Insect Conservation and Diversity (2013) **6**, 502–512

doi: 10.1111/icad.12007

High within- and between-trunk variation in the nematoceran (Diptera) community and its physical environment in decaying aspen trunks

PANU HALME,[1,2]* NOORA VARTIJA,[1] JUKKA SALMELA,[3] JOUNI PENTTINEN[4] and VEERA NORROS[5] [1]Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland, [2]Centre for Macroecology, Evolution and Climate, University of Copenhagen, Copenhagen, Denmark, [3]Department of Biology, Zoological Museum, University of Turku, Turku, Finland, [4]Metsähallitus, Natural Heritage Services, Jyväskylä, Finland and [5]Metapopulation Research Group, Department of Biosciences, University of Helsinki, Helsinki, Finland

Abstract. 1. Dead wood is a primary habitat for a large number of insects, including species from many nematoceran (Diptera) groups. The species living in dead wood must be adapted to the ephemeral and ever-changing nature of their substrate. There is a growing body of knowledge about the effects of dead wood quality and the surrounding landscape on the saproxylic beetle community, but we know very little about the other saproxylic insects. Moreover, we know only very little about the variation in the insect community between different parts of decaying wood pieces.

2. Using emergence traps, we studied the saproxylic nematoceran communities occupying different parts of decaying fallen aspen trunks in a boreal forest. To explain the variation in the detected assemblages, we also studied the variation in the physical environment in different parts of one of the studied trunks during the season.

3. We found out that the overall variation in assemblages was very high and also the similarity between the base and top of the same trunk was usually low. Dissimilarity arose more from differences in species richness than from species turnover. The greatest contrasts in the physical conditions of the study trunk were between the inside and the upper and lower surface of the trunk base.

4. Due to high variation within the trunks and especially between the trunks, the sampling effort in studies on the ecology of saproxylic insects should be high to have a reliable estimate of the local community.

Key words. Crane fly, dead wood, eclector trap, emergence trap, fungus gnat, SDR-simplex, similarity analysis.

Introduction

Dead wood is the primary resource or habitat for a vast number of forest-dwelling species throughout the world (Lonsdale *et al.*, 2008; Lassauce *et al.*, 2011). In addition to other species groups, dead wood is also an important habitat for larval development and adult overwintering of a diverse insect community. There is a massive number of insect species using the dead wood for nutrition (Grove, 2002). Many of these species are currently threatened due to intensive forest management actions, which reduce the volume of this important resource. For example, in Fennoscandia, the lack of dead wood is one of the most important reasons driving species closer to (local) extinctions (Rassi *et al.*, 2010).

In boreal forests, decaying aspens are regarded as biodiversity hotspots inhabited by exceptionally high insect,

*Correspondence: Panu Halme, Department of Biological and Environmental Science, P.O. Box 35 FI-40014, University of Jyväskylä, Finland. e-mail panu.halme@jyu.fi

© 2012 The Royal Entomological Society

fungus, and epiphyte diversity (Kuusinen, 1994; Siitonen & Martikainen, 1994; Kouki *et al.*, 2004; Junninen *et al.*, 2007). Yet, the abundance of aspen has been decreasing in boreal forests due to modern forest management practises. Due to its low economic value, it has been discriminated against in the forest management practises, and its abundance is currently clearly higher in natural than managed boreal forests (Kouki *et al.*, 2004; Vehmas *et al.*, 2009). As the natural forest cover is very low in the Fennoscandian boreal zone, the whole aspen-dependent community is under threat and many aspen-dependent species from many species groups have been recently red-listed in Fennoscandia (Gärdenfors, 2010; Rassi *et al.*, 2010).

The diversity patterns of saproxylic insects have been actively studied. For example, it has been shown that the species richness is highest in natural forests and connected landscapes (Grove, 2002). Moreover, there has also been extensive research on how the log- and stand scale factors affect the saproxylic insect community (e.g. Grove, 2002; Abrahamsson & Lindbladh, 2006; Foit, 2010; Hjälten *et al.*, 2010). Most of this research has been conducted on one especially well-known saproxylic insect group, beetles (Coleoptera). Many studies have been conducted using window traps or other trapping systems which do not control the variation within the trunk, and are not able to ensure that the resulting fauna truly inhabits the particular trunk. Studies using emergence (eclector) traps, shifting or peeling as data collection methods have a clear benefit in controlling the biological role of the detected fauna in the studied substrate (e.g. Jonsell *et al.*, 2005; Alinvi *et al.*, 2007; Gibb *et al.*, 2008; Foit, 2010). On the basis of these studies, we know pretty well how the saproxylic beetle community varies between the adjacent trunks lying in the same forest. Still, there are no studies focusing on the variation in the nematoceran community within the forests, and in general the knowledge about the variation in insect community between different parts of individual decaying trunks is poor (although see Foit, 2010).

The nematoceran flies are a very diverse insect group, including several groups with a high number of saproxylic species. Two representatives of such groups are crane flies and fungus gnats. The vast majority of crane flies (Tipuloidea) are dwellers of wetlands and moist biotopes. Yet, larvae of certain species are saproxylic, living in the dead wood itself (Krivosheina, 2008) or in fruiting bodies of wood-decaying fungi (Ševčík, 2003, 2006). Except species-poor cylindrotomids, saproxylic and fungivorous species are represented in all tipuloid families. Considering the Finnish fauna, of 332 species, 13% (44 spp.) are saproxylic or fungivorous (J. Salmela, unpubl. data). Most of these belong to Limoniidae (23 spp.), followed by Tipulidae (16 spp.), and Pediciidae (5 spp.). Fungus gnats (Sciaroidea: Bolitophilidae, Diadocidiidae, Ditomyiidae, Keroplatidae, and Mycetophilidae) is a highly species-rich insect group typical of forest environments. Fruit bodies of wood-inhabiting fungi and dead wood impregnated with fungal mycelium are very important microhabitats for fungus gnats although it is unclear how large a part of the species are actually feeding on fungi and how many species are in fact not mycetophagous, but are in fact predatory or saprophagous (Jakovlev, 1994, 2011). Several rare and threatened species in both crane flies and fungus gnats are associated with deciduous dead wood and among these several seem to be specialised on inhabiting decaying aspen trunks (Penttinen *et al.*, 2010).

