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Occurrence patterns of aspen-feeding wood-borers (Coleoptera: Cerambycidae) along the wood decay gradient: active selection for specific host types or neutral mechanisms?

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Abstract. 1. Determinants of host-use patterns in plant-feeding insects have been extensively studied, usually within the framework of optimality theory. Comparatively, factors driving host selection in saprophagous insects have received little attention.

2. In this study, mechanisms creating occurrence peaks of saprophagous wood-borers (Cerambycidae: Coleoptera) in standing dead aspen in the middle and late stages of decay were investigated by correlating insect occurrence with variations in substrate-related nutritional and physical parameters. Twenty-four snags at four decay stages were dissected from a mature stand in western Quebec, Canada. Wood samples were taken to measure levels of nitrogen, non-structural carbohydrates, phenols, wood density, water content and snag age.

3. Several nutritional and physical parameters varied significantly along the decay gradient and were correlated with insect occurrence, but all significant parameters were also strongly correlated with snag age and wood density. Model selection using Akaike's second order information criteria was used to rank the different models; the model including snag age only performed best, with a w_i of 0.873.

4. This importance of snag age gives support to a proposed hypothesis of host selection in which temporal autocorrelation in probability of insect occurrence explains peaks observed in the middle and late stages of decay. However, further studies will be needed to confirm the prevalence of such neutral mechanisms over active selection in the determination of host-use patterns in decaying aspen.

Key words. Boreal forest, Cerambycidae, coarse woody debris, dead-host species, host selection, insect nutrition, optimality, saproxylic insects.

Introduction

Host-use patterns and host-selection behaviour have been extensively studied in plant-feeding insects. Most insects show some degree of specialisation in their choice of host, whether it is as feeding or oviposition material (Jaenike, 1990; Bernays & Chapman, 1994). Host selection and specialisation have typically been approached within the framework of optimality theory (Pianka, 1976; Thompson, 1988; Mayhew, 2001; Scheirs & De Bruyn, 2002), which states that behaviours should be interpreted in terms of the contributions they make to the inclusive fitness of organisms (Maynard Smith, 1978). The preference–performance hypothesis of host selection, which predicts that ovipositing females should select hosts on which larval performance would be the greatest in order to maximise their fitness (Jaenike, 1978), is a direct application of optimality theory. Specialisation may arise from trade-offs between abilities in dealing with different physical and/or nutritional contexts. Specialisation thus produces smaller-breadth niches that can

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result in successional-type patterns when different groups of organisms evolve trade-offs leading to specialisation on different parts of an environmental gradient.

Among insects, species which directly feed on wood play important functional roles in forest ecosystems, as they contribute to wood decay by acting as vectors for wood-decaying fungi and by weakening the wood structurally by excavating extensive gallery networks (Rayner & Boddy, 1988; Haberkern *et al*., 2002). Because of this, dead trees colonised by wood-feeding insects usually exhibit a high rate of decay (Edmonds & Eglitis, 1989; Dajoz, 2000). Insects are also particularly diversified in dead wood, as assemblages found often comprise several trophic levels and vary according to the tree species, the anatomical region of the tree and the stage of decay (Dajoz, 2000).

In standing dead aspen (*Populus tremuloides* Michaux), host use by saprophagous wood-feeding Coleoptera has been shown to be concentrated in middle and late stages of decay (Saint-Germain, 2007). However, the mechanisms creating these host-use patterns are not currently understood. Although insects that feed on dead plant material do not face the same constraints as those that feed on living plant tissue (e.g. no induced defence mechanisms), the optimality theoretical framework should still be relevant. To date it has received little attention in studies focusing on host-use by saprophagous Coleoptera. Several environmental factors known to vary along the wood decay gradient may create opportunities for active selection and specialisation by wood-boring insects. Links between nutritional and physical substrate-related factors and species occurrence and/or larval performance have been suggested in the literature. Studies have shown a positive impact of higher nitrogen (N) content on larval growth rates of some Cerambycidae (Coleoptera) (Becker, 1977; Hosking & Hutcheson, 1979; Forcella, 1982; Shibata, 1998), and the N content of dead wood generally varies significantly along the decay gradient (Lambert *et al*., 1980; Fahey, 1983; Alban & Pastor, 1993; Holub *et al*., 2001). The importance of non-structural carbohydrates (NSCs) has also been suggested for some wood-feeding species that lack the ability to digest structural polysaccharides (Parkin, 1940); however, variations of NSCs along the decay gradient are poorly documented. Some physical characteristics, including wood density and water content, obviously vary along the decay gradient (Lambert *et al*., 1980), and may also have an influence on host selection and larval performance (Graham, 1925; Becker, 1977).

Little is known, however, on how these nutritional or physical factors influence wood-boring insect occurrence patterns, and, particularly, whether active selection by individual species for specific parts of the decay gradient plays a role in creating the apparently non-random patterns seen in aspen. In this study, this issue was approached by considering two conceptual models of host selection (Fig. 1), and discussing the relative support obtained by each in correlative analyses relating the physical and nutritional qualities of dead wood to insect occurrence over the decay gradient. A brief description of these models follows.

