Effects of stand tree species composition and diversity on abundance of predatory arthropods

Harri Vehviläinen, Julia Koricheva and Kai Ruohomäki

H. Vehviläinen, Biometrical Genetics, Biotechnology and Food Research, MTT Agrifood Research Finland, FI–31600 Jokioinen, Finland.
– J. Koricheva (julia.koricheva@rhul.ac.uk), School of Biological Sciences, Royal Holloway Univ. of London, Egham, Surrey, UK, TW20 0EX.
– K. Ruohomäki, Dept of Biology, Univ. of Turku, FI–20014 Turku, Finland.

Diverse plant communities are predicted to have higher abundance of predators as compared to species-poor ones. In this study we explored whether this prediction holds true for the abundance of predatory arthropods in forest ecosystems, which have been poorly studied in this respect. We collected ground-dwelling arthropods using pitfall traps from six long-term forest diversity experiments in Finland, Sweden and UK. The effects of tree species diversity on abundance of five main groups of predatory arthropods (ants, spiders, carabids, staphylinids and opilionids) were examined by means of meta-analysis. Overall, the diversity of tree species did not affect abundances of predators with the exception of staphylinids, which were more abundant in mixed stands than in monocultures. However, the effects of stand diversity on predator abundance became apparent when analyses were conducted on tree species basis. Preference for stands containing particular tree species was clear in the case of opilionids, carabids and staphylinids, and these preferences overruled the effects of tree species diversity in comparisons between monocultures and mixed stands containing the same tree species. Tree species diversity effects on predator abundance were furthermore mediated by the tree age, plot size and planting density used in the experiment. Overall, our results show that predator abundance does not increase uniformly with increase in tree species diversity, but rather suggest that predators have distinct preferences for stands composed of particular tree species and that these species preferences may overrule the effects of diversity.

Plant diversity may have profound impact on the abundance and species richness of both herbivores and their natural enemies (MacArthur 1955, Elton 1958, Hutchinson 1959, Root 1973, McCann 2000). The enemies hypothesis (Elton 1958, Root 1973, reviewed by Russell 1989) predicts that generalist predators and parasitoids should be more abundant in diverse plant communities compared to simpler ones. This might be due to higher abundance and species richness of herbivores, more favourable microclimate and shelter as well as availability of alternative feeding sources (e.g. nectar and pollen) in diverse plant communities.

The enemies hypothesis has been experimentally tested mainly in agricultural (Risch et al. 1983, Russell 1989, Andow 1991, Bommarco and Banks 2003) and grassland (Siemann et al. 1998, Koricheva et al. 2000) ecosystems. The results from agricultural systems largely support the enemies hypothesis (Risch et al. 1983, Russell 1989, Andow 1991). Risch et al. (1983) and Andow (1991) predicted that relative importance of enemies hypothesis would be greater in perennial than in annual systems. However, Koricheva et al. (2000) found that numbers of spiders and carabids declined with increase in diversity in perennial grasslands. Meta-analysis by Bommarco and Banks (2003) revealed that spatial scale modifies the impact of plant diversity on predators: generalist insect predators were affected by plant diversity in intermediate-sized (28–196 m²) but not in large (>256 m²) plots. Bommarco and Banks (2003) hypothesised that predators redistribute themselves more easily in experiments with smaller plot size and aggregate in more diverse plots that may harbour alternative prey and resources.

Plant diversity effects on natural enemies have received considerably less attention in forest ecosystems. The results from a few existing studies on forest diversity effects on natural enemies (Stamps and Linit 1998, Quayle et al. 2003, Finch 2005, Riihimäki et al. 2005, Koricheva et al. 2006, Kaitaniemi et al. 2007) indicate that the results from other ecosystems do not apply to forests and that the tree species composition effects may be more important than effects of tree species diversity per se. Moreover, previous studies have focused on effects of plant diversity on abundance and movements of individual species of natural enemies, on species richness of predators or their effects on particular herbivores. In contrast, the aim of our study is to explore more general patterns of abundance of most common groups of predatory arthropods in pure and mixed forest stands.

