Host-selection behaviour and host-use patterns of saproxylic beetles in snags of aspen (*Populus tremuloides* Michaux) and black spruce (*Picea mariana* (Miller)) in the province of Québec, Canada.

Michel Saint-Germain

Department of Natural Resource Sciences
McGill University, Montreal

February 2007

A thesis submitted to McGill University in partial fulfilment of the requirements of the degree of PhD in Entomology.

Abstract

The general objectives of this thesis project were to describe and to understand the dynamics creating occurrence patterns of saproxylic wood-feeding Coleoptera in snags (i.e., standing dead trees) of black spruce and aspen along the decay gradient. The first part of this thesis focuses on pre-landing host-selection behaviours in coniferophagous species, i.e. the use of host-produced volatiles to locate potential hosts. Results presented suggest that most saproxylic wood-feeding beetles studied herein use volatiles to orient towards potential habitat patches but that olfactive information does not allow the identification of suitable hosts at close range prior to landing. The second part of the thesis focuses on the occurrence patterns themselves and on underlying mechanisms. Sampling was conducted using snag dissection, a novel method allowing a better characterization of larval stage wood-feeding assemblages. Opposite patterns were observed between the two host species studied, as abundance and species richness were highest in early stages of decay in spruce, and in middle to late stages of decay in aspen. In aspen, numerous nutritional and physical parameters of dead wood correlated significantly with wood-borer occurrence. However, most of these parameters were strongly auto-correlated, and the explanatory model most highly ranked by model selection consisted of only a snag age term. Also, a simple neutral model based on temporal autocorrelation in occurrence probability produced patterns similar to those observed through sampling. In the last original paper presented, results suggest that wood-boring larvae select for specific types of substrate in highly variable aspen snags. This selection on the part of the larvae likely decreases the impact of the oviposition site on subsequent larval performance, and could explain the lack of strong selection seen on the part of the mother. My results suggest very different host-selection dynamics in black spruce and aspen, as assemblages of the former were dominated by early-decay species with volatiles-driven colonization dynamics, while middle- to late-decay species dominated the later, seemingly through mostly neutral colonization mechanisms. Some of my findings suggest that patterns observed in black spruce and aspen could be extrapolated to a coniferous/deciduous host dichotomy in colonization dynamics of wood-feeding species, based on divergent secondary chemistry and wood structure.

Résumé

Les objectifs de cette thèse consistaient à décrire et comprendre les méchanismes créant les patrons d'utilisation d'hôte chez les coléoptères saproxylophages utilisant l'épinette et le peuplier au long du gradient de décomposition. La première partie étudie l'utilisation des volatiles relâchés par l'hôte dans le processus de sélection d'hôte de ces insectes. Les résultats obtenus suggèrent que les insectes saproxylophages utilisent ces volatiles pour identifier une parcelle contenant un hôte potentiel, mais qu'ils ne peuvent être utilisés pour localiser un hôte en particulier à courte distance. La deuxième partie se concentre sur les patrons d'occurrence et les méchanismes sous-jacents. L'échantillonnage s'est effectué par dissection, méthode originale permettant une meilleure caractérisation des assemblages d'espèces saproxylophages, en particulier de stade larvaire. Des patrons opposés ont été observés entre les deux espèces d'arbre, les insectes étant concentrés en début de décomposition chez l'épinette, et davantage en fin de gradient chez le tremble. Chez le tremble, plusieurs paramètres nutritionels et physiques du bois étaient corrélés avec l'occurrence d'insectes. Cependant, la plupart de ces paramètres étaient corrélés entre eux, et le modèle le plus performant identifié ne comprenait que l'âge des chicots. Aussi, les patrons observés ont pu être re-créés par un simple modèle neutre basé sur l'autocorrelation temporelle dans la probabilité d'occurrence. Les résultats du dernier article suggèrent que les larves saproxylophages effectuent une sélection pour des types de substrats spécifiques au sein de chicots de tremble hautement variables. Cette sélection larvaire diminue l'impact du site d'oviposition originel sur la performance des larves, et pourrait expliquer le faible degré de sélection observé chez les espèces se développant dans le tremble. Mes résultats suggèrent des dynamiques de sélection d'hôte très différentes entre l'épinette et le tremble, les assemblages étant dominés chez l'épinette par des espèces de début de décomposition ayant des comportements de sélection axés sur les volatiles relâchés par leur hôte, et par des espèces de décomposition avancée aux dynamiques en apparence plutôt neutres chez le tremble. Ces divergences pourraient s'extrapoler à une dichotomie conifères/feuillus plus large basée sur les différences au niveau de la chimie secondaire et de la structure du xylème.