1. *Active selection model*. Two conditions are prerequisites for active selection of a specific decay stage. At least one biologically significant parameter must vary along the environmental gradient considered, and the ovipositing female must be able to detect these variations. If both conditions are met, then a basis exists for actual specialisation to take place. If different species specialise for different parts of the gradient, a succession-type pattern occurs (Fig. 1a). In this model, increased insect occurrence seen in mid to late stages of decay in dead aspen is a result of active selection of such hosts by the female, based on her evaluation of one or several parameters, either physical or nutritional.
2. *Temporal autocorrelative neutral model*. In this model, the female does not discriminate among dead aspen, regardless of any variations in nutritional or physical quality. Increased insect occurrence in mid and late stages of decay is solely the result of dispersal constraints and of some elements of behaviour seen in wood-borers feeding on dead deciduous hosts that increase the probability that a snag used 1 year will still be used by the same species the following year. This temporal autocorrelation effect

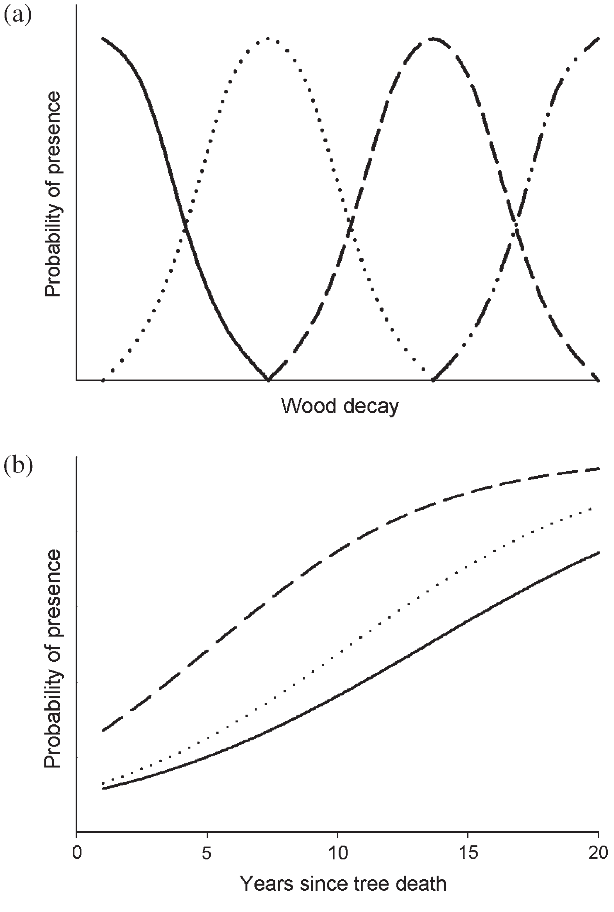

Fig. 1. Conceptual models describing the occurrence of dead-host cerambycid species along the decay gradient. (a) Active selection model, in which specialisation of different groups of species for successive parts of the gradient creates a successional pattern. (b) Neutral model based on temporal autocorrelation in the probability of insect presence in which colonised snags remain so until they exit the system. The shape of the curve varies with the annual probability of colonisation, indicated on the figure, and thus is linked with dispersal constraints.

> results in older snags having higher probabilities of being used by larvae, without any active selection for substrate quality beyond choosing a dead deciduous tree, and can be explained by larval development spanning several years, or by the tendency of emerging adults to oviposit on the same host from which they emerged (Hanks, 1999). In the model presented in Fig. 1b, each snag has a given probability of being colonised each year, but, once colonised, it remains so for the following years until it is no longer suitable (i.e. snags fall).

To assess the relative support given to these two models, occurrence patterns of wood-boring beetles (Coleoptera: Cerambycidae) were first described by dissecting 24 snags of all standing decay stages from a nearly pure aspen stand in western Quebec, Canada. Changes occurring in dead wood as decomposition increases were characterised by measuring the nutritional and physical parameters of the snags sampled for insects. Relationships between species occurrence and the measured parameters were assessed using model selection and hypothesis-testing approaches to identify underlying mechanisms leading to the host-use patterns observed along this decay gradient. Interpreting the observed species occurrence patterns in the light of the aforementioned conceptual models may give some insight into mechanisms driving the host-use patterns of aspen-feeding dead-host species.

Materials and methods

In May 2004, a mature, closed-canopy aspen stand was selected in the Lake Duparquet Research and Teaching Forest (Université du Québec en Abitibi-Témiscamingue, western Quebec, Canada; 48°28′N, 79°16′W). This stand harboured a high density of snags of all decay stages, with average diameters > 25 cm, and was located in a landscape mainly composed of similar (~85-year-old) aspen stands. Transects were established perpendicular to the edge of the stand 40 m apart, along which 24 snags were selected arbitrarily, composed of 6 snags of each of the four decay classes covering all standing stages of decay (Table 1) as described in Maser *et al*. (1979) (classes 1 and 2 refer to living and declining trees).

