Hoplothrips polysticti (Thysanoptera) on the wood-rotting polypore *Trichaptum abietinum* infesting dead *Picea abies* in Norway

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The fungivorous thrips *Hoplothrips polysticti* has previously been reported only from Scotland and Sweden. During a survey in forests of different ages in southeastern Norway, the thrips species was found to be common in dead *Picea abies* infested by *Trichaptum abietinum*, especially in a semi-old forest. *Hoplothrips unicolor* was also recorded for the first time in Norway. The occurrence of *H. polysticti* is discussed in relation to the age of the forests, and to the biochemical interference between fungi impacting the nutrient quality for the thrips. *H. polysticti* is proposed as a vector for *T. abietinum*.

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1. Introduction

Many forest invertebrates are dependent on dead wood and wood-rotting fungi (Kaila *et al*. 1994, Lindblad 1997). In modern managed forests, dead wood of certain qualities, e.g. large trunks in moist habitats, is scarce, and thus organisms depending on them may suffer due to lack of substrate for reproduction (Haila 1994, Økland 1995, Midtgaard 1996).

Several species of thrips of the suborder Tubuliferae live on dead wood, and for some of them, wood-rotting fungi are given as hosts (Mound *et al*. 1976, Scliephake & Klimt 1979). Most species are found in the tropics. In Scandinavia, species representing the genus *Hoplothrips* are fungivorous. *Hoplothrips pedicularius* (Haliday) live in colonies on *Stereum* sp., where the dominant males fight to defend the oviposition areas against competing males (Crespi 1986), but biological information on other species is scarce. Several of the *Hoplothrips* species are considered rare, but some of them are more likely to be overlooked. *Hoplothrips carpathicus* Pelikán 1961 was recently recorded from Sweden as new to northern Europe, but it is definitely not rare (Kobro & Nittérus 1999).

Hoplothrips polysticti (Morison) was described as a new species in 1949, and also as being in danger of extermination due to modern forestry in Scotland (Morison in Qvick 1977). This may be surprising, as the species forage on the polypore *Trichaptum abietinum* (Morison 1949) which is one of the most common wood-rotting fungi on Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Ryvarden & Gilbertson 1994). Later on, *H. polysticti* was found in Sweden (Qvick 1977). Qvick found 29 specimens, but did not report the sampling effort or the degree of management of the forest in which he found them. *H. polysticti* is not recorded from other countries (zur Strassen pers. comm.), but the results of Qvick (1977) indicated that the species was not rare, and that it should be possible to find *H. polysticti* in other Scandinavian countries as well. Thus, a sampling program was designed with two objectives: firstly, to find *H. polysticti* in southeastern Norway and secondly, to study its abundance in relation to the age of the forest.

2. Materials and methods

Bark from logs of spruce, infested with *T. abietinum*, was investigated for the presence of *H. polysticti* during 1997 and 1998. In this context the term "infested log" means lying dead spruce infested with *T. abietinum* unless otherwise stated. The infestation was judged from the presence of basidiocarps. Approximately 0.15 m^2 of bark, from positions on the log where basidiocarps were present, was removed and deposited in Berlese funnels for one to two weeks. One bark sample was taken from each of 72 logs selected from three different areas including four degrees of forestry management, representing an increasing age and an increasing amount of dead wood.

The forests of Nesodden (EIS 28) have been heavily exploited for over a century (Berner 1924, Røer pers. comm.), with a resulting low level of dead wood of quality necessary for wood-rotting fungi. Arbitrarily found, infested logs were investigated in these managed forests. The area of Nesodden was investigated in order to find patches of older forest for conservation purposes (Haugan 1996). Wood-rotting fungi were used as indicators of the age of the forest, and Haugan (1990) found nine patches in recessments or small valleys that had been protected against logging. The size of the patches varied from 0.02 to 0.73 ha (0.20 ha on average), and contained dead wood of all stages of decay. Only a few old signs of logging were present, and the patches had higher densities of dead wood than the managed forests around them. I sampled infested bark from these patches, too.