Here, we studied the nematoceran (crane fly and fungus gnat) communities and their physical environment on decaying aspen logs in a mixed boreal forest in Finland. We hypothesised that the communities living on a same trunk would be more similar than communities living on different trunks. Moreover, we hypothesised that the communities living in similar parts of different trunks would be more similar with each other than communities living in different parts of different trunks. We discuss our results both from the methodological and ecological point of view.

Materials and Methods

Study site

The research site (Kuusimäki) is located in the southern boreal vegetation zone (Ahti *et al.*, 1968) in the municipality of Muurame in Central Finland. It is a state-owned 80 ha large conservation site, with a history of slash and burn cultivation in the 19th century which was abandoned around the 1860s. The site was conserved as an old-growth forest in 1980s. At present, the forest is of high conservation value, mostly due to the occurrence of a high number of threatened saproxylic species. Compared to the managed forests around the study site, decaying birch (*Betula* spp.), Norway spruce (*Picea abies*), and Scots pine (*Pinus sylvestris*) trunks are abundant in the forest. The number of decaying aspen (*Populus tremula*) trunks is also considerable. According to the measurements made by the Finnish forest and park service, the volume of dead wood in the study site is around 50–80 m^3 ha^{-1}.

Study trunks and sampling

Trunk-emergence traps were used to study the dipteran communities on decaying fallen aspen logs. The trap model used was made entirely of transparent and highly air permeable green polyester cloth to prevent the modification of microclimatic conditions inside the trap (Fig. 1). The length of the trap was 1 m, meaning that the trap covers a section of about 1 m of a log. The vertical walls of the trap are long and have at their lower edges a selvage, which functions so that the long edges are folded beneath a log and attached firmly to the underside of the log. At both ends of the trap there is a collar, each having a selvage with a rope. The ropes are wound around the log so that the collar is attached tightly around the log.

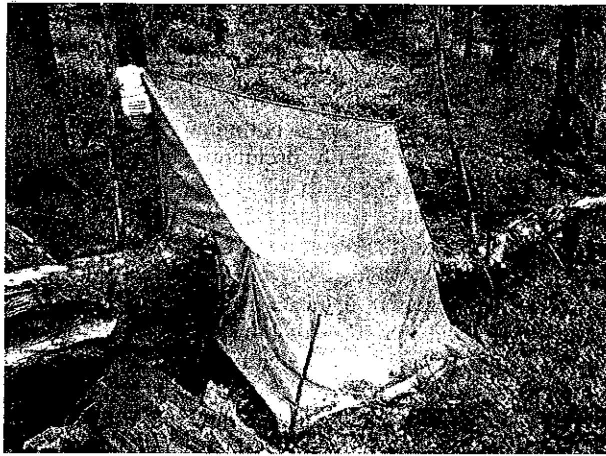

Fig. 1. Trap placed on the top part of an aspen trunk (trap number 2 in this study).

As a result, all insects hatching from the log section covered by the trap are captured in the trap while keeping the insects hatched elsewhere outside.

In all, we used 14 traps, which were placed on seven trunks (Table 1) so that one trap was always placed on the base of a trunk and the other to the top. The trunks were selected based on the earlier knowledge of the authors about the locations of suitable, large decaying aspen trunks in the study forest. The exact locations of the traps were selected so that they could be positioned properly. This meant, for example, selecting a place where the underside of the trunk was either visible or could be exposed to cover also the underside with the trap. We also avoided branches since they hinder the proper installation of the trap. Moreover, the locations were selected so that each trap could be positioned on a completely bark-covered section of the trunk. As a result of these conditions, the base traps were placed on average 4.1 m (SD 1.38) from the base, and the top traps on average 5.8 m (SD 2.53) from the top. The distance between the traps was on average 13.9 m (SD 2.83). The trunk diameter at base traps was on average 43.8 cm (SD 5.16) and at top traps 22.9 cm (SD 2.88). The difference in trunk diameter between the two traps was on average 20.9 cm (SD 4.45).

Table 1. Trap numbers, trap positions, trunk diameters, and decay stages at the trap.

Trap number	Trap position and trunk number	Trunk diameter (cm)	Decay stage
1	Base 1	40.0	2
2	Top 1	23.5	2
3	Base 2	40.0	2
4	Top 2	22.0	2
5	Base 3	36.0	2
6	Top 3	19.5	2
7	Base 4	46.0	3
8	Top 4	25.0	3
9	Base 5	50.5	2
10	Top 5	25.0	2
11	Base 6	47.0	2
12	Top 6	26.5	2
13	Base 7	47.0	2
14	Top 7	19.0	2

The decay stage of the trunks was measured at the traps based on the five class classification (Renvall, 1995) that is commonly used in similar studies. Based on these measurements, the decay stages of the trunks were found to be relatively similar: stage 2 on six trunks and stage 3 on one trunk. The decay stage was always similar on both traps of one trunk. We do not know the exact time of death or falling of these trunks, but based on our personal experience and the decay stages we estimate that they had been fallen for 5–15 years at the time of the sampling.

The traps were installed in the beginning of May (5–7 May 2008). Collecting jars were emptied five times (8.6., 7.7., 4.8., 20.8., and 5.10.). A solution of 50% ethylene glycol + a few drops of detergent was used as a preservative in the traps. The collected material was finally stored in 80% ethanol. The crane fly and fungus gnat specimens were sorted from the material in the laboratory and were identified to species level by the authors (crane flies by JS and fungus gnats by NV and JP). Considering crane flies, all individuals were identified to species level, but considering fungus gnats, only males could be identified to species level as their identification is to large extent based on male genitals. The voucher specimens are preserved in the Jyväskylä University Museum's Section of Natural Sciences, Zoological Museum, University of Turku or in the personal collections of authors.