Contribution of authors

This thesis mainly consists of five original papers co-authored by me and my supervisors, Dr. Christopher Buddle and Dr. Pierre Drapeau. Chapter 3 of this thesis had already been pulished at the time of submission (*Environmental Entomology*, 35: 478-487, 2006). For each of the papers presented within, I planned the experimental designs, conducted fieldwork, identified most of the specimens collected and performed all analyses presented with feedback from my supervisors. I alone wrote the first drafts of all manuscripts. Final drafts incorporated the useful comments and in some cases direct contributions of my supervisors. All others who contributed to the production of these papers through field or laboratory work, or through an input of ideas or financial support are acknowledged within each original paper.

Acknowledgements

A doctoral thesis cannot be completed within 3 years without the contribution of numerous people. The planning and completion of my doctoral research evolved through discussions and experiences involving students from the laboratories of both my supervisors, Drs Christopher Buddle (McGill) and Pierre Drapeau (UQAM). I especially want to thank Maxim Larrivée, Virginie-Arielle Angers and Antoine Nappi for their input. Numerous other undegraduate and graduate students and technicians also contributed to sampling efforts and laboratory work: Elise Bolduc, Marianne Cheveau, Chris Cloutier, Andrea Dechêne, Valerie Evans, Helene Lalande, Daniel LeSieur, Tania Motchula, Alexandre Renaud, Zach Sylvain, Marie-Andrée Vaillancourt and Annie Webb. I especially want to thank E. Bolduc, V. Evans, Z. Sylvain and A. Webb as well as Drs. C. Buddle and Timothy Work for the cubic meters of wood they helped dissect. I greatly appreciated the general enthusiasm and openness my supervisors showed towards the ideas I had regarding the orientation of my research, their commitment towards its successful completion, and the invaluable scientific input they provided. Other committee members, including T. Work (UQAM) and Terry Wheeler (McGill), also contributed positively in terms of ideas. I also want to aknowledge the support provided by the GREFi (Groupe de recherche en écologie forestière interuniversitaire), which financial assistance allowed me to present the results of my research in several conferences, particularly in France and western Canada. I also want to thank my family for their unfaltering support during these last few years.

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1. **Introduction**

Widespread interest in saproxylic insects is relatively recent, especially in terms of their diversity and their ecological functions. Following a few pioneer studies published early in the twentieth century which focused on host-use patterns and succession (Graham 1925, Savely 1939, Howden and Voigt 1951, Wallace 1953), literature on saproxylic insects shifted in focus for several decades, looking mostly at the damage some species cause in specific context to commercial lumber (Parmalee 1941, Gardiner 1957, Ross 1960, Cerezke 1977). In the 1980's and 1990's, an increasing awareness of the effects of intensive forest management on biodiversity then sparked a 'renaissance' in insect biodiversity work, particularly in Fennoscandia (Heliövaara and Väisänen 1984, Haila 1994, Niemelä 1997), but also to some degree in North America (Spence *et al*. 1996). Some researchers began to focus their work specifically on saproxylic insects, which were considered among the taxa most vulnerable to forest management (Berg *et al*. 1994). Papers on saproxylic insects published in international journals became more numerous (Väisänen *et al*. 1993, Kaila *et al*. 1994, Siitonen 1994, Siitonen and Martikainen 1994). Despite the ever-increasing number of papers published on saproxylic insects by Fennoscandian authors, interest in these taxa remains limited in other regions of the world, with some notable exceptions (Hammond 1997, Hammond *et al*. 2001, 2004, Grove 2002b, Lachat *et al*. 2006).

Although some of the knowledge about community structure and colonization dynamics of saproxylic insects, mostly acquired in Fennoscandia on tree species *Picea abies* (L.) (Norway spruce) and *Populus tremula* L. (aspen) and reviewed in the following section,

may very well be applicable to North American communities, the generality of observations made in other systems cannot be taken for granted without a minimum amount of research. Also, despite two decades of intensive research in Fennoscandia, our understanding of the local communities and colonization dynamics of these insects is still fragmentary, for several reasons. First, saproxylic insects are particularly difficult to study, largely because of sampling limitations. An important proportion of saproxylic taxa live most of their life as larvae, enclosed in their woody substrate. Adults are usually short-lived; some do not feed at all, and in the few days of their adult life, all they will do is disperse to find a mate and an appropriate host for their offspring (Hanks 1999). Some others will breed for several generations within the same substrate, and thus will not even leave the log or snag in which they developed (e.g., Ranius and Hedin 2001). Largely because of logistic and taxonomical constraints, adults are almost always the main target of biodiversity studies focusing on saproxylic species (e.g., Siitonen and Martikainen 1994, Martikainen 2001, Hammond *et al*. 2004, Lindhe and Lindelöw 2004). However, because of the life history of numerous species, such an approach is likely to produce fragmentary results. When sampling saproxylic insects at the host scale using trunk-window traps, a method based on activity and targeting adults, a very high proportion of transient species and individuals are to be expected (e.g., see Martikainen 2001). Untangling such data requires a high level of knowledge concerning the ecology and natural history of those species, a level which may exist in Fennoscandia, but is lacking in other parts of the world, including eastern North America. Concurrently, methods providing more direct and complete information, e.g., eclector traps or dissection of larval hosts, cannot always be conducted because of the rarity and endangered status of some species (Ranius *et al*. 2005). Even such methods have important limitations; for example,

