruleocarpus Hartig	*Salix*
Nematus leucotrochus Hartig	*Ribes*
Nematus melanaspis Hartig	*Salix*, *Populus*, *Betula*
Nematus melanocephalus Hartig	*Salix*, *Betula*, *Corylus*, *Populus*
Nematus olfasciens Benson	*Ribes*
Nematus pavidus Lepeletier	*Salix*
Nematus ribesii (Scopoli)	*Ribes*
Nematus salicis (L.)	*Salix*
Nematus spiraeae Zaddach	*Arundus*
Nematus tibialis Newman*	*Robinia*

Appendix III. *continued*

Species name	Host plant genus
Paranematus caerulaeus Zinovjev	*Lonicera*
Pontania vesicator (Bremi)	*Salix*
Pontania proxima (Lepeletier)	*Salix*
Pristiphora angulata Lindqvist	*Spiraea*
Pristiphora carinata (Hartig)	*Vaccinium myrtillus*
Pristiphora conjugata Dahlbom	*Salix, Populus*
Pristicampus incisus (Lindqvist)	*Potentilla fruticosa*
Pristiphora mollis (Hartig)	*Vaccinium myrtillus*
Pristiphora rufipes (= *pallipes*) Lepeletier	*Ribes*
On angiosperm trees	
Apethymus filiformis (= *abdominalis*) Klug	*Quercus*
Apethymus serotinus (= *braccatus*) (O.F. Müller)	*Quercus*
Caliroa annulipes (Klug)	*Tilia, Salix, Betula, Quercus*, etc.
Caliroa cerasi (L.)	*Pyrus, Malus, Prunus, Crataegus*, etc.
Caliroa varipes (Klug)	*Quercus, Salix, Betula*
Croesus septentrionalis (L.)	*Betula*
Dineura virididorsata (Retzius & Degeer)	*Betula*
Eriocampa ovata (L.)	*Alnus*
Fenusa dohrnii (Tischbein)	*Alnus*
Fenusa pusilla (Lepeletier)	*Betula*
Harpiphorus lepidus (Klug)	*Quercus*
Hemichroa crocea (Geoffroy)	*Betula, Alnus, Corylus*
Heterarthrus aceris (Kaltenbach)	*Acer*
Heterarthrus flavicollis (Gussakovskij)	*Acer*
Heterarthrus nemoratus (Fallén)	*Betula*
Heterarthrus ochropodus (Klug)	*Populus*
Heterarthrus vagans (Fallén)	*Alnus*
Hoplocampa alpina (Zetterstedt)	*Sorbus*
Hoplocampa brevis (Klug)	*Pyrus, Malus*
Hoplocampa flava (L.)	*Prunus*
Hoplocampa minuta (Christ)	*Prunus*
Hoplocampa testudinea (Klug)	*Malus, Pyrus*
Kaliofenusa ulmi (Sundevall)	*Ulmus*
Macrophya punctum-album (L.)	*Fraxinus*
Mesoneura opaca (Klug)	*Quercus*
Messa hortulana (Klug)	*Populus*
Micronematus monogyniae (Hartig)	*Prunus*
Nematinus abdominalis (Panzer)	*Alnus*
Nematinus luteus (Panzer)	*Alnus*
Nematus umbratus (Thomson)	*Betula, Ulmus, Corylus, Alnus*
Periclista andrei Konow	*Quercus*
Periclista dusmeti Konow	*Quercus*
Periclista lineolata (Klug)	*Quercus*
Platycampus luridiventris (Fallén)	*Alnus*
Pristiphora abbreviata (Hartig)	*Pyrus, Malus*
Pristiphora geniculata (Hartig)	*Sorbus.*
Pristiphora testacea (Jurone)	*Betula*
Profenusa pygmaea (Klug)	*Quercus*
Scolioneura betuleti (Klug)	*Betula*
Stauronematus compressicornis (Fabricius)	*Populus, Salix*
Tomostethus nigritus Fabricius	*Fraxinus*
Trichiocampus viminalis (Fallén)	*Populus, Salix*
Trichiocampus ulmi (L.)	*Ulmus*
On gymnosperm trees	
Anoplonyx destructor Benson	*Larix*
Anoplonyx duplex (Lepeletier)	*Larix*
Anoplonyx ovatus (Zaddach)	*Larix*
Pachynematus scutellatum (Hartig)	*Picea*
Pikonema montanum (Zaddach)	*Picea*
Pikonema imperfectum (Zaddach)	*Larix*
Pristiphora abietina (Christ)	*Picea*
Pristiphora ambigua (Fallén)	*Picea*
Pristiphora erichsonii (Hartig)	*Larix*
Pristophora glauca Benson	*Larix*

Appendix III. *continued*

Species name	Host plant genus
Pristiphora laricis (Hartig)	*Larix*
Pristiphora subarctica (Forsslund)	*Picea*
Pristiphora wesmaeli (Fischbein)	*Larix*
Polyphagous species	
Allanthus cinctus (L.)	*Rosa, Rubus, Fragaria*
Allanthus rufocinctus (Retzius)	*Rosa, Rubus*
Ametastegia glabrata (Fallén)	Chenopodiaceae, Polygonaceae, *Plantago, Salix, Lythrum, Solanum*
Cladius pectinicornis (Geoffroy)	*Rosa, Fragaria, Poterium, Filipendula, Lamiastrum*
Monophadnoides rubi (Harris)	*Rubus, Geum, Filipendula*
Priophorus pallipes (Lepeletier)	*Betula, Cotoneaster, Prunus, Rubus, Sorbus, Fragaria, Crataegus, Corylus, Rosa, Laurus, Aronia*

[1]Sources: as in Table 2. *The only introduced Tenthredinidae in Europe (Liston 1995).