To examine the variation in the physical conditions surrounding the dipteran community inhabiting the trunks, we conducted temperature and relative humidity measurements on one of the study trunks (trunk 1, see Table 1). These measurements were conducted 2 years after the species data was collected, but according to the Finnish Meteorological Institute, the weather conditions in these two summers were generally similar (http://ilmatieteenlaitos.fi/vuositilastot). For the measurements, we used data loggers (HOBO U12-012, Onset Computer Corporation, Cape Cod, MA, USA) that we set to record the temperature and relative humidity every 10 min. We placed two data loggers at each end of the trunk, one on the upper and one on the lower surface of the trunk. At each end, we also attached to one of the data loggers an external temperature probe that we placed inside the trunk, in a horizontal hole drilled up to the centre of the trunk from one side. The hole was then filled with sawdust and covered with tape to minimise the effects of the drilling on the conditions inside the trunk. The data loggers remained in the field from May 18th to October 20th, thus covering almost the whole snowless season in the study area. During this time, we downloaded the recorded data from the loggers and reset them at ca. monthly intervals.

Analyses

Sample-based rarefaction (Gotelli & Colwell, 2001; Magurran, 2004) was used to investigate accumulation of species in top and base trunks. Means and SDs were calculated by using Mao-Tau method (Colwell, 2011). Sample-based rarefaction was calculated by using EstimateS 8.2.0 (Colwell, 2011).

To analyse the similarity between the pairs of traps within different categories of the data, we calculated the *Chao-Jaccard abundance-based similarity estimator index*, which enables pairwise comparisons of communities (here traps) that take into account the possibility of undetected species (Chao *et al.*, 2005). We argue that estimating the effect of undetected species on the similarity of two communities is crucial when analysing this kind of data that includes several species with only one or a few individuals. Moreover, the effect of undetected species may jeopardise all conclusions if the sampling effort is different in compared groups (Chao *et al.*, 2005). In our case, the sampling effort is partly different because we standardised the length of the trunk covered by the trap, thus having a larger volume (or trunk surface) sampled from the bases than from the tops. We used this index to describe the variation between pairs of traps belonging to different categories (within a trunk, between base and top on different trunks, between base and base of different trunks, and between top and top of different trunks). The indexes were calculated using EstimateS 8.2.0 (Colwell, 2011).

As the pairwise Chao-Jaccard similarity values are not independent of each other, we adopted the randomisation-based Mantel test to study the similarity patterns (Quinn & Keough, 2002).The Mantel test assesses the statistical significance of the correlation between a data matrix, here the matrix of the pairwise similarities of the trap communities, and a model matrix. We conducted three separate tests. First, we tested whether similarities between trap pairs were different for within-trunk pairs compared to between-trunk pairs. In this test, the model matrix contained ones for the within-trunk pairs and zeros for the between-trunk pairs. Second, we tested whether the similarity of within-trunk, base-base, and top-top pairs was different from the similarity of the remaining pairs, that is those where the traps were at the top and base of different trunks. The model matrix for the second test contained ones for within-trunk, base-base, and top-top pairs and zeros for the other the pairs. Third, we tested whether the physical distance between trap pairs was associated with their similarity. Here, the model matrix contained the distances between the trap pairs in metres. In each test, we made 5000 randomisations of the data matrix, and used the Pearson correlation coefficient (r) to measure the correlation between the matrices.

To further analyse the community similarity between different trap pairs, we used SDR-simplex approach presented recently by Podani and Schmera (2011) (Fig. 4a). By partitioning the gamma diversity between two communities into additive components, this approach enables studying simultaneously how beta diversity, nestedness, and similarity contribute to the differences detected between two communities. We used the method to produce ternary plots which illustrate the roles of these three community indexes (similarity, nestedness, beta diversity) in the communities that we studied. Because also nestedness and beta diversity values are based on presence–absence data, the similarity measure used in this approach must be based on similar data. The similarity measure used here is the classic Jaccard similarity index. Podani and Schmera (2011) do not encourage conducting any significance testing on the results, but to use the plots for more illustrative purposes. Nevertheless, to clarify the role of randomness in the assemblages on our study trunks, we created also random assemblages for comparison. As the random beta diversity, nestedness or similarity is dependent on the fill (proportion of ones) in the species-by-sites matrix, we created the random assemblages separately for the communities occupying the top and base trunks. The randomisation was done by shuffling among the whole matrix so that the fill was retained. Because the randomised values are used for illustrative purposes instead of significance testing, we show only 100 randomly selected values for the first 20 randomly assembled matrices in the figures to retain clarity. The SDR values were calculated with SDR-simplex program (Podani & Schmera, 2011) and the ternary plots illustrating the values were drawn with Tri-plot version 1.4 (Graham & Midgley, 2000).

Trap number 12 (top trap in trunk six, Tables 1 and 2) included only one individual and made us suspect some possible damage in the trap even though no holes or other damages were detected. Such a small number of emerging individuals may not be exceptional, as some other top traps also resulted in relatively low numbers of individuals (Table 2). Still, we conducted all the analyses with and without trap 12 to see its effect on the results. The deletion of trap 12 changed the results of the Mantel tests and therefore we report their results both with and without trap 12. The SDR analyses are utilising presence–absence data and focusing on community similarity between different samples and therefore they are presented without trap 12.

Results

The 641 individuals which we could identify to species level belonged to 59 species of fungus gnats and 17 species of crane flies. Considering fungus gnats, most of the species were rare in the data and 31 species were detected only based on one individual. Only 23 species were detected on more than one trunk, and even the two most abundant species were presented by only 14 and 12 individuals (Table 2). On the other hand, there were totally 925 unidentified fungus gnat females, 555 and 370 individuals in the base and top trunks, respectively. The female-biased abundance in some nematoceran groups is known

Table 2. The numbers and abundances of different species detected in different traps. For clarity, the values considering the base traps are in italics.