In this study, we tested the predictions of the enemies hypothesis in forest ecosystems by pitfall sampling of five...
main groups of ground-dwelling predatory arthropods (ants, spiders, carabids, staphylinids and opilionids) from six long-term forest experiments that contained both tree monocultures and mixed species stands. In our previous study using the same experiments (Vehviläinen et al. 2007) we have found that tree species composition affects the abundance and damage of herbivores and in the present study we examine the possibility that these effects are mediated to some extent via the tree diversity effects on the third trophic level. The groups of predators that we have sampled may have considerable impact on foliar herbivores. For example, ants forage both on the ground and on the trees and have been shown to affect survival of foliar herbivores in our experiments (Riihimäki et al. 2005, Kaitaniemi et al. 2007). Additionally, pupae of many foliar herbivores overwinter in soil and predation by ground-dwelling predators (e.g. carabids) has been shown to affect herbivore densities (Tanhuanpää et al. 1999).

To combine the results from the six experiments where the sampling has been conducted, we used the method of meta-analysis which allows general conclusions to be drawn from a collection of independent datasets testing the same hypothesis. The main aim of our study is to explore whether the tree species diversity affect the abundance of predatory arthropods. Specifically, our study addressed the following questions: 1) Do predators show preference for stands composed of certain tree species? 2) Does response to the tree species diversity differ between the five predator groups? 3) Does the presence of particular tree species in a stand affect abundance of predators more than diversity of stand per se? 4) Do plot size, tree age or planting density affect the magnitude or direction of the effects of tree species diversity on predator abundances?

Material and methods

Experiments

In 1999–2003 we have sampled predatory arthropods from six long-term forest experiments (Table 1). The majority of the above experiments have been established by the foresters from the Finnish Forest Research Institute, the Swedish Univ. of Agricultural Sciences and the Forestry Commis-}

Arthropod sampling procedure

Arthropods were sampled using pitfall traps. Each trap consisted of a 175 ml polyethylene container (Ø 67 mm) filled with concentrated sea salt solution. A drop of detergent was added in each pitfall to reduce surface tension. Acrylic covers (100 × 100 mm) were positioned few centimetres above the traps to prevent rain water entering the traps and to reduce evaporation. Three (the Satakunta experiment) or five (other experiments) traps were placed at the central part of each plot, in such a way that individual traps were located ≥ 5 m from each other. As the scale of experimental plots was fairly small, the number of pitfalls per plot should be adequate for comparison of abundances of ground-dwelling arthropods between treatments (Niemelä et al. 1996, Rainio and Niemelä 2006). Pitfalls were left in the field for five days (Table 1), after which they were removed and arthropods were preserved in 75% ethanol until identification. Because the duration of the pitfall trapping was rather short, we have conducted two trappings per season in three out of six experiments and over several years in the Satakunta experiment (Table 1).

Pitfall traps measure ‘activity densities’ and not ‘absolute densities’. As a result they are more likely to detect actively foraging predators whereas sit-and-wait or ambush predators would be underrepresented. However, we are mainly interested in relative differences in abundance between monocultures and mixed stands and not in absolute densities of predators.

The predatory arthropods were separated in the laboratory into five main taxonomic groups: ants (Formicidae), opilionids (Opiliones), carabids (Carabidae), staphylinids (Staphylinidae) and spiders (Araneida) and their numbers in each trap were calculated. The fairly broad taxonomic resolution was chosen in order to draw general conclusions on the effects of tree species diversity on the most abundant groups of predators. The predator groups examined also represented different foraging strategies. For instance, ants were selected to represent social insects foraging both on the ground and in tree canopies and having complex interactions with the trees ranging from predation on herbivores to aphid tending. Carabids and staphylinids represent solitary insects that can be regarded as generalist and facultative predators, respectively, foraging mainly on the forest floor, spiders and opilionids were selected as obligatory predators which often have highly specialised hunting tactics.