In July 2004, three wood samples (~20 ml each) were systematically taken around the bole of each snag at 120 degrees from each other 0.5 m above ground to measure nutritional parameters. These samples included the last growth rings of the sapwood to a depth of 1 cm. Samples were kept on dry ice during transport and frozen at −80 °C once back in the laboratory. Phloem and cambium were excluded because they are generally present only in the first decay classes and are not the main object of dead-host species nutrition. Sapwood samples were taken at the surface of the snag to measure nutritional parameters as they would be assessed by an ovipositing female during host selection.

At the end of July, the 24 snags were cut down and a 1-m section (at 0.5–1.5 m above ground level) was taken to the laboratory for insect sampling. Three 4-cm-thick wood discs, two over the 1-m section and one at 5 m above ground, were also taken to determine the time of tree death and to measure physical parameters. The presence of fruiting bodies of wood-decaying fungi was noted for all snags. Insect sampling was performed by first peeling the bark and examining the subcortical tissues for insects (adults and larvae). The bole was then cut into segments (~20 cm long) and these were carefully dissected with axes and hatchets, following galleries or other signs of use. All insects found were collected.

Determination of the age of snags

The time of death of the 24 snags was estimated using dendrochronology. For each snag, growth rings were measured on four radii on two of the wood discs, taken at 1.5 m and 5 m respectively. Measurements were cross-dated using the software COFECHA (Grissino-Mayer, 2001) with master chronologies previously produced at these same sites (Bergeron *et al*., 2002; Lecomte *et al*., 2005).

Measurement of physical parameters

Three physical parameters of dead wood were measured: wood density, the capacity of the wood to absorb water, and the capacity of wood to hold water. All were measured using the same samples, three ~50-ml wood blocks taken systematically at 120 degrees around the bole from the remaining wood disc taken at ~1.5 m above ground. Wood density was measured by averaging the density (dry weight/volume) of these three samples. Volume was measured by water displacement. Wood density was used in subsequent analyses to represent the decay gradient. Reliable measurements of water content could not be taken at the moment of sample collection. Instead, the capacity of the wood to absorb water was measured by saturating the wood samples by immersing them in water for 72 h. They were then weighed and oven-dried them at 60 °C to weight constancy. Their capacity to absorb water was calculated as millilitres of water held by 1 cm^3 of wood when saturated. To complement this information, the water loss rate of saturated wood put to dry in an oven at 60 °C (capacity to hold water) was also measured. Samples were weighed every hour for 8 h, and the loss rate was measured as the slope of a regression made on the percentage of total water held lost every hour.

Measurement of nutritional parameters

Three parameters related to the nutritional quality of the substrate were measured: total N; total NSCs, and total phenols. Nitrogen and carbohydrates are among the most important and limiting nutrients for insects and phenols constitute an important class of secondary compounds, which often have negative effects on insect performance (Haack & Slansky, 1987). Wood samples (see above) were oven-dried at 60 °C, milled to a fine powder, and then stored at −80 °C until analysed. For N, 50 mg of wood powder was digested in 10 ml of acid mix as described

Table 1. Characterisation of all 24 snags sampled, and species and number of insects collected through wood dissection. Decay classes follow Maser *et al*. (1979). Diameter was measured at breast height. Wood density = dry weight/volume (g cm^{-3}).

Snag	Decay class	Diameter	Years since tree death	Wood density	Presence of fruiting bodies	*Anthophylax attenuatus* (Haldeman)	*Bellamira scalaris* (Say)	Others
1	3	40.1	3	0.283	No	0	0	0
2	3	21.0	9	0.287	No	0	0	0
3	3	19.9	4	0.291	Yes	0	0	0
4	3	20.2	3	0.351	No	0	0	0
5	3	33.5	3	0.388	No	0	0	0
6	3	19.8	3	0.404	No	0	0	0
7	4	24.2	8	0.237	No	27	2	0
8	4	35.3	14	0.262	No	11	0	0
9	4	31.5	4	0.314	No	0	0	0
10	4	25.3	6	0.333	Yes	6	0	1
11	4	19.6	2	0.355	No	0	0	0
12	4	21.4	2	0.405	No	0	0	0
13	5	25.3	11	0.187	No	18	1	0
14	5	31.0	19	0.203	No	1	0	0
15	5	22.4	7	0.255	Yes	1	0	0
16	5	31.7	10	0.276	Yes	59	1	1
17	5	22.0	12	0.282	Yes	1	0	0
18	5	27.2	10	0.285	Yes	7	0	0
19	6	28.4	13	0.175	Yes	8	0	0
20	6	29.6	21	0.194	Yes	1	0	0
21	6	33.6	22	0.224	No	3	0	1
22	6	23.6	19	0.232	No	1	4	0
23	6	20.0	11	0.248	No	14	0	0
24	6	29.2	21	0.265	Yes	4	0	0

in Parkinson and Allen (1975). Samples were then diluted to 100 ml with de-ionised water and N levels were measured with a Lachat QuickChem 8000 flow injection auto-analyser (Hach Company, Inc., Loveland, CO, U.S.A.). For NSCs, which include glucose, fructose, sucrose and starch, 50 mg of wood powder was extracted in 20 ml of distilled water. The suspension was heated at 60 °C for 1 h to aid extraction. A 200 µl aliquot was then successively treated with invertase, phosphoglucose-isomerase and amyloglucosidase to convert starch, fructose and sucrose to glucose, as described in Wong (1990). Glucose levels were then photometrically assessed at 340 nm after treatment with a hexokinase. For total phenols, 50 mg of wood powder was extracted in 50% methanol (v/v) for 16 h in an orbital shaker. One hundred microlitre aliquots were then assayed using the Folin–Ciocalteu method, as described in Waterman and Mole (1994).