destructive methods like bark sieving or dissection cannot be repeated in time, and thus give only a snapshot of assemblages that vary seasonally. Also, a majority of studies will usually consider whole saproxylic assemblages altogether (with some exceptions, e.g., Vanderwel *et al*. 2006) although they are composed of several trophic guilds having very distinct ecologies. Thus, diverging responses of individual guilds may be lost in pooled analyses.

The general objectives of this thesis were to investigate host-use patterns of saproxylic insects using snags of black spruce, *Picea mariana* (Miller), and aspen, *Populus tremuloides* Michaux, over the decay gradient and to understand processes driving insect species succession along that same gradient. These two tree species were chosen for their ecological and economical prevalence in the region of Quebec where this project initially started, i.e., the Clay Belt region of western Quebec (Abitibi), dominated by aspen, and adjacent northern regions of the Canadian Shield (southern James Bay area), dominated by black spruce and to a lesser extant jack pine (*Pinus banksiana* Lambert). Aspen and black spruce are also major constituents of the boreal and boreal mixed-wood forests across Canada, from Newfoundland to the Rocky Mountains (Farrar 1995). To circumvent the aforementioned methodological problems associated with saproxylic insects, I decided early in project development to sample a definite series of snags using two approaches, first using sticky traps to investigate which insect species landed on specific snag types on which they may oviposit, and then at the end of the sampling season using a destructive method, dissection, to determine which species were present in the snag. Following preliminary sampling, these original intents eventually led to more precise objectives and sampling designs which included aspects of the host-selection

behaviour of these species, to which host-use patterns are inextricably linked. Also, what was collected through dissection in our first sampling efforts convinced me to focus my research on specific saproxylic trophic guilds: bark-feeders and wood-borers.

Non-random patterns of occurrence result from specialization of species along the studied environmental gradient. Most phytophagous (or saprophagous) insect species show some degree of specialization in their oviposition host choice (Jaenike 1990). For specialization to occur, the individual must be able to detect variations between potential hosts in suitability. Mechanisms of host appraisal can be divided as pre-landing and post-landing processes (Saint-Germain *et al*. 2004a). In an effort to understand processes driving host-selection and subsequent host-use patterns seen in saproxylic Coleoptera, with special attention given to wood-feeding groups, the original papers presented within this thesis first investigate pre-landing host-selection processes (chapters 3 and 4), while the last three focus on post-landing processes or selection in a broader, evolutionary context (chapters 5 through 7).

The impact of host-produced volatiles on host-location behaviour has been well described in primary species of Scolytidae (Wood 1982, Byers 1995), but their importance in host-selection of saproxylic insects is less understood. In chapter 3, the specificity of the assemblages of insects landing on old and new snags of five different tree species, in addition to inert (i.e., not releasing volatiles) stovepipe trap controls, was investigated using sticky traps. The mode of action of sticky traps can be compared to those of flight-intercept traps fixed on a potential host, as they theoretically target adults that are approaching or leaving a potential host. However, sticky traps are one step closer to

actual oviposition, as the insect must land on the snag to be caught, while it is not necessarily the case in flight-intercept traps. This method was expected to give us information on the importance of host-produced volatiles in host-selection by saproxylic insects. Indeed, if these insects, or at least some components of the saproxylic assemblage, use volatiles to select hosts to some degree while in flight, this behaviour should be reflected by capture rates on different host types. Results for chapter 3 suggested that the use of volatiles may be scale-dependent, and these observations prompted me to design a new experiment to test this hypothesis, presented in chapter 4. Again, in this chapter, sticky traps were used to sample insects landing on potential hosts. Here the response of wood-feeding Coleoptera to volatiles was tested both at the stand scale and the host scale. In relatively young stands of jack pine showing low densities of fresh snags, 11 trees per plot were selected to form concentric circles around one tree that was either mechanically-killed, baited with a commercial mix of attractants designed for wood-borers, or left untouched. Assemblages of beetles that were captured were first compared between active treatments and controls to assess insect response at stand level, and then, within each plot, landing rates of wood-feeding species were correlated to the hosts' distance to the baited central tree. Results from this experiment allowed an important clarification on the use of host-produced volatiles in secondary wood-feeding insects and helped explain some contradictory results reported in the literature.