Statistical analyses

Averaging

Numbers of predators in pitfalls were first averaged over each plot and then over treatments. If the experiment was sampled more than once, the values for plots were averaged over the sampling periods before averaging plot values over treatments.
<table>
<thead>
<tr>
<th>Experiment</th>
<th>Established</th>
<th>Anthropod sampling</th>
<th>Treatments</th>
<th>No. pitfalls / plot</th>
<th>No. plots</th>
<th>Plot size (ha)</th>
<th>Planting interval (m)</th>
<th>No. trees per ha</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gisburn 54°N, 02°E</td>
<td>1991</td>
<td>28.6-3.7.2003</td>
<td>Alder100%, Oak100%, Pine100%, Spruce100%, Sitka100%, Sitka50%-Pine50%, Oak50%-Spruce50%, Oak50%-Pine50%, Spruce50%-Pine50%, Oak50%-Alder50%, Alder50%-Spruce50%, Alder50%-Pine50%</td>
<td>5</td>
<td>36</td>
<td>0.2</td>
<td>0.75</td>
<td>4153</td>
<td>Moore et al. 1991, Vehviläinen et al. 2007</td>
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<td>England</td>
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<tr>
<td>Vimpeli 63°N, 24°E</td>
<td>1982</td>
<td>20.-25.7.2003</td>
<td>Birch100%, Pine 100%, Spruce 100%, Birch33%-Pine33%-Spruce33%</td>
<td>5</td>
<td>36</td>
<td>0.16</td>
<td>2.22</td>
<td>2025</td>
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<td>Östad 57°N, 16°E</td>
<td>1989</td>
<td>8.–13.7.2002</td>
<td>Birch100%, Pine 100%, Spruce100%, Birch77%-Pine23%, Birch77%-Spruce23%</td>
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<tr>
<td>Jokioinen 60°N, 23°E</td>
<td>1982</td>
<td>6–11.6. and 8–13.8.2002</td>
<td>Birch100%, Pine100%, Birch50%-Pine50%, Birch25%-Pine75%</td>
<td>5</td>
<td>8</td>
<td>0.21–0.38</td>
<td>2.2</td>
<td>2000</td>
<td>Vehviläinen et al. 2006, 2007</td>
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<tr>
<td>Satakunta 61°N, 21/22°E</td>
<td>1999</td>
<td>6/7.–11/12.6. and 25/26.–30./31.7.2001</td>
<td>Birch100%, Pine100%, Spruce100%, Larch100%, Alder100%, Birch50%-Pine50%, Alder50%-Spruce50%, Birch50%-Spruce50%, Birch50%-Alder50%, Spruce50%-Larch50%, Pine50%-Spruce50%, Pine50%-Larch50%, Birch33%-Pine33%-Spruce33%, Birch33%-Pine33%-Larch33%, Birch33%-Pine33%-Alder33%, Birch33%-Larch33%-Alder33%, Alder33%-Spruce33%-Larch33%, Pine33%-Spruce33%-Larch33%, Birch20%-Alder20%-Pine20%-Spruce20%-Larch20%</td>
<td>3</td>
<td>114</td>
<td>0.04</td>
<td>1.5</td>
<td>4225</td>
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<tr>
<td>*Oak = sessile oak (Quercus petraea), Alder = black alder (Alnus glutinosa), Pine = Scots pine (Pinus sylvestris), Spruce = Norway spruce (Picea abies), Birch = silver birch (Betula pendula), Sitka = Sitka spruce (Picea sitchensis).</td>
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Meta-analysis

Standardized mean difference in predator abundance between treatments (Hedges’ d, Gurevitch and Hedges 1993) was used as a measure of the effect size. Three different comparisons were conducted. First, we compared predator densities between different monocultures in order to understand whether predators preferred stands composed of particular tree species. In this analysis predator abundance in monoculture of species A was compared to mean predator abundance in monocultures of all other species. Negative values of effect size indicated that predators were more abundant in that particular monoculture as compared to other tree species’ monocultures. Second, we tested for the overall diversity effects by comparing predator abundance in a particular tree species mixture with the mean predator abundance in monocultures of tree species composing that mixture. Positive effect sizes thus indicated higher predator abundance in mixtures compared to monocultures (a result consistent with the predictions of the enemies hypothesis). Third, the tree species-specific responses were calculated by comparing the abundance of predators in a specific monoculture with the mean predator abundance in mixtures that contained that tree species. In addition, the effects of plot size and tree age on predator abundance were analysed by using them as continuous variables in meta-analyses.