Østmarka forest reserve (EIS 29) has not been exploited for approximately 60 years. Therefore, it contains larger amounts of dead wood than the managed forests (Økland 1994). The age of the forest may be comparable to the patches of older forest in Nesodden. The Østmarka forest reserve is hereafter classified as a "semi-old forest".

The area between the lakes Katnosa and Spålen (EIS 36) is a forest reserve with old-growth characters similar to virgin forest. In this area, bark was collected from infested logs in two stands with an average age being 100 and 120 years (Hatlinghus pers. comm.).

Uninfested logs, found arbitrarily in the managed forests of Nesodden, were used as controls.

Additionally, spruces and pines from 13 other EIS quadrats in southeastern Norway, and also fungus-infested dead trees of other species, were sampled.

The investigated logs represented the decay stage 1, i.e. hard wood and with intact bark or with bark beginning to break up (Lindblad 1997). The logs were scattered in the forests.

Localities are given as EIS quadrats according to Økland (1976). The identification of the representatives of the thrips species was verified by zur Strassen (pers. comm.). For statistical comparisons, two-sample *t*-tests were used, with a significance level of 99%.

Table 1. Fungus-dwelling thrips from 60 logs of *Picea abies* infested with *Trichaptum abietinum*.

Species	Specimens	From no. of logs
Hoplothrips fungi (Zetterstedt, 1828)	1	1
Hoplothrips pedicularius (Haliday, 1836)	11	4
Hoplothrips polysticti (Morison, 1949)	300	48
Hoplothrips ulmi (Fabricius, 1781)	6	4
Hoplothrips unicolor (Vuillet, 1914)	3	2
Maderothrips longisetis (Bagnall, 1910)	4	4

3. Results

A total of 325 adult specimens from six species of the family Phlaeothripidae (suborder Tubuliferae) were recorded from *T. abietinum*-infested bark of

Table 2. *Hoplothrips polysticti* from logs of *Picea abies* infested with *Trichaptum abietinum* from four types of forest.

Logs in type of forest	No. of logs	Imagines per sample
Managed, uninfested	12	0.3 a
Managed, infested	12	2.0 b
Patches of older	24	3.7 b
Semi-old	12	12.5 c
Old	12	3.2 b

Numbers followed by different letters are significantly different at the 99 % level (two-sample *t*-test).

spruce (Table 1). A similar number of larvae of the same family were recorded but not identified. Several other thrips species belonging to the family Thripidae (suborder Terebrantia) were also recorded, but as these do not forage on fungi, they will not be discussed here.

H. polysticti constituted 92% of the specimens. Other species recorded were *Hoplothrips fungi* (Zetterstedt), *H. pedicularius*, *H. ulmi* (Fabricius), *H. unicolor* (Vuillet) and *Maderothrips longisetis* (Bagnall) (Table 1).

In the samples constituting adults of *H. polysticti*, the infested logs in the managed forest, patches of older forest did not differ significantly from each other. A higher average number of adults was recorded in the semi-old forest. Only a few specimens were recorded from the uninfested logs (Table 2).

In all localities, a majority of *H. polysticti* individuals were brachypterous. In semi-old forest, however, the proportion of macropterous specimens was somewhat higher (Table 3), and the only macropterous males were found there.

From spruce trees infested by other fungi and other fungal-infested dead trees (altogether 60 logs), only 14 specimens of *H. polysticti* were found, of which eight were found from pines (Table 4). Thrips were also found in 11 out of 13 other EIS quadrats in southeastern Norway (Fig. 1).

Fungal spores were present on prepared thrips.

4. Discussion

4.1. The thrips

Despite not being recorded from Norway before, this survey showed that *H. polysticti* is a common thrips species in spruce logs infested by *T. abietinum*. Also *H. unicolor* is new to the Norwegian fauna, and was, together with *H. fungi*, *H. pedicularius*, *H. ulmi* and *M. longisetis* found only sporadically. Thus, *H. polysticti* was a dominating thrips species in infested dead spruce trees in the study localities (Table 1).