The last three original papers (chapters 5 through 7) deal with host-use patterns in specific host types along the decay gradient and with processes driving these patterns. Chapter 5 presents results from the dissection of a total of 160 snags of black spruce and aspen, collected in 10 sites disseminated within the provincial distribution range of each tree

species. This allowed for an unprecedented characterization and understanding of the patterns of occurrence of saproxylic wood-feeding Coleoptera in those two tree species along the decay gradient. Chapter 6 looks more into the processes driving such occurrence patterns in aspen. In this part of the study, measurements were made on 24 snags to quantify changes in important physical and nutritional parameters of the substrate occuring as dead wood decays. Relationships between these parameters, which potentially could affect larval performance and thus host selection according to optimality theory, and insect occurrence patterns were then analyzed with hypothesis testing and model selection. The last original paper presented (chapter 7) complements the first four papers as it investigates the variability in decay within single snags and whether larvae show some form of substrate selection. To answer this question, I produced density profiles of 20 aspen snags of middle- to late-decay stages, within which I also sampled cerambycid larvae (Coleoptera) according to the wood density in which they were found. The two distributions were then compared for each snag and with pooled data. According to optimality theory, selection by the larvae should have important implications regarding host selection by the mother; chapter 7 discusses such issues in the light of the results obtained, which sheds some light on some results obtained in chapters 5 and 6.

1.1 Summary of objectives and hypotheses

Chapter 3 aims at characterizing landing patterns of saproxylic Coleoptera assemblages between fresh and old snags of 5 tree species, including two deciduous and three coniferous, and black stovepipe controls. Results are to be interpreted in the context of pre-landing host-selection behaviour, as diverging assemblages found on different snag types should mainly be the result of active selection taking place before the insect is captured (lands on the potential host).

H_{1A} – Significant differences can be found in species composition between some or all snag types.

H_{1B} – Extent of divergence in species composition between snag types varies between predatory, fungivores and wood-feeding assemblages.

The first objective of chapter 4 was to determine whether wood-feeding Coleoptera were more frequently captured in stands baited with either natural or synthetic attractants than in unbaited control stands. The second objective was, at a finer scale, to determine to what extent insects attracted to a baited stand would directly land on the baited tree compared to neighboring unbaited trees (i.e., efficiency in locating volatile source at close range).

H_{1A} – Landing rates of wood-feeding species are higher in baited stands than in control unbaited stands.

H_{1B} – Wood-feeding insects land more frequently on central trees than predicted by the random landing null model.

Objectives of chapter 5 were to characterize occurrence patterns of wood-feeding Coleoptera in aspen and black spruce snags along a wood density gradient and among different regions within the provincial distribution of the two tree species.

H_{1A} – Insect occurrence probability is higher in early stages of decay for both tree species.

H_{1B} – Stressed-host guild is dominant in terms of density and species richness in both tree species relatively to dead-host guild.

H_{1C} – Insect occurrence patterns along the decay gradient differ between regions in both tree species.

Objectives of chapter 6 were to investigate the relationships between dead-host species occurrence patterns in aspen along the decay gradient to nutritional and physical characteristics of dead wood, and to evaluate whether the observed patterns are more likely to be produced by active selection on the part of the insect or by neutral mechanisms.

H_{1A} – Insect occurrence is positively correlated with concentrations of important nutrients (nitrogen, non-structural carbohydrates).

H_{1B} – Insect occurrence is significantly correlated with physical parameters (wood density, water content).

H_{1C} – Insect occurrence is significantly correlated with snag age, with a higher correlatioon coefficient than nutritional or physical parameters.

Objectives of chapter 7 were to quantify the degree of variability in wood density in aspen snags of mid- to late-stages of decay, and to determine if larvae of two cerambycid species, *Anthophylax attenuatus* (Haldeman) and *Bellamira scalaris* (Say), occur more frequently in some types of decay than would be predicted by chance.

H_{1A} – Larvae of *A. attenuatus* are found more frequently in some categories of wood density than would be predicted by chance.

H_{1B} – Larvae of *B. scalaris* are found more frequently in some categories of wood density than would be predicted by chance.