Statistical analyses

Probability plots from logistic regressions were used to illustrate host-use patterns of Cerambycidae along the decay gradient, with wood density and snag age as independent variables and the presence/absence of larvae (all dead-host species combined) as the dependent variable. All nutritional and physical variables were related to wood density using linear regressions to see how these parameters changed over the decay gradient. These parameters (snag age, wood density, water content, water loss rate, snag diameter, N, phenols and NSCs) were also related to occurrence (presence/absence) of insects using simple logistic regressions, and to log-transformed abundance with linear regressions. Correlations were used to build a correlation matrix between all measured parameters.

To test how several models including different sets of parameters fit the observed patterns of presence/absence along the decay gradient, both model selection and standard hypothesis testing were used. Model selection is an analytical approach in which several competing hypotheses are simultaneously confronted with data (Johnson & Omland, 2004). Models are then ranked according to their relative weighted support. Aikake's second order information criteria (corrected for low sample sizes) were used to compare competing models. Each model was also tested using simple or multiple logistic regressions. Tested models are described in Table 2. Analyses of variance and linear regressions were performed in SPSS 10.0.5 for Windows (SPSS, Inc., Chicago, IL, U.S.A.). Logistic regressions were performed in SYSTAT 11.00 (Systat Software, Inc., Point Richmond, CA, U.S.A.).

Results

Host-use patterns along the decay gradient

A total of 173 dead-host cerambycid larvae were found in the 24 snags. The assemblages were species-poor, as *Anthophylax attenuatus* represented 93.6% of larvae found, and *Bellamira*

Table 2. Presentation of all models included in model selection, with underlying theoretical basis.

Model	Theoretical basis	References
Nutritional		
Nitrogen	Larval performance ↑ with higher N levels	Hosking & Hutcheson (1979), Shibata (1998)
Non-structural carbohydrates (NSCs)	Some species dependent on high NSC concentrations	Parkin (1940)
Phenols	Defence compounds; may influence larval performance	Haack & Slansky (1987)
Nitrogen + phenols	Combined nutritional effects	See above
Nitrogen + NSCs + phenols	Combined nutritional effects	See above
Physical		
Diameter	Diameter affects species composition	Araya (1993), Hammond *et al*. (2004)
Volume	Correlate of diameter	See above
Wood density	Decay stage affects species composition	Graham (1925), Vanderwel *et al*. (2006)
Water content + water loss	Water content affects survival rates	Chararas (1981)
Wood density + water content	Combined physical effects	See above
Diameter + wood density + water content	Combined physical effects	See above
Wood density + water content + water loss	Combined physical effects	See above
Others		
Age	Temporal autocorrelation hypothesis	See Introduction
Presence of fruiting bodies	Species composition affected by fungal flora	Jonsell *et al*. (2005)

scalaris 4.6% (Table 1). Occurrence of these species was concentrated at the end of the decay gradient (low wood density). Most snags of early decay stages contained no or few larvae, whereas all snags with a wood density <0.282 g cm^{-3} contained larvae (covered density range: 0.405–0.175). As *A. attenuatus* was numerically dominant and there were no differences in occurrence patterns between the two main species, further analyses were carried out with pooled species data. Fig. 2a illustrates the probability of occurrence along a wood density gradient as calculated using a binary logistic regression ($\chi^2_1 = 17.375$; $P < 0.001$). Probability of occurrence (presence of at least one larva) is close to 0 at the beginning of the gradient, and increases in a sigmoid fashion to close to 1 in the middle to late stages of decay. This increase is steeper when the probability of occurrence is calculated with snag age and reaches 1 at around 10 years of age (Fig. 2b). Log-transformed abundance increases in the second half of the covered decay gradient ($F_{1,23} = 8.505$; $P = 0.008$) (Fig. 2c). However, there is no apparent trend in abundance within the part of the gradient in which all trees are colonised. This relationship is not significant when snag age is used as the independent variable (Fig. 2d).