Weighted meta-analyses were performed so that each treatment-wise effect size was weighted by the inverse of its variance. We used mixed models because they assume that there exists random variation among studies within class in addition to sampling variance, which is a realistic assumption in ecological data (Gurevitch et al. 2001). Randomization tests were used to estimate the significance of the homogeneity statistics ($Q_b$). Confidence intervals around the effect sizes were created by bias-corrected bootstrapping with 9999 iterations. MetaWin 2.0 statistical software (Rosenberg et al. 2000) was used to conduct the meta-analyses.

Results

During the course of the study, 158 560 predatory arthropod individuals were collected in total (ants: 149 842, spiders: 5520, carabids: 1231, staphylinids: 1287, opilionids: 680). The average number of arthropods collected per pitfall at different experiments and collection periods reflected adequate sampling effort despite the fairly short collection time [average (min–max) / pitfall: ants: 100.5 (3.6–472.0), spiders: 3.1 (0.1–8.0), carabids: 0.58 (0.0–2.6), staphylinids: 1.1 (0.1–3.1), opilionids: 0.4 (0.1–1.3)].

Comparison of predator abundance between monocultures

Abundance of staphylinids, opilionids and carabids varied greatly between monocultures of different tree species (Fig. 1a). Staphylinid abundance was higher in alder and pine monocultures and lower in spruce monocultures. Opilionids were less abundant in spruce monocultures than in other monocultures. Both opilionids and carabids were more abundant in birch monocultures. Ants and spiders did not show preferences for any of the tree species, although they tended to be more abundant in spruce monocultures.

Overall effects of tree species diversity on predator abundance

When abundances of predators were analysed across all tree species, only abundance of staphylinids was significantly affected by tree species diversity and was higher in mixed stands compared to monocultures (Table 2). The difference between the responses of various predator groups was not significant ($Q_b = 3.35; DF = 4; p = 0.307$).

When tree species diversity effects on predators were compared between the 2- and 3-species mixtures, staphylinids were significantly more abundant in 2-species mixtures than in monocultures ($E_+ = 0.272; 95\% CI = 0.071,0.491; DF = 19$), but the difference in their densities between monocultures and 3-species mixtures was not significant ($E_+ = 0.122; 95\% CI = -0.174,0.437; DF = 6$). Diversity effects on other groups of predators did not differ between the 2- and 3-species mixtures.

Tree species-specific responses of predators to diversity

Comparisons between specific monocultures and mixed stands containing those tree species revealed that the effects of tree species diversity on predator abundance differed between the tree species (Fig. 1b). The preference of predators for stands composed by a particular tree species could explain most effects. However, few cases, such as spider abundance being higher in mixed stands containing alder than in alder monocultures, could not be accounted for by either spider avoidance of alder or preference of other tree species. The only predator group showing no tree species-specific response was ants that were not affected by the tree species diversity in any of the tree species comparisons.

Effect of experimental plot size

In overall analysis of all tree species, opilionids were the only predator group affected by the plot size; the larger the experimental plot, the more abundant opilionids were in mixed stands as compared to monocultures (Slope (SE) = 1.828 (1.377), $p = 0.056$, DF = 27). Plot size had no significant effect on responses to tree species diversity in other predator groups ($p \geq 0.140$ in all cases). However, when plot size effects were analysed separately for different tree species, a pattern emerged: in general, plot size affected responses of ants and other predator groups to tree species diversity in the opposite way. For instance, for spruce the effects of diversity on ant abundance declined with increase in plot size whereas diversity effects on abundance of opilionids, carabids and spiders were enhanced. In other words, the larger was the spruce plot, the more abundant the ants were in spruce monocultures as compared to mixed
stands containing spruce and vice versa for other predators (Table 3).

**Effect of tree age**

Similarly to the effects of plot size, the age of the trees affected the responses of ants and other predator groups to tree species diversity in the opposite way. For example, the older was the spruce stand, the more abundant ants were in monocultures as compared to spruce-containing mixtures while the opposite was true for opilionids and carabids (Table 3). The effects of tree age were, however, rather small compared to the effects of plot size. Interestingly, neither tree age nor plot size affected the responses of staphylinids to tree species diversity, although they were the only group of predators affected by the overall tree species diversity.