2. **Literature review**

2.1 Defining saproxylic insects

The term saproxylic was proposed by Dajoz in 1966 and has been widely adopted since (Grove 2002a). Saproxylic insects are defined as being dependent, during some part(s) of their life cycle, on dead or dying wood, on wood-inhabiting fungi or on other saproxylic species (Speight 1989). They typically include bark- and phloem-feeders, wood-borers, fungivores, and their associated predators, parasites and commensals. Saproxylic insects include species of numerous insect orders. Coleoptera are the most important, as they can represent around 95% of saproxylic insect biomass in some systems (Brustel and Dodelin 2005). Species of Coleoptera are present in all trophic guilds found in dead wood, although parasites are extremely rare within this order [e.g. *Phloeopora testacea* (Mannerheim), Staphylinidae; Wallace 1953]. Nearly one hundred families of Coleoptera have been reported to include saproxylic species (Howden and Vogt 1951, Hammond 1997, Kaila *et al.* 1997, Hammond *et al*. 2001, Grove 2002, Lindhe and Lindelöw 2004, Lachat *et al*. 2006, Tykarski 2006). Diptera also include species of all trophic guilds. Cecydomyiidae, Sciaridae and Mycetophilidae are often cited as the most species-rich families (Irmler *et al*. 1996, Hövemeyer and Schauermann 2003, Økland *et al*. 2005, Vanderwel *et al*. 2006). Hymenoptera include a few wood-boring species (especially family Siricidae), numerous parasitic species (e.g., families Braconidae, Icneumonidae), and some other species using wood as shelter (Formicidae) (Howden and Vogt 1951). Several families of Lepidoptera include wood-feeding species, the most common being Cossidae and Sessidae (Howden and Vogt 1951, Haack and Slansky 1987). Other orders,

like Hemiptera, Homoptera and Psocoptera, are minor components of the saproxylic fauna. Termites (Isoptera) are an important group of saproxylic insects but are mainly restricted to warmer climates (Breznak 1982).

2.2 Diversity patterns of saproxylic Coleoptera at stand scale

Saproxylic Coleoptera assemblages have traditionally been studied at two different spatial scales. At the scale of the stand, local assemblages are described using trapping methods that intercept dispersing adults. Methods commonly used include flight-intercept traps, either free-standing or fixed to a tree or snag (Martikainen *et al*. 2000, Similä *et al*. 2003, Saint-Germain *et al*. 2004b), and occasionally multiple-funnel traps (Chénier and Philogène 1989a) or Malaise traps (Ohsawa 2004, Ulyshen *et al*. 2004). Assemblages have often been studied within comparisons between naturally- or anthropogenically-disturbed habitats and more-or-less pristine controls, or along successional gradients. In most studies looking at the effect of management, overmature natural stands (controls) generally harbor more abundant and/or species-rich assemblages than young or intensively managed stands. Similar responses were observed in boreal forests of Fennoscandia (Martikainen *et al*. 1999, Martikainen 2000), in temperate mixed forests of Japan (Maeto *et al*. 2002) and in tropical rainforests in Australia (Grove 2002b) and Africa (Lachat *et al*. 2006). Some other studies found few differences in abundance or richness, but striking ones in terms of species composition (Väisänen *et al*. 1993, Similä *et al*. 2003, Hammond *et al*. 2004, Zeran *et al*. 2006). In studies looking at assemblages over different successional stages, most found an increase in species richness in late successional stages (Gutowski 1995, Similä *et al*. 2003), but others found early-

successional sites having higher abundance and species richness (Similä *et al*. 2002, Saint-Germain *et al*. 2004b). These differences are likely to be related to the nature of the early-successional sites considered, as both of the above-mentioned studies used recent burns in their sampling design, habitats well-known for their highly specialized and abundant fauna (Wikars 1992; Muona and Rutanen 1994; Wikars 1997).

Whether the context of the study be related to different management regimes or different successional stages, almost all studies seem to point, either implicitely or explicitely, at the availability of dead wood and the diversity of decay stages found within stands as the main factors explaining higher diversity and abundance in saproxylic insect assemblages. Most of the studies that tested statistically the relationship between dead wood availability and either species richness or composition found it to be significant and positive (Økland *et al*. 1996, Martikainen 2000, Sippola *et al.* 2002, Similä *et al*. 2003, Lachat *et al*. 2006). Another classic example of the importance of dead wood availability is the study of Siitonen and Martikainen (1994) in which they sampled saproxylic insects in both Finnish and Russian Karelia. The Finnish side of the border had been intensively managed for decades, with drastic effects on dead wood volume, while the Russian side had been only sporadically managed. With similar methods and sampling efforts, four times more rare species were found on the Russian side, along with several species considered extinct in Finland. This importance of the availability of dead wood is seen from another angle in a few studies that tackled connectivity issues. Schiegg (2000) showed that, at a scale of 150 m, plots having higher connectivity between pieces of dead wood, measured as average nearest neighbor distance (Diggle 1983), had richer saproxylic insect assemblages, and connectivity also affected species composition. One of