Changes in wood quality along the decay gradient

All physical parameters varied significantly along the decay gradient. Wood density decreased with snag age, going from ~0.4 g cm^{-3} at tree death to ~0.2 g cm^{-3} in older snags ($F_{1,23} = 27.52$; $P < 0.001$; Fig. 3a). Wood density was further used to describe the decay gradient, as the decay rate is expected to vary between trees depending on intrinsic and extrinsic factors, and thus wood density may reflect the extent of decay more precisely than snag age. Wood absorbency increased with decreasing wood density ($F_{1,23} = 35.19$; $P < 0.001$; Fig. 3b), whereas the water loss rate decreased ($F_{1,23} = 11.88$; $P = 0.002$; Fig. 3c); thus wood in late stages of decay absorbs more water and loses it more slowly in dry conditions. Among nutritional parameters, N concentration levels were low in wood in early stages of decay and decreased significantly as wood decayed ($F_{1,23} = 18.51$; $P < 0.001$; Fig. 3d). Non-structural carbohydrates were also found in low concentrations, and decreased significantly as wood decayed ($F_{1,23} = 5.57$; $P = 0.028$; Fig. 3e). Phenols were rather stable throughout the gradient, at around 10 mg g^{-1}, except for in a few trees with much higher concentrations ($P > 0.05$; Fig. 3f).

Relationships between wood quality and occurrence of cerambycid larvae

Relationships between insect occurrence, insect abundance and wood quality were first assessed separately using simple logistic regressions. Significant relationships between insect occurrence and snag age, wood density, water content, water loss rate and N were observed (Table 3). Probability of occurrence of larvae decreased with increasing wood density ($\chi^2_1 = 17.38$; $P < 0.001$) and water loss rate ($\chi^2_1 = 12.68$; $P < 0.001$), and increased with increasing snag age ($\chi^2_1 = 22.67$; $P < 0.001$), water content ($\chi^2_1 = 15.33$; $P < 0.001$) and N level ($\chi^2_1 = 9.83$; $P = 0.002$). Relationships with insect abundance were weaker. Log-transformed abundance increased with higher water content ($F_{1,23} = 5.33$; $P = 0.031$), and decreased with higher wood density ($F_{1,23} = 8.51$; $P = 0.008$). Interpretation of these results is difficult because most of these variables were strongly correlated (Table 3).

Different multivariate models with suspected biological significance were tested with both multivariate logistic regressions and model selection (Aikake's second order information criteria). Models are listed with results in Table 4. Several logistic regression models had a $P \leq 0.001$, including different combinations

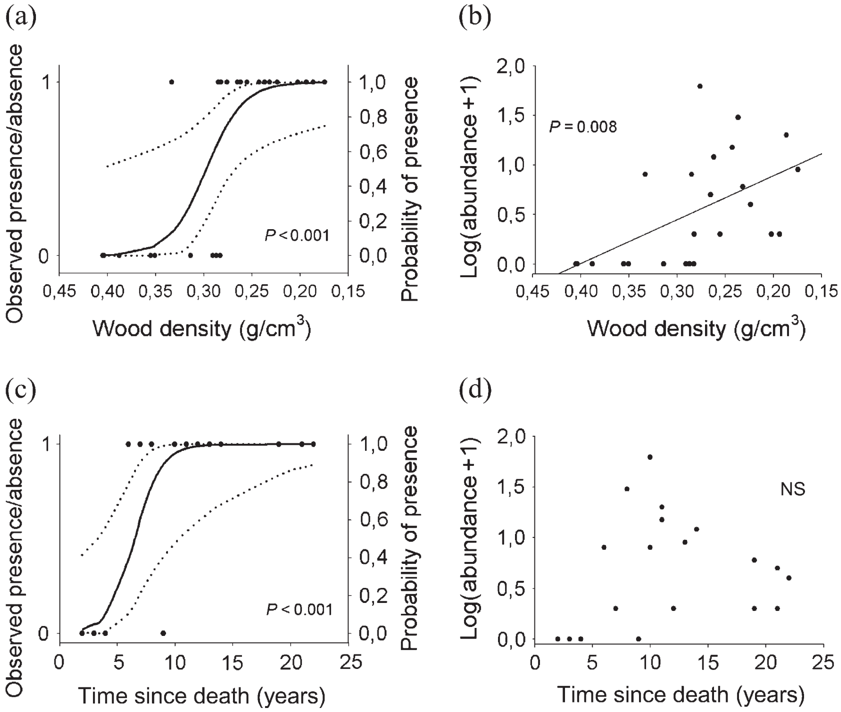

Fig. 2. Relationships between (a) wood density and presence/absence of all dead-host species (left y-axis), and probability of occurrence with confidence intervals as determined by logistic regression (right y-axis); (b) wood density and log-transformed abundance of larvae; (c) snag age (time since death) and presence/absence of all dead-host species (left y-axis), and probability of occurrence with confidence intervals as determined by logistic regression (right y-axis); (d) snag age (time since death) and log-transformed abundance of larvae.

of physical and nutritional parameters, and snag age. The best models included snag age, wood density, N and water-related parameters. The model including only snag age showed the strongest relationship with insect occurrence (Table 4). Snag age was also the most highly rated in model selection, with a w_i of 0.873. The model including only wood density was rated second, with a w_i of 0.062. All other models had a $w_i < 0.050$ (Table 3).