**Effect of planting density**

Effects of planting density could be tested only in birch- and pine-containing experiments. Planting density did not modify effects of tree species diversity on abundances of most predator groups (Fig. 2) with the exception of spiders, which were more abundant in monocultures of birch at low
planting densities and in mixtures at high planting densities (Fig. 2a).

**Discussion**

Overall, the diversity of tree stands did not affect abundances of ground-dwelling predators with the exception of staphylinids, which were more abundant in mixtures than in monocultures. The fact that the abundances of most of the predator groups were not affected by the diversity of stands suggests that the enemies hypothesis may not hold as a general phenomenon in forest ecosystems. While there is a debate on how diverse predator assemblages have to be to exhibit an effective control of herbivore populations (Cardinale et al. 2003, Rosenheim et al. 2004, Finke and Denno 2005, Snyder et al. 2006), the abundance of predators should be a fairly straightforward measure of their effectiveness. The lack of consistent response by predator groups does not imply that individual species do not respond to tree species diversity in forest ecosystems (Niemelä et al. 1996). For instance, individual species responding to the same extent but to opposite directions within group would result in zero effect size of tree species diversity. However, the enemies hypothesis (Root 1973) does not explicitly predict variation in responses of generalist predators to plant diversity, and thus higher level classification should reveal general trends accurately.

In the analyses at the tree species level the effects of stand diversity on predator abundances were more variable. While ants and spiders were not showing any preference for stands composed of certain tree species as compared to individual monocultures, staphylinids, carabids and opilionids showed distinct preferences for stands composed of particular, although different, tree species. Moreover, these preferences were apparent in comparisons between monocultures and mixtures at the tree species level. If the predator group was less abundant in a monoculture of a particular tree species, it was more abundant in mixtures than in monocultures containing that tree species. For instance, staphylinids were relatively less abundant in monocultures of spruce than in monocultures of other tree species and also more abundant in spruce mixtures compared to spruce monocultures. It seems that in the forest ecosystem the identity of tree species within stands may be more important to predators than the number of different tree species per stand. This result agrees well with our previous studies on foliar predators (Riihimäki et al. 2005, Kaitaniemi et al. 2007) and on insect herbivore abundance and damage in the same forest diversity experiments (Vehviläinen et al. 2007), which also showed higher relative importance of stand composition over effects of tree species diversity per se. Later this finding has been substantiated also by Jactel and Brockerhoff (2007).

Jactel et al. (2005) list three mechanisms that could explain greater abundance and richness of natural enemies in forest ecosystems: 1) alternative hosts for generalists, 2) complementary food for specialists, and 3) diversity of shelter. They also comment on potential negative effects of reduced foraging effectiveness in complex-structured plant associations. The diversity of herbivores is expected to increase with increase in tree species diversity of stand thereby providing alternative hosts for predators for example at the times when their main host is temporarily unavailable due to its life cycle. Likewise, the availability of aphids providing honeydew as complementary food for predators can be expected to be more stable in time in mixed stands, in which different tree species harbour different species of aphids (Jactel et al. 2005). The microclimate within stands composed of different tree species can be expected to be fairly different and in a seasonal environment both the prevention of desiccation during summer as well as suitable overwintering sites may be important in determining the abundance of predatory arthropods in temperate–boreal forests (Koivula 2002). In addition to shelter from the elements, the safety from predation by vertebrates may promote the preference of predatory arthropods for stands composed by certain tree species (Gunnarsson 1996). Similarly to probability of being predated, also the predation efficiency of the arthropod predators themselves may be highly dependent on the particular tree species within a stand (Halaj et al. 2000, Kaitaniemi et al. 2004, Riihimäki et al. 2006). Should a predator be familiar with the structure and type of

**Table 2. Effects of tree species diversity on abundance of different predators.** Values reported are the mean effect sizes (E_\(\text{a}\)) and lower (lcl) and upper (ucl) limits of the bias-corrected 95% confidence intervals. Significant effects are shown in bold.