her conclusions was that the spatial arrangement of wood pieces seemed to matter as much or even more than dead wood volume alone. Other studies aimed at determining at which spatial scale insect species responded to forest cover. Holland *et al.* (2004, 2005) used computer software that analyzes abundance data and information on forest cover at multiple spatial scales to determine at which scale the species is more responsive to the explanatory variable, while avoiding the non-independence of measurements at different scales. For 27 species of Cerambycidae, they determined that the insects responded at scales ranging from 20 to 2000 m, while the scales associated with the greatest number oft species were well under 1000 m. These results demonstrate the importance of spatial and temporal connectivity between potential hosts for the local persistence of these species, and suggest low dispersal capabilities, at least in species with small body size.

However, among the relatively large body of literature produced about determinants of abundance and species composition of saproxylic assemblages, contradicting results and disappointingly weak trends are common. Furthermore, more detailed information about, for example, the effect of forest cover composition or fragmentation, is absent or inconclusive. Some of this confusion is certainly linked to the subsets of species used and to the efficiency of sampling methods. Most studies usually tackle entire saproxylic beetle assemblages altogether, despite the fact that it would be reasonable to expect differential responses among the numerous trophic guilds included in the saproxylic community, especially since some studies of insect succession detected an important turnover among trophic guilds along the decay process (see below). Also, methods based strictly on activity capture insects in their dispersal phase, i.e., insects which may not be closely associated with the local habitat. In that sense, studies using eclector traps (i.e., rearing)

always give stronger patterns than studies using flight-intercepts. It thus seems that researchers studying saproxylic beetles must make a choice whether to go either for large samples and reduced logistical difficulties, and then deal with the blurred response produced by activity-based trapping methods, or for smaller sample sizes and sometimes heavy logistical restrictions associated with rearing or dissections, which yield much more direct information.

2.3 Diversity patterns of saproxylic Coleoptera at the host scale

Studying saproxylic Coleoptera at the host scale is more difficult, as techniques to be used are more logistically-demanding and usually produce much less specimens. Methods traditionally used are eclector traps, either *in-situ* (Lindhe and Lindelöw 2004) or *ex-situ* (Hammond *et al.* 2004, Saint-Germain *et al*. 2004c), trunk-window traps (Kaila *et al*. 1994, Økland 1996, Ranius and Jansson 2002), and occasionally sticky traps (Waters and Hyche 1984, Shepherd and Goyer 2003) and bark sieving (Jonsell and Weslien 2003, Jonsell *et al*. 2004). Several factors influence abundance, species richness and/or species composition of saproxylic insect assemblages collected from specific hosts (Table 2.1).

Table 2.1 Summary of studies in which saproxylic beetles were sampled at the host scale, with reported relationships between abundance, species richness, species composition and explanatory variables.

Study	Region	Host species	Decay stages	Abundance	Sp. richness	Sp. composition
Graham 1925	Minnesota, USA	*Pinus strobus* L. *Pinus resinosa* Aiton *Pinus banksiana* Lambert *Picea glauca* (Moench) *Abies balsamea* (L.)	Logs monitored for 5 years	-	-	Decay stage Host species Sun exposure
Savely 1939	North Carolina, USA	*Pinus echinata* Miller *Pinus tadea* L. *Quercus* spp.	Undetermined	-	-	Decay stage Host species
Howden & Vogt 1951	Maryland, USA	*Pinus virginiana* (Mill.)	1-10 years old	Decay stage -	Decay stage -	Decay stage
Wallace 1954	England	*Pinus nigra* Arnold *Pinus sylvestris* L.	3 classes	-	-	Decay stage Sun exposure
Zhong & Schowalter 1989	Oregon, USA	*Abies amabilis* (Douglas) *Pseudotsuga menziesii* (Mirbel) *Thuja plicata* Donn *Tsuga heterophylla* (Raf.)	Only fresh	Host species	-	Host species
Araya 1993	Japan	*Fagus crenata* Blume *Quercus mongolica* Fisch.	By rot types	-	-	Diameter Rot type
Kaila *et al*. 1994	Finland	*Betula pendula* Roth	Undetermined	-	Sun exposure +	Sun exposure
Irmler *et al*. 1996	Germany	*Alnus glutinosa* (L.) *Fagus sylvatica* L. *Picea abies* Karst.	4 classes	Decay stage +	Decay stage +	Snag vs. log
Hammond *et al*. 2001	Alberta, Canada	*Populus tremuloides* Michaux	Only fresh	-	Logs +	Snag vs. log
Martikainen 2001	Finland	*Populus tremula* L.	4 classes (bark cover)	-	Sun exposure +	Decay stage Sun exposure