Discussion

There was a low occurrence of cerambycid larvae in the first stages of decay but a high occurrence, rapidly reaching a probability of presence of 1, in the mid to late stages. The observed concentration of larvae in mid to late stages may represent the result of active selection for the later stages of decay (Fig. 1a, but with only one group of species and thus no succession), or may be produced by neutral autocorrelative mechanisms, as modelled in Fig. 1b. Active selection is possible when at least one biologically significant parameter varies along the studied environmental gradient, and when a given species has the ability to detect these variations. Several of the measured parameters did vary significantly along the studied gradient.

Among nutritional parameters, both N and NSCs varied significantly along the decay gradient. A positive relationship was observed between N concentrations and insect occurrence. This nutritionally important compound has been linked to increased insect performance in the literature. Shibata (1998) showed that larval and adult body masses of the cerambycid *Semanotus japonicus* Lacordaire were higher in hosts with higher levels of N. Hosking and Hutcheson (1979) also observed an increase in larval growth in N-enriched substrates for *Arhopalus ferus* Mulsant. However, these two species belong to a different behavioural guild (stressed-host species, *sensu* Hanks, 1999) and will generally feed on subcortical tissues, at least in their first instars. Although these studies documented the positive impact of higher N levels on cerambycid larval growth, they did not assess the importance of N content in host selection per se, and thus the real impact of N on insect occurrence patterns remains unknown. Furthermore, some studies suggest that cerambycid larvae associated with dead hosts have the ability to acquire N through other sources than the wood they ingest. Some cerambycid species have been observed to develop and reach adulthood in wood containing as little as 0.03% N (Becker, 1963), and it is likely that in such contexts they acquire atmospheric N through symbiotic micro-organisms living in their gut (Mishra *et al*., 1985). The N content of dead sapwood observed in this study was very low compared with levels observed in other systems, where N content is believed to drive occurrence patterns. Nitrogen concentrations generally represent 1–5% of dry weight in subcortical tissues (Haack & Slansky, 1987) and around 3% in aspen foliage (Hemming & Lindroth, 1999), in comparison with an average of 0.15% in dead wood in our study. Because of such low levels and aforementioned behaviours regarding alternative sources of N, the variations in N content we observed may have limited biological significance.

Non-structural carbohydrates also showed significant variations along the decay gradient. However, NSCs were negatively correlated with insect occurrence, and thus are unlikely to be a driving factor for the host-use patterns of dead-host species. Although the importance of NSCs for larval survival has been

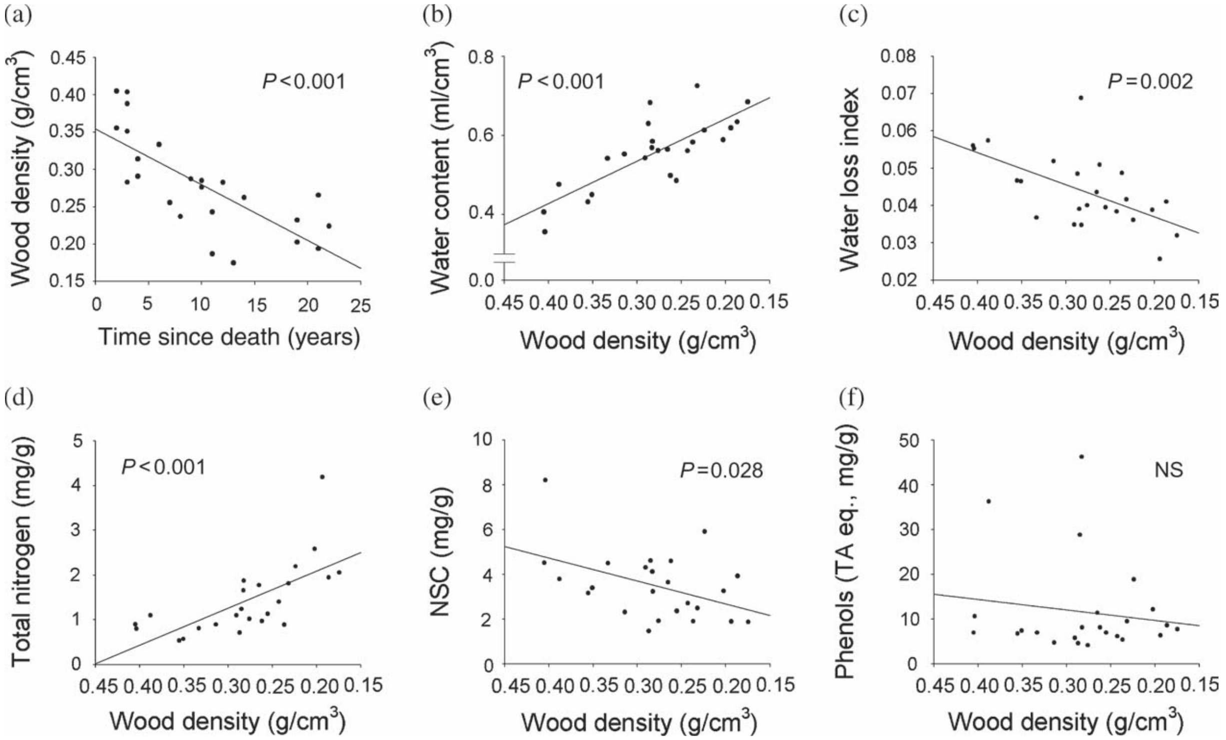

Fig. 3. Simple linear regressions between wood density and major explanatory variables measured: (a) snag age (time since death); (b) water content; (c) water loss; (d) total nitrogen; (e) non-structural carbohydrates (NSCs); (f) phenolic compounds. Each data point represents an individual snag. NS, non-significant.