Trap number (higher), trunk number (lower), and trap position (base/top)															
	Abundance	1 1 Base	2 1 Top	3 2 Base	4 2 Top	5 3 Base	6 3 Top	7 4 Base	8 4 Top	9 5 Base	10 5 Top	11 6 Base	12 6 Top	13 7 Base	14 7 Top
Abundance	641	*74*	34	*22*	43	*176*	31	*23*	11	*47*	5	*13*	1	*23*	138
Species		*19*	24	*9*	21	*8*	6	*14*	8	*17*	4	*6*	1	*11*	4
Fungus gnats															
Anatella ankeli	6			*1*				*1*		*3*				*1*	
Apolephthisa subincana	2					*2*									
Boletina basalis	2				1				1						
B. dispecta	1					*1*									
B. gripha	4		1		1			*1*				*1*			
B. jamalensis	1				1										
B. nigricans	3				1						1			*1*	
B. sciarina	1				1										
B. silvatica	4				2						1	*1*			
B. triangularis	1				1										
Brevicornu sericoma	1			*1*											
Dynatosoma reciprocum	14	*5*		*5*		*2*									2
Ectrepesthoneura pubescens	3									*3*					
Exechia contaminata	2				1	*1*									
E. dorsalis	5	*1*	1		1			*1*				*1*			
E. fusca	3	*2*								*1*					
E. exiqua	1							*1*							
E. parva	1				1										
Exechiopsis aemula	1		1												
E. clypeata	6	*1*	1	*1*	1	*1*								*1*	
E. januarii	1								1						
E. pseudopulchella	1		1												
E. seducta	1							*1*							
E. subulata	7		6					*1*							
E. (Xenexechia) leptura	1	*1*													
Leia cylindrica	1		1												
Macrocera pilosa	1						1								
Mycetophila abiecta	3		1							*2*					
M. brevitarsata	1														1
M. fungorum	1							*1*							
M. laeta	1								1						
M. luctuosa	2	*1*	1												
M. sumavica	1	*1*													
M. triseriata	1	*1*													
M. uliginosa	3						1				2				
Mycomya annulata	2		1		1										
M. nitida	1				1										
M. shermani	2				1									*1*	

Continued

Table 2. (continued)

Trap number (higher), trunk number (lower), and trap position (base/top)															
	Abundance	1 1 Base	2 1 Top	3 2 Base	4 2 Top	5 3 Base	6 3 Top	7 4 Base	8 4 Top	9 5 Base	10 5 Top	11 6 Base	12 6 Top	13 7 Base	14 7 Top
M. trivittata	1				1										
Myrosia maculosa	1		1												
Neuratelia nemoralis	1													*1*	
Neoplatyura flava	1													*1*	
Notolopha cristata	3		1	*1*					1						
Orfelia falcata	1						1								
O. unicolor	1	*1*													
Palaeodocosia janickii	5	*2*				*1*				*2*					
Phronia biarquata	2			*2*											
P. braueri	2							*2*							
P. obscura	3			*3*											
P. strenua	5	*3*						*1*					1		
P. triangularis	1									*1*					
Phthinia congenita	1	*1*													
Pseudorymosia fovea	4		1						1	*2*					
Rymosia bifida	1		1												
R. setiger	3		1											*2*	
Sciophila ochracea	2		1		1										
Syntemna stylatoides	12		2					*3*	3	*4*					
Tarnania fenestralis	1							*1*							
Trichonta girscheri	1		1												
Crane flies															
Epiphragma (Epiphragma) ocellare	6	*3*			2					*1*					
Euphylidorea phaeostigma	1													*1*	
Achyrolimonia decemmaculata	1														1
Atypophthalmus (Atypophthalmus) inustus	1									*1*					
Discobola annulata	14	*6*	3				1	*2*		*2*					
Elephantomyia (Elephantomyia) krivosheinae	6							*6*							
Limonia badia	339					*167*	22			*2*		*5*		*9*	134
Metalimnobia (Metalimnobia) charlesi	1		1												
Metalimnobia (Metalimnobia) quadrimaculata	1									*1*					
Rhipidia (Rhipidia) maculata	25						5			*17*		*3*			
R. (Rhipidia) uniseriata	12			*1*	11										
Tipula (Dendrotipula) flavolineata	2	*1*			1										
T. (Lunatipula) limitata	1		1												
T. (Pterelachisus) irrorata	9	*2*	2					*1*	2	*2*					
T. (Pterelachisus) stenostyla	35	*19*	2		9					*1*	1			*3*	
Ula (Ula) bolitophila	40	*22*	1	*7*	3				1	*2*		*2*		*2*	
U. (Ula) sylvatica	1	*1*													
Chodopsycha lobata	1					*1*									

for a while (Kjærandsen, 1993; Ekrem *et al.*, 2010), but no reasonable explanations have been given.

Considering specimens identified to species, crane flies were on an average much more abundant in the data. Even though seven species were detected by only one individual, the two most abundant species were presented by 339 and 40 individuals, respectively. Base and top trunks were numerically dominated by crane flies, *Limonia badia* was the most abundant species in both.

An average of 12.0 (SD 4.8) species were detected in the individual base traps and 9.7 (SD 9.0) in the top traps. The species richness in base and top traps was not significantly different (Paired samples t-test: $t = 0.727$, d.f. = 6, $P = 0.495$). When the data from the two traps from each trunk were combined, an average of 19.6 species (SD 9.6) was detected on one trunk.

According to sample-based rarefaction, both base and top trunks are characterised by rather similar rarefied species richness (Fig. 2). The rarefied richness curve of the base trunks lies above that of the top trunks, but the difference is not especially notable due to the overlapping standard deviation error bars. Rarefaction curves in both assemblages are showing no signs of flattening out, thus indicating the presence of undetected species (Fig. 2).