Table 2.1 (*continued*)

Study	Region	Host species	Decay stages	Abundance	Sp. richness	Sp. composition
Koenigs *et al.* 2002	California, USA	*Abies concolor* (Gordon) *Pinus ponderosa* (Douglas)	3 decay classes	Decay stage Host species	-	Decay stage
Sverdrup-Thygeson & Ims 2002	Norway	*Populus tremula* L.	Undetermined	-	Logs +	Snag vs. log Sun exposure
Jonsell & Weslien 2003	Sweden	*Picea abies* Karst.	Sampling at years 1 and 4	Logs +	Decay stage + Logs +	Decay stage Snag vs. log
Hammond *et al*. 2004	Alberta, Canada	*Populus tremuloides* Michaux	3 classes	Decay stage – Snags +	Decay stage + Logs +	Decay stage Diameter
Lindhe & Lindelöw 2004	Sweden	*Picea abies* Karst. *Betula pendula* (L.) *Populus tremula* L. *Quercus robur* L.	Mechanically-created high stumps monitored for 7 years	-	Diameter + Host species Sun exposure + Fungi divers. +	Host species
Saint-Germain *et al*. 2004c	Québec, Canada	*Picea mariana* (Miller)	Only fresh, fire-killed	Diameter + Fire severity – Height along stem –	Diameter + Fire severity – Height along stem –	Fire severity
Jonsell *et al*. 2005	Sweden	*Picea abies* Karst.	6 y-old stumps	-	-	Wood-decay fungi
Lindhe *et al*. 2005	Sweden	*Picea abies* Karst. *Betula pendula* (L.) *Populus tremula* L. *Quercus robur* L.	Mechanically-created high stumps followed for 7 years	Diameter Sun exposure	-	Host species Sun exposure
Gibb *et al*. 2006	Sweden	*Betula pendula* Roth *Picea abies* Karst.	Only fresh	-	-	Host species Sun exposure
Vanderwel *et al.* 2006	Ontario, Canada	*Pinus strobus* L. *Pinus resinosa* Aiton *Pinus banksiana* Lambert	4 classes logs only	Decay stage –	-	Decay stage

An important fraction of the saproxylic fauna is somewhat specialized in terms of the tree species it can use as hosts. Two general statements can be derived from the literature. First, a single species is rarely found to use both coniferous and deciduous tree species as hosts. Most studies comparing different tree species report very distinct assemblages that utilize deciduous and coniferous hosts (Savely 1939, Lindhe and Lindelöw 2004, Gibb *et al*. 2006). In a behavioural study involving the cerambycid *Arhopalus syriacus* (Reitter), Chararas (1981a) observed that adults were attracted by volatiles from numerous coniferous species, including species of the genera *Pinus*, *Abies* and *Larix*, but showed no response to sympatric non-coniferous *Eucalyptus* or *Quercus* species. This sharp boundary between assemblages using the two host groups might be explained by differences in secondary compounds produced by coniferous and deciduous trees, and possibly by the different cell structures found in their sapwood (tracheids in conifers vs. sieve elements in deciduous trees). Second, the degree of specialization is generally thought to be higher in fresh than in old dead wood (Brustel and Dodelin 2005). However, there is limited published empirical support for this statement. To my knowledge, there has been no study including several tree species in which assemblages were characterized over the entire decay gradient. Several early-successional coniferophagous species, including *Arhopalus foveicollis* (Haldeman), *Monochamus scutellatus* (Say), *Rhagium inquisitor* (L.) and *Tetropium cinnamopterum* Kirby, reproduce on hosts of different tree genera (Belyea 1952, Gardiner 1957, Vlasak and Vlasakova 2002, Nappi *et al*. unpublished data). Also, in a study using mechanically-killed spruce [*Picea abies* (L.)], birch (*Betula pendula* Roth), aspen (*Populus tremula* L.) and oak (*Quercus robur* L.), Lindhe and Lindelöw (2004) observed a high degree of similarity in assemblages associated with the three deciduous host species. High degrees

of specialization are well documented for wood-borers using living hosts (Hanks 1999), but whether or not it can be observed in early saproxylic wood-borers remains doubtful. There is also limited support for specialization in trophic groups other than wood-feeding. Parasites and predators are closely tied to their prey species, while fungivores are more likely to be tied to specific wood-decay fungus species rather than to specific tree species (Komonen *et al*. 2004, Jonsell *et al*. 2005).