<table>
<thead>
<tr>
<th>Predators</th>
<th>E_(\text{a})</th>
<th>lcl</th>
<th>ucl</th>
<th>DF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ants</td>
<td>-0.0289</td>
<td>-0.2043</td>
<td>0.1444</td>
<td>27</td>
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<tr>
<td>Spiders</td>
<td>0.0130</td>
<td>-0.1508</td>
<td>0.1773</td>
<td>27</td>
</tr>
<tr>
<td>Carabids</td>
<td>0.0062</td>
<td>-0.1684</td>
<td>0.1837</td>
<td>27</td>
</tr>
<tr>
<td>Staphylinids</td>
<td>0.2132</td>
<td>0.0446</td>
<td>0.3876</td>
<td>27</td>
</tr>
<tr>
<td>Opilionids</td>
<td>0.0258</td>
<td>-0.1161</td>
<td>0.1816</td>
<td>27</td>
</tr>
</tbody>
</table>

**Table 3. Effects of plot size and tree age on predator abundance in monocultures vs mixtures.** Reported values are slopes of the regression and their standard error. The more positive is the slope, the more abundant predators are in mixtures vs monocultures with increase in plot size or tree age. Significant (p < 0.05) values in bold.

<table>
<thead>
<tr>
<th>Predators</th>
<th>Birch</th>
<th>Pine</th>
<th>Spruce</th>
<th>Alder</th>
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<tr>
<td>Ants</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>age</td>
<td>-0.002 (0.021)</td>
<td>-0.973 (1.928)</td>
<td>-0.011 (0.021)</td>
<td>-0.125 (0.028)</td>
</tr>
<tr>
<td>age</td>
<td>0.037 (0.021)</td>
<td>2.054 (1.922)</td>
<td>-0.018 (0.021)</td>
<td>0.046 (0.027)</td>
</tr>
<tr>
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<td>0.116 (2.134)</td>
<td>2.569 (2.060)</td>
<td>3.673 (2.578)</td>
<td>6.031 (3.514)</td>
</tr>
<tr>
<td>Carabids</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>age</td>
<td>-0.008 (0.021)</td>
<td>1.704 (1.954)</td>
<td>0.022 (0.021)</td>
<td>0.046 (0.027)</td>
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<td>0.082 (0.028)</td>
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<td>age</td>
<td>-3.180 (2.149)</td>
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<td>-0.036 (0.026)</td>
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<td>-1.485 (2.172)</td>
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<td>-0.037 (0.024)</td>
<td>4.998 (2.678)</td>
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<tr>
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<td>-3.180 (2.149)</td>
<td>-0.491 (1.928)</td>
<td>-0.022 (0.021)</td>
<td>-0.036 (0.026)</td>
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<table>
<thead>
<tr>
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<th>Staphylinids</th>
</tr>
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<tbody>
<tr>
<td>age</td>
<td>0.004 (0.060)</td>
</tr>
<tr>
<td>age</td>
<td>0.003 (0.059)</td>
</tr>
</tbody>
</table>
prey fauna of a particular tree species, increase in diversity of tree species within stand may hamper its foraging efficiency as in Huffaker’s (1958) classic experiments (Halaj et al. 2000, Kaitaniemi et al. 2004). The abundance and effectiveness of ants in reducing herbivore numbers has, however, been shown to be higher in birch–pine mixtures compared to monocultures in our earlier studies in the Satakunta experiment (Riihimäki et al. 2005, Kaitaniemi et al. 2007).