shown for stressed-host species *Arhopalus syriacus* Reitter (Chararas, 1981), a prevalence of enzymes degrading structural polysaccharides is suspected in dead-host species (Parkin, 1940; Chararas *et al*., 1983; Haack & Slansky, 1987; Kukor *et al*., 1988; Zverlov *et al*., 2003). Consequently, NSCs may not be a key factor in host selection for this behavioural guild, as these insects can obtain glucose from cellulose and hemicellulose constituting the cell walls. As phenolic concentrations were not significantly related to insect occurrence and observed N and NSC variations do not seem to cover biologically significant levels, measured nutritional parameters apparently do not offer any basis for nutrition-based active selection among aspen-feeding dead-host species, despite the significant relationship observed between N and insect occurrence in hypothesis testing.

All physical parameters varied significantly with snag age and wood density. Snags in later stages of decay had the capacity to hold more water and lost their water at slower rates than snags in the early stages of decay. Consequently, older snags represent more stable environments for wood-feeders. Some species have been shown to respond to moisture gradients. The cerambycid genus *Asemum* was found to be more abundant in conditions of high moisture (Graham, 1925), and Chararas (1981) showed that mortality of *Arhopalus rusticus* (L.), *A. syriacus* and *Ergates faber* L. decreased significantly with an increase in water content. Some species are sensitive to rapid changes in moisture content. Several species, including *Monochamus titillator* (F.) and *Acanthocinus nodosus* (F.), have been shown to lose water rapidly when exposed to high temperatures (Savely, 1939). Again, evidence shows that water content does affect insect performance, but its possible role in host selection has not been clearly established. It may seem doubtful that cerambycids would have evolved host-selection behaviours based on the appraisal of moisture content in a snag, which is so dependent, especially near the surface of the wood, on recent meteorological conditions. Like N, moisture content probably influences larval performance but not host-selection per se and thus may create non-random patterns through differential mortality.

Interpretation of our results is complicated by the high number of autocorrelated variables. Nine different models including different sets of nutritional and physical parameters were deemed highly significant in hypothesis testing. The use of model selection allowed us to relativise actual support for each of these models. Only two models had $w_i > 0.05$, and the model consisting of only snag age received what can be considered as overwhelming support ($w_i = 0.873$). The selection of snag age as the best predictor of insect occurrence can be explained either by its involvement in neutral mechanisms in which time elapsed since the death of the tree has a major influence, or by the existence of another parameter correlated with age that was not measured.

Few of the parameters known to be biologically significant for wood-borers were not measured in our study. Among these are host-produced volatiles, which are a dominant factor in host selection for other behavioural guilds, especially stressed-host

Table 3. Relationships between all nutritional and physical variables measured and insect occurrence (presence/absence, all species pooled; binary logistic regression) and insect abundance (log-transformed; simple linear regression). The second part of the table shows correlation matrices between all measured parameters.

	Age	Density	Water content	Water loss rate	Diameter	Nitrogen	Phenols	NSCs
Presence (logistic regression)	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	NS	$P = 0.002$	NS	NS
Log (abundance + 1) (linear regression)	$P = 0.065, R^2 = 0.147$	$P = 0.008, R^2 = 0.279$	$P = 0.009, R^2 = 0.270$	NS	NS	NS	NS	NS
Non-structured carbohydrates	NS	$P = 0.028, R^2 = 0.202$	$P = 0.023, R^2 = 0.213$	NS	NS	NS	NS	—
Phenols	NS	NS	NS	$P = 0.013, R^2 = 0.248$	$P = 0.002, R^2 = 0.354$	NS	—	—
Nitrogen	$P < 0.001, R^2 = 0.551$	$P < 0.001, R^2 = 0.457$	$P = 0.010, R^2 = 0.263$	$P = 0.008, R^2 = 0.282$	NS	—	—	—
Diameter	NS	NS	NS	NS	—	—	—	—
Water loss rate	$P = 0.003, R^2 = 0.338$	$P = 0.002, R^2 = 0.351$	$P = 0.003, R^2 = 0.337$	—	—	—	—	—
Water content	$P = 0.001, R^2 = 0.396$	$P < 0.001, R^2 = 0.615$	—	—	—	—	—	—
Density	$P < 0.001, R^2 = 0.556$	—	—	—	—	—	—	—

NS, non-significant; NSCs, non-structured carbohydrates.

species (Allison *et al*., 2004). Host volatiles produced by aspen have mostly been studied as deterrents to coniferophagous species (e.g. Huber *et al*., 2000), and the use of such volatiles as kairomones for aspen-feeding species has not been documented in the literature. A study by Saint-Germain *et al*. (2006) suggested that host-produced volatiles are not an important driver of pre-alightment host selection in saproxylic species. Similar assemblages were captured using sticky traps on old snags of five different tree species, including coniferous species, and inert stovepipe controls. These results suggest the absence of pre-alightment host selection, although assemblages captured contained few wood-boring species. In addition, host volatiles in fact act in proxy of another biologically significant factor related to performance, and cannot be considered as a basis for host selection in themselves.