Appendix IV. Diprionid species in Europe, all on tree host plants, regarded as pests or outbreak species in the literature.[1] All species are native for Europe

Species name	Host plant group
Diprion pini (L.)	*Pinus*
Diprion similis (Hartig)	*Pinus*
Gilpinia frutetorum (Fabricius)	*Pinus*
Gilpinia hercyniae (Hartig)	*Picea*
Gilpinia pallida (Klug)[2]	*Pinus*
Gilpinia polytoma (Hartig)	*Picea*
Monoctenus juniperi (L.)	*Juniperus*
Microdiprion pallipes Fallén	*Pinus*
Neodiprion sertifer (Fourcroy)	*Pinus*

[1]Sources as in Table 2.
[2]Larsson *et al.* (1993) list *Gilpinia verticalis* as a 10th outbreak species, but this species is synonymized with *G. pallida* by Liston (1995), so it is not included in this table.

Appendix V. Tenthredinid species in Japan regarded as pests or outbreak species in the literature.[1] All are native species to Japan

Species name	Host plant genus
On herbs and grasses	
Allantus albicinctus Matsumura	*Spirea, Filipendula*
Athalia infumata Marlatt	*Rorippa, Brassica*
Athalia japonica Klug	*Arabis, Cardamine, Rorippa, Raphanus, Brassica*
Athalia rosae ruficornis Jakovlev	*Raphanus, Brassica*
Dolerus ephippiatus Smith	*Hordeum, Triticum, Secale,* and other grasses
Dolerus lewisii Cameron	Poaceae
Eutomostethus apicalis Matsumura	*Juncus*
Lagidina platycerus Marlatt	*Viola*
Pachyprotasis fukii Okutani	*Petasites*
Takeuchiella pentagona Malaise	*Glycine*
Tenthredo nigerrima Forsius	*Petasites*
Tenthredo providens Smith	*Oenanthe, Cryptotaenia, Peucedanum, Angelica*
On angiosperm shrubs	
Allantus meridionalis Takeuchi	*Rosa*
Cladius pectinicornis Geoffroy	*Rosa*
Perineura okutanii Takeuchi	*Hydrangea*
Tenthredo hiralis Smith	*Aucuba*
On angiosperm trees	
Allantus nakabusensis Takeuchi	*Prunus*
Amauronematus fallax Lepeletier	*Salix*
Apethymus kuri Takeuchi	*Castanea*
Caliroa cerasi L.	*Prunus, Pyrus, Cydonia, Sorbus*
Caliroa matsumotonis Harukawa	*Prunus, Pyrus*

Appendix V. *continued*

Species name	Host plant genus
Caliroa zelkovae Oishi	*Zelkova*
Conaspidia murotai Togashi	*Kalopanax*
Croesus japonicus Takeuchi	*Alnus*
Eriocampa mitsukurii Rohwer	*Alnus*
Fenusa dohrni Tischbein	*Alnus*
Fenusa pusilla Lepeletier	*Betula*
Hoplocampa pyricola Rohwer	*Pyrus*
Nematus crassus Fallen	*Salix*
Pareophora gracilis Takeuchi	*Prunus*
Parna kamijoi Togashi	*Tilia*
Stauronematus compressicornis Fabricius	*Populus, Salix*
Trichiocampus flaviventris Togashi	*Populus*
Trichiocampus populi Okamoto	*Populus*
On gymnosperm trees	
Anoplonyx orientis Smith	*Larix*
Pachynematus itoi Okutani	*Larix*
Pristiphora erichsoni Hartig	*Larix*
Pristiphora ezomatsuvora Togashi	*Picea*
Pristiphora politivaginata Takeuchi	*Larix*
Pristiphora wesmaeli (= *takagii*) Tischbein	*Larix*

[1]Sources: as in Table 3.

Appendix VI. Diprionid species in Japan, all on tree host plants, regarded as pests or outbreak species in the literature[1]

Species name	Host plant genus
Diprion nipponicus Rohwer	*Larix, Pinus*
Gilpinia daisetusana Takeuchi	*Pinus*
Gilpinia tohi Tacheuchi	*Picea*
Monoctenus itoi Okutani	*Chamaecyparis*
Neodiprion sertifer Geoffroy	*Pinus*
Nesodiprion japonicus Marlatt	*Pinus, Cedrus, Larix*

[1]Sources: as in Table 3.