Due to the nature of forest ecosystems (i.e. the main component being long-lived trees covering considerable areas) differences in the plot size and tree age may be expected to modify the effects of tree species diversity on predatory arthropod abundance (Punttila 1991, Oxbrough...
et al. 2005, Derunkov 2005). Indeed, both plot size and tree age were found to have effects on abundance of predators in this study, but the effects were not uniform. A general pattern seems to be that when response of ants to tree species diversity changes due to plot size or tree age, the response of other predators to tree species diversity changes also, but to the opposite direction. This suggests that the ants may cause the competitive displacement of other groups to some extent, although the question of importance of ant abundance in shaping the arthropod predator community is still open (Halaj et al. 1997, Lenoir et al. 2003, Mody and Linsenmair 2004). The effects of plot size and tree age can be explained only partly by different preferences of predators for particular tree species. For example, ants clearly favour large and old alder mixtures over monocultures, but as they did not show any general avoidance of stands containing alder or preference for stands composed of other tree species, there must be a mixture effect either making older and bigger alder mixtures more favourable or monocultures unfavourable. Overall, the plot sizes of spruce and alder seemed to have the strongest effects on the predators. Out of the six tree species analysed here, these two are at the opposite ends of the spectrum: spruce represents the end of succession as a shade tolerant conifer whereas alder is a nitrogen-fixing early succession deciduous tree. A plausible explanation for both the plot size and the tree age effects may be the differences in predator community composition with increase in space and time (Puntila 1991, Lenoir et al. 2003).

Our results of increase in diversity effects with increase in plot size are somewhat contradictory to the findings of Bommarco and Banks (2003), who found in their meta-analysis of agricultural systems that the effects of plant diversity on predators tend to disappear in larger plots, which highlights the difference between these two systems, for instance in temporal variability. In annual systems predators must be adapted to effective search of suitable habitats, whereas in more temporally stable systems predators do not have to find suitable habitat every year and may thus be also less eager to move between experimental plots.

Concentrated resources are predicted to attract more animals (Tahvanainen and Root 1972). When we analysed data on herbivores from the same experiments as used here, we found that some herbivore groups were less abundant in monocultures of birch compared to birch-containing mixtures at low planting densities, but the tree species diversity did not generally have effect on herbivores at high planting densities (Vehviläinen et al. 2007). As this reduction in herbivore abundance is hypothesised to be at least to some extent due to effects of the predators, it is somewhat surprising to find that planting density of birch or pine affected strongly only abundance of spiders. The spiders, however, were more abundant in birch monocultures than in mixtures at low planting densities and vice versa at high planting densities, as predicted by the response seen in herbivores (Vehviläinen et al. 2007). The effects of planting density on spiders may be due to their foraging tactics: at high planting densities spiders may benefit from a mixture of tree architectures and close proximity of branches as they most probably forage to some extent also on trees and use ambush tactics and nets in contrast to other predatory groups studied here (Halaj et al. 2000, Oxbrough et al. 2005).

Overall, our results suggest that while the abundance of some predatory arthropods can be affected by tree species diversity, the tree species composition of the stand is a more important determinant of the abundance of predators in forest ecosystems. The preference of predators for stands composed of particular tree species may be due to several non-mutually exclusive mechanisms such as more abundant and diverse prey fauna, favourable microclimate, higher foraging efficiency and better shelter. The relative importance of these factors may furthermore be specific for predators, tree species and their interaction. Therefore, it seems that the extent to which predator preferences for particular tree species overrule the effects of increased diversity and vice versa in forest ecosystems is not straightforward to assess. In the light of idiosyncratic effects of diversity on different predators, such as birds (Greenberg et al. 2000, Perfecto et al. 2004), more information on the relative importance of predator preference for stands composed of particular tree species should be gathered before applying these results to forestry situations. We especially encourage further studies that could pinpoint the mechanisms behind the results found in this study.

Acknowledgements – We are grateful to Samuli Helle, Päivi Immonen, Pekka Kaitaniemi, Andre Koppe, Liisa Laukkonen, Elina Mäntylä, Aila Oravala, Henna Piekäinen, Janne Riihimäki, Paula Salminen, Lassi Suominen and Elena Valkama for their help in collecting and handling the vast amount of arthropods. We thank the staff of the Satakunta Environmental Research Institute of Univ. of Turku and the Östad field station of the Swedish Univ. of Agricultural Sciences for their hospitality and Forestry Commission (UK) and Finnish Forest Research Institute for the permission to use their experiments. The study was financially supported by the Academy of Finland (project 76735), the Finnish Society of Forest Science, the Satakunta Cultural Foundation and the Turku University Foundation (grants to HV).

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