The Chao-Jaccard abundance-based similarity estimator values between the assemblages detected from different traps were mostly very low (Fig. 3). The average similarity between communities occupying the same trunk tended to be higher than for communities occupying different trunks ($r = 0.119$, $P = 0.054$, Fig. 3; $r = 0.229$, $P = 0.045$ without trap 12). But, the similarity of the pairs within groups (within-trunk, trunk bases, trunk tops) was not generally higher than that of the other pairs ($r = 0.043$, $P = 0.687$, Fig. 3; $r = 0.055$, $P = 0.612$ without trap 12). The distance between the traps did not have any effect on the similarity of the communities occupying them ($r = -0.069$, $P = 0.520$; $r = -0.111$, $P = 0.303$ without trap 12).

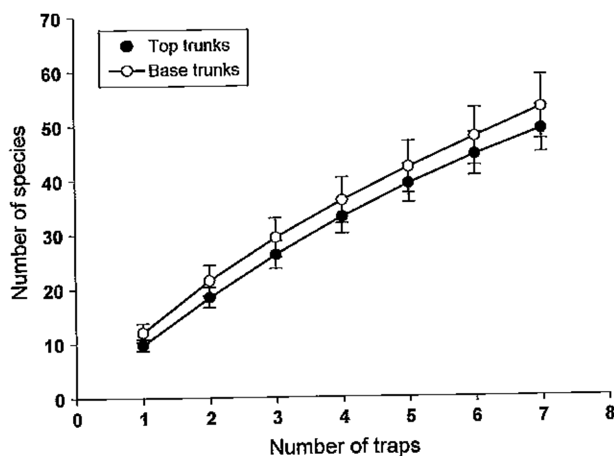

Fig. 2. Observed mean (±SD) species richness accumulation curves of base and top aspen trunks.

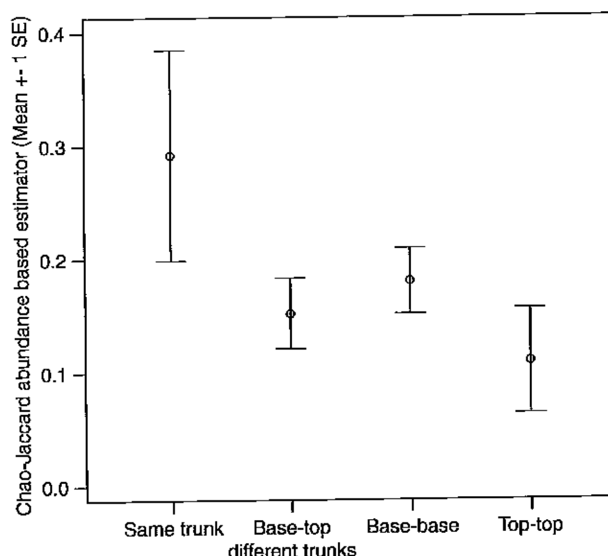

Fig. 3. The Chao-Jaccard abundance-based similarity estimator values between trap pairs belonging in different categories. 'Same trunk' means the base and top traps within a trunk, 'base-top different trunks' means similar base-top pairs, but calculated so that the base and top traps are always from different trunks. 'Base-base' pairs are pairs of two base traps and 'top-top' pairs of two top traps.

Looking at presence–absence data instead of abundance data, the similarities between the trap pairs were even lower (Fig. 4a–f). The fact that community similarity between sample pairs was low means also that beta diversity between the communities was very high (Fig. 4a–f). The beta diversity of the traps was on the level that could be expected from totally random assemblies when the fill of the data matrix is as low as in this data. Therefore, the community assemblies can be argued to be somewhat random and, for example, top traps were not more similar with each other than with base traps. Yet, there were several trap pairs among the top traps which did not share a single species (Fig 4f). Moreover, the communities in top traps seemed to have higher species richness differences among them than expected randomly (Fig 4f). Other than that, there were no clear differences between the communities occupying different parts of the trunks.

The physical environment was clearly different in different parts of the monitored log (Fig 5). On a daily scale (Fig. 5b), the greatest contrast was between the centre of the trunk base, where temperature remained fairly constant, and the other parts of the log which experienced pronounced daily cycles in temperature. In fact, inside the base the remaining low-amplitude daily cycle was reversed: the warmest time was shortly after midnight, the coldest in the early afternoon. Another clear difference can be seen between the upper and lower surface of the trunk base, the former having a markedly warmer and dryer microclimate than the latter. In fact, the upper surface of the base