The presence of fungal fruiting bodies on the sampled snags was noted. Presence of fruiting bodies and insect occurrence were significantly and positively correlated, but only weakly so, and this parameter was rejected by model selection. However, some polypores are seasonal and may have been overlooked. Additionally, hyphae may grow for some years before the fungus actually fructifies. Lindhe *et al*. (2004) showed that fungal species richness peaked about 7 years following the death of the tree in snags of different tree species, including aspen, a timeframe that coincides with a sharp increase in occurrence observed in this study for dead-host wood-borers. Significant relationships between the species composition of the fungal flora and saproxylic beetles on spruce snags have been shown using a correlative approach (Jonsell *et al*., 2005), but whether fungi are the primary causal parameter or only a correlate of a more determinant one has not been established.

Most nutritional and physical parameters measured in our study received marginal relative support when compared with snag age in model selection as predictors of insect occurrence. These results suggest that the measured parameters may not offer a basis for active selection for mid to late stages of decay for dead-host wood-borers. Snag age by itself cannot be the basis of active selection; if the pattern observed is assumed not to be linked to some unmeasured parameter, then it is possible that it was produced through neutral mechanisms related to the time elapsed since the death of the tree. Host-use patterns observed in this study and at other sites (Saint-Germain, 2007) can be reproduced by a simple model in which no active selection takes place (Fig. 1b). Because the larval developmental time of most dead-host species usually lasts for >1 year and because adults in some cases oviposit on the host from which they emerged (Hanks, 1999), a strong temporal autocorrelation in occurrence of larvae within a single snag can be expected. A snag containing larvae in 1 year thus has a much higher probability of still containing some the following year. When this is taken into account in an iterative model, it tends to create patterns such as that observed in our study, where there is no form of selection by the ovipositing female beyond identification of the tree as dead and deciduous. Further studies on the behaviour of these species will be needed to test this neutral autocorrelative hypothesis.

Because of its correlative nature, our study cannot provide decisive evidence in support of neutral mechanisms as drivers of the host-use patterns observed for aspen-feeding, dead-host,

Table 4. Ranking of different models including measured nutritional and physical parameters using model selection (Aikake's second order information criteria). All models were also tested using logistic regression (right). Aikake weight (w_i) refers to the relative probability of each model to perform best.

	Model selection					Logistic regression		
	K	Log-likelihood	AIC$_c$	ΔAIC$_c$	w_i	χ^2	d.f.	Significance (P)
Age	2	–4.54	13.652	0	0.873	22.674	1	$<$0.001
Wood density	2	–7.19	18.952	5.300	0.062	17.375	1	$<$0.001
Water content, water loss, wood density	4	–5.08	20.255	6.603	0.032	21.641	3	$<$0.001
Wood density, water content	3	–7.19	21.578	7.926	0.017	17.377	2	$<$0.001
Water content, water loss	3	–6.28	19.754	10.265	0.005	15.038	2	0.001
Nitrogen, phenols	3	–8.39	23.974	10.322	0.005	14.981	2	0.001
Wood density, water content, diameter	4	–7.15	24.397	10.745	0.004	17.463	3	0.001
Nitrogen	2	–10.96	26.494	12.842	0.001	9.832	1	0.002
Nitrogen, NSCs, phenols	4	–8.35	26.809	13.157	0.001	15.051	3	0.002
Presence of fruiting bodies	2	–13.50	31.578	17.926	$<$0.001	4.748	1	0.029
NSCs	2	–15.31	35.197	21.545	$<$0.001	1.129	1	0.288
Phenols	2	–15.39	35.343	21.691	$<$0.001	0.983	1	0.321
Diameter	2	–15.51	35.584	21.932	$<$0.001	0.743	1	0.398
Volume	2	–15.60	35.762	22.110	$<$0.001	0.564	1	0.453

AIC, Aikake's information criteria, NSCs, non-structured carbohydrates.

wood-feeding beetle species. However, based on the information provided by this study, the involvement of several nutritional and physical parameters in the host-selection behaviour of these species can be questioned. Nitrogen and NSCs, so often involved in host selection by phytophagous species (Bernays & Chapman, 1994), were found at very low levels in dead wood throughout the decay gradient and received minimal support in model selection as drivers of insect occurrence. Models including physical parameters only were ranked higher than nutritional models, but lower than the model including snag age only. Although most of the parameters generally regarded as important for wood-feeding species were measured, no basis for active selection along the decay gradient was clearly identified. Further study of occurrence patterns and behaviours of these species will be needed to confirm that neutral mechanisms effectively drive the preference of these species for middle and late stages of decay.

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