Only three specimens of *H. polysticti* were caught from uninfested logs. As the infestation of fungus was judged from the presence of basidiocarps only, these logs may also have been infested without yet having produced visible basidiocarps. The uninfested control logs may therefore not be true controls of infestation.

Many insects with close association to fungi consume fungal tissue (Martin 1979), but host specificity is not typical for thrips living on wood-rotting fungi (Graves & Graves 1970, Mound 1974). Therefore, other infestations of dead wood were investigated for the presence of *H. polysticti*. Fourteen specimens were recorded (Table 4), of which a majority was found from pines with well-developed infestations of *T. abietinum*. Morison (1949) recorded *H. polysticti* only on pines infested by this fungus. Birch (*Betula*) and aspen (*Populus*), can also occasionally be a substrate

Table 3. Proportion of macropterous *Hoplothrips polysticti* from infested logs of *Picea abies* in four types of forest.

Forest type	% macropterous
Managed	11
Patches of older	10
Semi-old	29
Old	13

Table 4. *Hoplothrips polysticti* sampled from other fungus-infested dead spruce and other tree species.

Species	Fungus	No. of samples	No. of thrips
Picea abies	*Fomitopsis pinicola*, *Phellinus*, *Stereum* and others	14	0
Pinus silvestris	*Trichaptum abietinum*	12	8
Pinus silvestris	*Stereum* and others	10	1
Prunus domestica	*Phellinus*	1	0
Alnus sp.	Unidentified polypore	1	0
Betula sp.	*Fomes fomentarius*	12	2
Populus sp.	*Fomitopsis pinicola* and others	8	3
Quercus sp.	Unidentified polypore	2	0

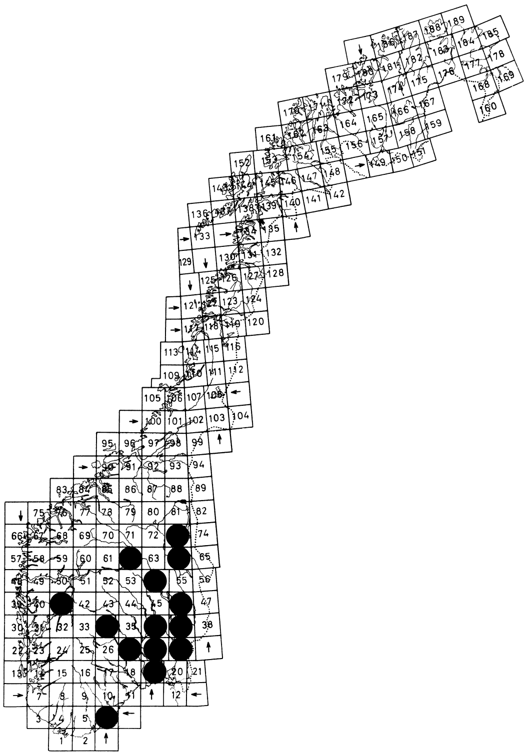

Figure 1. Records of *Hoplothrips polysticti* in Norway.

for *T. abietinum* (Ryvarden & Gilbertson 1994). Although it is possible that *H. polysticti* forage on several fungi, it is also possible that, since *H. polysticti* was occasionally found from dead birches and aspens and an "uninfested" spruce, these trees actually were infested by *T. abietinum*.

The few specimens recorded in logs without visible infestation of *T. abietinum* do not necessarily contradict with the other results presented in this paper, indicating that *H. polysticti* is monophagous on *T. abietinum* in the investigated area.

Since the majority of recorded adult thrips represented *H. polysticti*, probably nearly every larvae were of the same species. The abundance pattern was relatively similar among the study areas. Thus, the populations of *H. polysticti* were probably at least two times larger than shown in Table 2.

H. polysticti was present in forests other than those in which this study was focused. After the first recognition of the habitat of this species, it has been found in all except two EIS quadrats where it was sought in southeastern Norway (Fig 1).