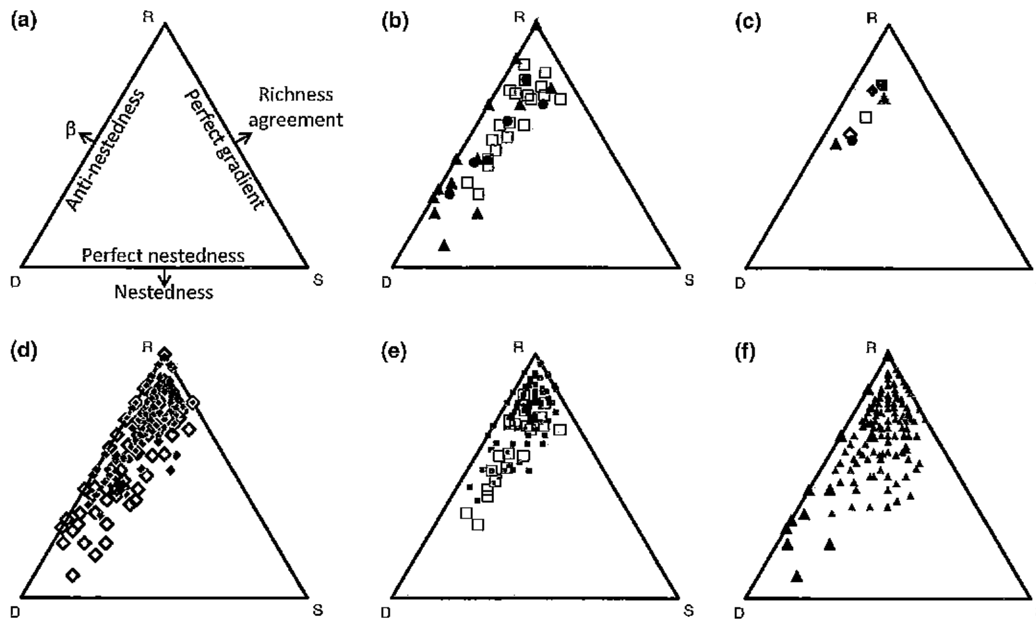

Fig. 4. SDR-simplex plots of the studied communities. (a) (modified from Podani & Schmera, 2011) illustrates the function of the plots. β = beta diversity, S = similarity, R = species replacement and D = species richness difference between the two communities. Each dot shows the relationship between two communities, here two traps. If, for example, the SDR value and thus the dot in the plot are close to the left side, the beta diversity between the studied communities is very high. The closer the dot is to R corner, the more beta diversity is resulting from species replacement instead of richness difference between the two samples. In (b and d–f) each dot represents a pair of two traps, ▲being values from pairs within the top data, □ values from pairs within the base data, • values from pairs within a trunk, and ◊ values from all possible pairs. To allow the comparison of our data with the null hypothesis of randomly assembled communities, the grey symbols are values from randomised top, base, and whole data matrices, respectively (for details of the randomisation, see text). In (c), the symbols represent mean values for each group. Thus, the figures represent (b) original data points from top data, base data, and within-trunk–trap pairs, (c) means of each original data category and each set of randomised values, (d) original values from the whole data showing every possible trap pair and randomised values from the same data, (e) original values from the base data and randomised values from the same data (f) original values from the top data and randomised values from the same data.

was usually the warmest and the lower surface the most humid of all measuring points. The amplitude of the daily cycle was also slightly reduced at the lower surface of the trunk. Conversely, there were no great microclimatic differences between the upper and lower surfaces and the inside of the trunk top. Considering the seasonal variation in the daily means (Fig. 5a), the ranking order of the measuring points was similar to that on the daily scale, both in terms of temperature and relative humidity. The upper surface of the trunk base had the warmest, the lower surface the coldest and most humid microclimate. Interestingly, a time lag in the temperature changes inside the trunk base can also be seen on the seasonal time scale. The daily mean temperature inside the base also typically did not drop as low as in other parts of the log. This effect was most striking towards the end of the season, when the inside of the base remained almost constantly warmer than the other measuring points.

Discussion

The nematoceran community on the decaying aspen logs seems to be species-rich and very variable already on the most local scale, that is within a log. Although communities within the same trunk were on average slightly more similar than communities in different trunks, there was considerable variation around this pattern, and in many cases the base and top traps shared only a few species. Looking at the abundance and estimating the effect of undetected species increased the similarity estimate compared to situation where only presence-absence information was used. This difference, however, is mostly resulting from *Limonia badia* being present in abundance in both traps of two trunks. The low similarity between the assemblages occupying bases and tops of the same trunks, evident in the SDR-simplex plots, was close to what was expected for randomly assembled data matrices with an equally low fill. Thus, based on our results, the communities of fungus gnats and crane flies appear to be mostly randomly and independently assembled on both ends of a trunk and are not dominated by species specialised either to base or top conditions.

When the focus was extended to the inter-trunk variation, but looking at the communities in similar parts of the trunks, the similarity between the samples was also very low. The communities in the tops were often even less similar with each other than the bases, and many

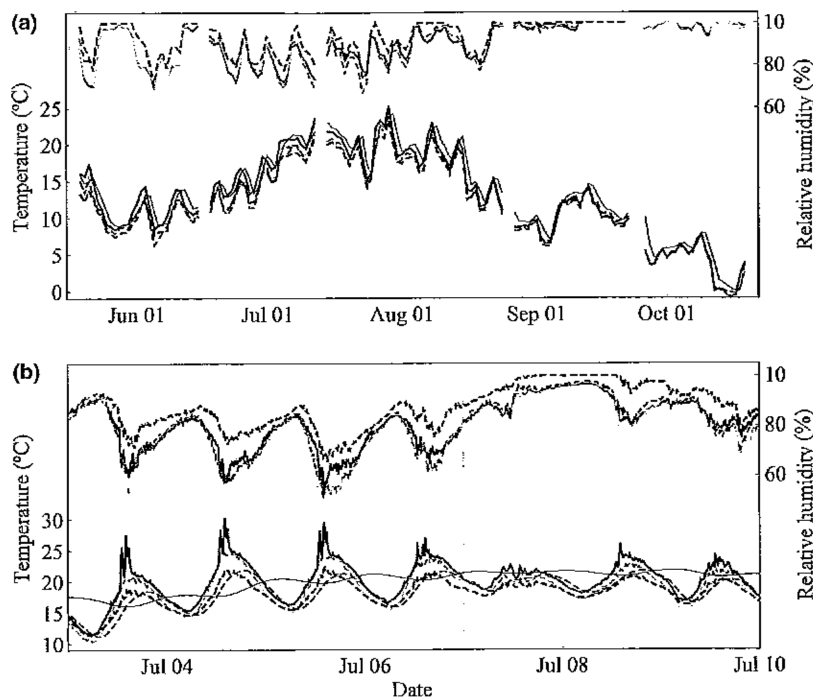

Fig. 5. Seasonal and daily variation in temperature (the lower curves) and relative humidity (the upper curves) at different parts of trunk 1. Red, solid = base, upper surface; blue, dashed = base, lower surface; black, solid = base, inside (temperature only); yellow, solid = top, upper surface; green, dashed = top, lower surface; black, dashed = top, inside (temperature only). (a) Daily mean values shown over the growth season. The small monthly gaps in all data series are due to the monthly logger resetting. The longer gaps in some data series are due to logger failure. (b) 10-minutely values shown over 1 week in July.

pairs of top traps did not include a single shared species. Yet, looking at the abundance data and estimating the effect of undetected species resulted in the similarities of top-top and base-base pairs to be on the same level. According to the SDR-simplex analysis, community assembly appears to be close to random also at the inter-trunk scale. There were also no evident spatial patterns in community composition within the study site.

Looking at the variation in the physical environment both between and within the base and top parts of the sampled trunk, it is easy to understand the low similarity between the communities occupying them. The nematoceran species are most likely partly adapted to different temperature and moisture conditions, and thus for example the base's ability to stabilise temperature lows and peaks may be meaningful for their success in this environment. Still, this variation in the physical environment was very high also on the different surfaces of the same parts of the trunk where the measurements were taken. One can easily see that a larva living just under the upper surface bark faces very different conditions than another living in the same niche below the trunk. This makes it questionable, what are the relevant different parts of the trunks after all. It may well be, that the lowest and highest quarter of the trunk in the base part would host at least as dissimilar communities as the highest quarter in the base and the top parts. This issue is not, however, easily studied with traditional emergence traps. Instead, an approach utilising novel high-throughput sequencing and seeking larval DNA from standardised tree samples from different parts of the trunks could be efficient (see e.g. Ovaskainen *et al.*, 2010 for this approach).

Nematoceran taxonomy is mostly based on the structure of male sexual organs, and the association of conspecific sexes may be ambiguous using morphological approach only (e.g. Kurina *et al.*, 2011). Due to this difficulty, over 900 collected fungus gnat female specimens were left unidentified. It is likely that this portion of our sample included species that were not represented by the males. Thus, the real species richness of our total sample would be higher than that of the observed richness. As shown by Ekrem *et al.* (2010), adult nematoceran samples may have biased sex-ratios and females may account for one-third of the observed species richness at minimum. The unidentified female samples are also a source which would probably reduce notably the number of species with only single individual in our data.

Our results were partly surprising because we expected to see some part of insect community to be specialised in the differently sized dead wood. If this would have been true, we should have detected some nestedness, for example, among the base samples. At least among fungi and beetles species specialising to different dead wood types have been shown to exist (Hjälten *et al.*, 2007; Hottola,

2009). It may of course be that the variation in the size between base and top samples is not high enough to detect such specialisation patterns, and as discussed earlier, the above and below surfaces of the trunks are in many respects at least as different as base and top. To find specialised species, we should have perhaps sampled, for example, the thin branches or only the below surface of the trunk base. Another reason may be that there are too many confounding factors affecting the situation. It may, for example, be that the fungal species occupying the particular part of the trunk are more important in determining the nematoceran community than the actual diameter, such has been earlier shown considering beetles (Jonsell *et al.*, 2005). Indeed, rearing experiments conducted during the last 15 years or so suggest that many fungus gnat species may be restricted to single species or a single genus of fungi (e.g. Ševčík, 2001; Jakovlev, 2011) even though it is often argued that polyphagy is a rule in mycetophagous insects because fruit bodies of fungi are ephemeral and highly unpredictable in occurrence (see e.g. Hanski, 1989). The lifespan of fruit bodies of many wood-inhabiting fungi for example perennial polypores is in fact considerably long, not to mention the fungal mycelium living inside dead wood which may inhabit the same log for several years or even decades. There may also be an interplay of physical factors such as temperature and moisture and the fungal assemblage inside a log, leading to differences in suitability between different logs and different sections of single log to nematoceran species, thereby creating great variation in nematoceran assemblages.

To conclude, nematoceran communities in different parts of dead wood are diverse and local variation is very high. We are far from understanding what are the factors determining the local species assemblages. The future studies should address the dead wood quality in more detailed manner. For example, more attention should be paid on the qualities that enable the occurrences of the rarest species. Only after understanding them can we promote for forest management to focus on maximising optimal dead wood types.

Acknowledgements

We are grateful to three anonymous reviewers for their constructive comments on an earlier version of the manuscript. We thank Panu Kuokkanen from Metsähallitus for research licences. This work was funded by the Finnish Entomological Society (grant to NV), Finnish Cultural Foundation (Post Doc Pool grant to PH) and the Centre of Excellence in Evolutionary Research.

References

Abrahamsson, M. & Lindbladh, M. (2006) A comparison of saproxylic beetle occurrence between man-made high-and low-stumps of spruce (Picea abies). *Forest Ecology and Management*, **226**, 230–237.

Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968) Vegetation zones and their sections in northwestern europe. *Annales Botanici Fennici*, **5**, 169–211.

Alinvi, O., Ball, J.P., Danell, K., Hjälten, J. & Pettersson, R.B. (2007) Sampling saproxylic beetle assemblages in dead wood logs: comparing window and eclector traps to traditional bark sieving and a refinement. *Journal of Insect Conservation*, **11**, 99–112.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.J. (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, **8**, 148–159.

Colwell, R.K. (2011) *Statistical estimation of species richness and shared species from samples. Version 8.2.0.* <http://viceroy.Eeb.Uconn.edu/estimates> 15th January 2012.

Ekrem, T., Stur, E. & Hebert, P.D.N. (2010) Females do count: documenting Chironomidae (Diptera) species diversity using DNA barcoding. *Organisms Diversity and Evolution*, **10**, 397–408.

Foit, J. (2010) Distribution of early-arriving saproxylic beetles on standing dead Scots pine trees. *Agricultural and Forest Entomology*, **12**, 133–141.

Gärdenfors, U.(ed.) (2010) *The 2010 Red List of Swedish Species.* Artdatabanken, Swedish Agricultural University, Uppsala, Sweden.

Gibb, H., Hilszczanski, J., Hjälten, J., Danell, K., Ball, J.P., Pettersson, R.B. & Alinvi, O. (2008) Responses of parasitoids to saproxylic hosts and habitat: a multi-scale study using experimental logs. *Oecologia*, **155**, 63–74.

Gotelli, N. & Colwell, R. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Graham, D.J. & Midgley, N.G. (2000) Graphical representation of particle shape using triangular diagrams: an excel spreadsheet method. *Earth Surface Processes and Landforms*, **25**, 1473–1477.