4.2. The fungus

T. abietinum is a common pioneer species on recently fallen spruce and pine trees causing white rot of dead sapwood, the annual basidiocarps most often occurring in the lower parts of the logs (Ryvarden & Gilbertson 1994). Andersson (1987) considered it an aggressive infestor. Polypores disperse passively as wind-borne spores, which may be a risky strategy to colonize recently dead trees, a substrate that is often spatially and temporally unpredictable. This is the case especially in managed forests where dead wood is scarce. For a recently fallen tree, the chance to be infested by *T. abietinum* decreases strongly when the distance to an already infested log exceeds 25 m, as most spores fall on the ground close to the basidiocarps from which they are released (Dahl 1997). When *T. abietinum* is common, the spore dispersal is probably very effective. In this study, uninfested logs were difficult to find in the managed forests.

4.3. The thrips and the fungus

In the investigated areas, the commonness of *H. polysticti* brings up at least two possible interpretations. Firstly, the population may be of a certain level on each infested log regardless of the age of the forest and secondly, the number of specimens may increase with increasing availability of infested dead wood.

4.3.1. Stable population of thrips

Among three of the four forest types, the abundance of *H. polysticti* was not significantly different (Table 2) and can be regarded as representing a normal or average level for the occurrence of *H. polysticti* in infested logs. In the semi-old forest, a windfall caused by a storm in 1969 (Christiansen & Bakke 1988) temporarily increased the availability of the substrate for the fungus and the thrips and, consequently, the population sizes of these species increased. Many logs had passed the stage of decay most suitable for these organisms at the time of this investigation. Thus, a greater population of thrips was concentrated on a limited number of logs, showing the last phase of an accidental population peak about to decrease to a lower level.

Macropterous imagines were more abundant in the semi-old forest, possibly indicating a difference between it and the other forests (Table 3). Aphids may have sequences of generations with apterous specimens on a host plant for some time, but due to the crowding or the reduced nutritional quality of the host plant, they may produce alate emigrants to disperse (Kawada 1987). Similarly, thrips living on dead wood fungi are adapted to changes in the availability of substrate that is necessary for their development. On a recently infested log, thrips probably have plenty of nutrients for several generations. It would thus be a waste of energy to produce wings during the first generations. Production of wings is probably induced by the lack of food available for the larvae (Mound 1976), or crowding (Ananthakrishnan 1984). When the population on a log increases with simultaneous depletion of the substrate, macropterous specimens will develop with increasing numbers (Lewis 1973), preparing for dispersal to new logs. This was possibly the case in the semi-old forest.

A temporary increase in a thrips population was also reported by Morison (Lewis 1973), who showed that seven species of Tubuliferae thrips, feeding on fungi on dead wood or bark, had population peaks of several years due to an increase in the availability of dead wood.

4.3.2. Increasing population of thrips

Another interpretation of the presence of *H. polysticti* in the investigated areas is that a forest with a high density of infested logs may support more fungi and fungus-dependent thrips per log than a forest with a low density of infested dead wood. Almost twice as many thrips per sample were collected in the patches of older forest than in the managed forest, although this difference was not statistically significant. Thus, the thrips abundance may increase from managed forests to patches of older forests, and reaching a peak in semi-old forests (Table 2). The increase in thrips abundance is possibly a response to the increased availability of substrate. However, the amount of dead wood in the old forest was highest. Therefore, it could be expected that also the population of thrips should be highest there. Since this was not the case (Table 2), I propose two explanations concerning change in the nutrient quality of the fungus, which may have a negative impact on the abundance of fungivorous thrips in the oldest forest.