Grove, S.J. (2002) Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics*, **33**, 1–23.

Hanski, I. (1989) Fungvory: fungi, Insects and Ecology. *Insect-Fungus Interactions* (ed. by N. Wilding), pp. 25–68. Academic Press, London, UK.

Hjälten, J., Johansson, T., Alinvi, O., Danell, K., Ball, J.P., Pettersson, R., Gibb, H. & Hilszczanski, J. (2007) The importance of substrate type, shading and scorching for the attractiveness of dead wood to saproxylic beetles. *Basic and Applied Ecology*, **8**, 364–376.

Hjälten, J., Stenbacka, F. & Andersson, J. (2010) Saproxylic beetle assemblages on low stumps, high stumps and logs: implications for environmental effects of stump harvesting. *Forest Ecology and Management*, **260**, 1149–1155.

Hottola, J. (2009) *Communities of wood-inhabiting fungi: ecological requirements and responses to forest management and fragmentation.* PhD thesis, University of Helsinki.

Jakovlev, J. (1994) *Palaearctic Diptera Associated with Fungi and Myxomycetes.* Karelian Scientific Centre of Russian Academy of Sciences, Petrozavodsk. (in Russian with an English abstract).

Jakovlev, J. (2011) Fungus gnats (Diptera: Sciaroidea) associated with dead wood and wood growing fungi: new rearing data from Finland and Russian Karelia and general analysis of

known larval microhabitats in Europe. *Entomologica Fennica*, **22**, 157–189.

Jonsell, M., Schroeder, M. & Weslien, J. (2005) Saproxylic beetles in high stumps of spruce – fungal flora important for determining the species composition. *Scandinavian Journal of Forest Research*, **20**, 54–62.

Junninen, K., Penttilä, R. & Martikainen, P. (2007) Fallen retention aspen trees on clear-cuts can be important habitats for red-listed polypores: a case study in finland. *Biodiversity and Conservation*, **16**, 475–490.

Kjærandsen, J. (1993) Diptera in mines and other cave systems in southern Norway. *Entomologica Fennica*, **4**, 151–160.

Kouki, J., Arnold, K. & Martikainen, P. (2004) Long-term persistence of aspen – a key host for many threatened species – is endangered in old-growth conservation areas in finland. *Journal for Nature Conservation*, **12**, 41–52.

Krivosheina, M.G. (2008) Biology of xylobiont larvae of limoniid flies the genus gnophomyia (diptera, limoniidae) with description of immature stages. *Entomological Review*, **88**, 778–792.

Kurina, O., Ounap, E. & Ramel, G. (2011) *Baeopterogyna mihalyii* Matile (Diptera, Mycetophilidae): association of sexes using morphological and molecular approaches with the first description of females. *Zookeys*, **114**, 15–27.

Kuusinen, M. (1994) Epiphytic lichen flora and diversity on populus-tremula in old-growth and managed forests of southern and middle boreal finland. *Annales Botanici Fennici*, **31**, 245–260.

Lassauce, A., Paillet, Y., Jactel, H. & Bouget, C. (2011) Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators*, **11**, 1027–1039.

Lonsdale, D., Pautasso, M. & Holdenrieder, O. (2008) Wood-decaying fungi in the forest: conservation needs and management options. *European Journal of Forest Research*, **127**, 1–22.

Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell Science, Oxford, UK.

Ovaskainen, O., Nokso-Koivisto, J., Hottola, J., Rajala, T., Pennanen, T., Ali-Kovero, H., Miettinen, O., Oinonen, P., Auvinen, P. & Paulin, L. (2010) Identifying wood-inhabiting fungi with 454 sequencing-what is the probability that BLAST gives the correct species? *Fungal Ecology*, **3**, 274–283.

Penttinen, J., Ilmonen, J., Jakovlev, J., Salmela, J., Kuusela, K. & Paasivirta, L. (2010) Thread-horned flies (*Diptera: Nematocera*). *The 2010 red list of Finnish species* (ed. by P. Rassi, E. Hyvärinen, A. Juslén and I. Mannerkoski), pp. 477–489. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki, Finland.

Podani, J. & Schmera, D. (2011) A new conceptual and methodological framework for exploring and explaining pattern in presence-absence data. *Oikos*, **120**, 1625–1638.

Quinn, G.P. & Keough, M.J. (2002) *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, UK.

Rassi, P., Hyvärinen, E., Juslén, A. & Mannerkoski, I. (eds) (2010) *The 2010 Red List of Finnish Species*. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki, Finland.

Renvall, P. (1995) Community structure and dynamics of wood-rotting basidiomycetes on decomposing conifer trunks in northern finland. *Karstenia*, **35**, 1–51.

Ševčík, J. (2001) Diptera (excluding Mycetophilidae s. str.) associated with fungi in Czech and Slovak Republics: a survey of rearing records from 1998–2000. *Acta Universitatis Carolinae Biologica*, **45**, 157–168.

Ševčík, J. (2003) Insects associated with wood-decaying fungi in the czech and slovak republics: a review of present knowledge. *Acta Facultatis Rerum Naturalum Universitatis Ostrava, Biology and Ecology*, **9**, 159–165.

Ševčík, J. (2006) Diptera associated with fungi in czech and slovak republics. *Casopis Slezskeho Zemskeho Muzea, Serie A, Vedy Prirodni*, **55**, 1–84.

Siitonen, J. & Martikainen, P. (1994) Occurrence of rare and threatened insects living on decaying *Populus tremula* – a comparison between Finnish and Russian Karelia. *Scandinavian Journal of Forest Research*, **9**, 185–191.

Vehmas, M., Kouki, J. & Eerikäinen, K. (2009) Long-term spatio-temporal dynamics and historical continuity of European aspen (Populus tremula L.) stands in the Koli national park, eastern Finland. *Forestry*, **82**, 135–148.

Accepted 4 October 2012
First published online 4 December 2012

Editor/associate editor: Simon R. Leather