4.3.2.1. Extracellular impact in the microhabitat

In an old forest, several fungi are often present on each infested log, and the two most common ones are *T. abietinum* and *Fomitopsis pinicola* (Andersson 1987). These held true in the old forests in this study (Dahl 1997, Lindblad 1997). The mentioned fungi decay wood material in different ways. *T. abietinum* decomposes cellulose, hemicellulose and lignin, resulting in a white rot, while *F. pinicola* decomposes carbohydrates only, resulting in a brown rot because of the remaining lignin (Kirk & Highley 1973). Fungi have an extracellular digestion and release their digestive enzymes from the hyphae to their environment (Martin 1979). The thrips may feed on the breakdown products of hyphal decay in the sub-cortical region (Mound 1976, Ananthakrishnan 1984). Metabolites from the decaying process of the white- and the brown-rot fungi are different, and if these types of fungi occur together, they may possibly influence the quality of the sub-cortical microhabitat of a thrips adapted only to one of these fungi. If *H. polysticti* forage only on the decay metabolites of *T. abietinum*, then *F. pinicola* decay metabolites might alter the microhabitat in an unfavourable way for the thrips. Waste products and other exudates of fungi may affect the biochemical microhabitat, too (Rayner & Boddy 1988).

A similar situation is found in another group of insects, the wood wasps (Hymenoptera) that live on fungi producing white rot only and are not found on brown-rot fungi. One explanation is that the decay metabolites with a high content of lignin are less nutritious for the wasp (Gilbertson 1984).

4.3.2.2. Intracellular impact in the microhabitat

The thrips may also forage directly on the basidiocarps or on the fungal hyphae. Another explanation to why *H. polysticti* was not most common in the old forest is a possible change in the nutritional quality of the fungus itself, caused by biochemical impacts from other fungi on the log.

Secondary substances in higher plants act as repellents or attractants to insects (Fraenkel 1969). The presence or absence of such chemicals is in principle governing the insects' choice of plants as food. A large number of secondary substances with allelopathic effects between plants is known (Mac'as 1999), and chemical compounds from one plant may be taken up, transported within a target plant and inhibited its growth by inhibiting photosynthesis or protein synthesis (Rice 1984).

Many similarities exist between fungi and plants regarding action of secondary metabolites (Dowd 1991). Neighbouring fungi may be antagonists, as hyphal interference between the species is common among wood-rotting fungi, resulting in an inhibition of one or both of the participants (Rayner & Boddy 1988). A variety of secondary substances are known in fungi (Martin 1979, Dowd 1991), and host chemistry is important for fungivorous insects (Thunes 1994, Jonsell 1999). Despite being difficult to find references to support the idea, allelopathic relationships may exist between fungi, too. Thus, compared to the same fungus in a younger forest, the nutrient quality of a fungus in an old forest may be reduced due to a biochemical interaction between several fungi on the same log in the old forest.

4.3.3. Dispersal of fungal spores

Fungal spores can be attached firmly to thrips, as they were found on prepared specimens, and can potentially be dispersed by the thrips *in vivo* (Kobro & Nittérus 1999). Insects may thus transport spores of *T. abietinum* from one log to another. Since other arthropods found in this study represented most often mites (Acari) and springtails (Collembola), e.g. beetles (Coleoptera) being scarce, the winged thrips are the most probable vector candidates, improving the substrate availability for the fungi. Several species of sporophagous thrips transport spores from a number of different fungi (Ananthakrishnan 1984), although none of the fungi mentioned by Ananthakrishnan (1984) were of the order to which the wood-rotting fungi in this study belong.

If *T. abietinum* had evolved for wind dispersal of the spores only, their reproductive organs would probably had grown more exposed to wind, as in grasses and trees. Instead, they are more or less hidden under the log, which supports the idea that a vector may be important for the distribution of the spores.

5. Conclusions

H. polysticti is a common fungivorous thrips in the investigated area in southeastern Norway, where it was most often recorded from dead *P. abies* infested by *T. abietinum*. The occurrence of *H. polysticti* varied with the age of the forest, and it was most common in the semi-old forest. Two interpretations for the presence of the thrips are suggested, both of them of importance in the biochemical interactions in the microhabitat on the log. *H. polysticti* probably acts as a vector for *T. abietinum*.

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