As wood decays, its structural and nutritional status changes drastically (see section below). Stage of decay can thus be expected to have an important impact on assemblage composition. Several studies report changes in abundance, species richness and species composition along the decay process. Some studies observed an increase in species richness as decay proceeds (Simandl 1993, Irmler *et al.* 1996, Jonsell and Wieslien 2003). A limited number of studies observed an inverse trend (e.g., Howden and Vogt 1951). Also, several studies, mainly focusing on coniferous hosts, observed changes in the relative importance of the different trophic guilds as decay proceeds (Graham 1925, Savely 1939, Howden and Vogt 1951, Vanderwel *et al*. 2006). Phloeophagous and xylophagous species (e.g., Buprestidae, Cerambycidae, Scolytidae) usually dominate the first phase, to be eventually replaced by fungivores, saprophages and predators (e.g., Elateridae, Lathridiidae, Melandryidae, Staphylinidae, Tenebrionidae) within a few years as dominant trophic guilds. Interestingly, Wallace (1953) clearly observed such a succession in pine stumps in open conditions, but the succession was indistinct under closed canopy. In parallel to this decay stage effect, some studies compared assemblages found in logs to those found in snags of the same host species. Sverdrup-Thygeson and Ims (2002) found richer beetle assemblages in snags. Jonsell and Weslien (2003)

observed higher densities of insects in logs, and found that some species were to some degree restricted to either logs or snags. Gibb *et al*. (2006) also observed differences in species composition. In all of these studies, logs and snags (high stumps) were mechanically created at the same time.

Some studies have also shown that assemblages vary with anatomical region within individual trees. Saproxylic assemblages were in some cases found to be stratified vertically. Simandl (1993) described the assemblages as being highly aggregated in specific parts of the stem along the vertical gradient in buckthorn. Also, in recently dead Japanese red pine (*Pinus densiflora* Siebold & Zuccarini), scolytids *Shirahoshizo* spp. and *Taenioglyptes fulvus* Niijima showed opposite vertical occurrence patterns, the first showing maximum emergence density near the ground, while the second was more common much higher on the stem. In the same trees, the cerambycid *Monochamus alternatus* Hope and the curculionid *Pissodes nitidus* Roelofs were concentrated in the middle part of the stem (Yoshikawa 1987). However, another study looking at vertical distribution in fire-killed black spruce (*Picea mariana* (Miller)) showed no such stratification of communities (Saint-Germain *et al*. 2004c). Whether or not this lack of vertical stratification is due to effects of fire is not known. Schiegg (2001) compared assemblages emerging from fallen trunks and limbs in European beech (*Fagus sylvatica* L.); here, insects emerging from limbs were both more abundant and diverse.

Another important factor reported frequently in the literature is sun exposure. Several studies stress the observation that insect species often show preference for substrates in open settings exposed to sunlight. Lindhe and Lindelöw (2004) collected more species-

rich assemblages on high stumps with high exposure. In their study, Lindhe *et al*. (2005) estimated that about two-thirds of collected species favoured sun-exposed conditions, while the remaining third favoured shaded conditions. Sun-exposure was also a better predictor of species occurence than host diameter. In Norway spruce [*Picea abies* (L.)], Sverdrup-Thygeson and Ims (2002) found that richness and abundance were stable throughout an exposure gradient, but observed a high turnover in species composition. They suggested that these changes in species composition could be related to humidity and temperature within the substrate, which is known to vary substantially in sun-exposed dead wood (Graham 1925, Savely 1939). Savely (1939) also showed that some insect species were unable to tolerate the high temperatures sometimes reached in subcortical tissues of exposed snags.

Different types of wood-decay fungi have different effects on woody tissue. Because of these differential effects, the types of wood-decay fungi present in dead wood could influence associated saproxylic insects. Fungi can be generally classified as brown or white rot depending on the compounds they attack. Brown rot fungi decompose cellulose and hemicellulose, but leave lignin untouched. White rot decomposes all three compounds (Rayner and Boddy 1988). Wallace (1954) observed that some fly larvae and some beetle species were consistently found either in brown or white rot. Araya (1993) reported that some species of wood-feeding Lucanidae were associated with a specific rot type, while others were not so restricted. A study by Jonsell *et al*. (2005) also suggests that wood-decay fungi can influence host-use, as the presence or absence of *Fomitopsis pinicola* Karst. and *Trichaptum abietinum* (Dickson) were the main drivers of species composition of saproxylic insect assemblages sampled on high stumps of Norway spruce.

However, few other variables were considered in their analysis, most notably describers of decay stage. It has not been investigated to this point whether this potential impact of wood-decay fungi on host-use patterns would be linked to changes in nutrient availability or rather on some aspects of their secondary chemistry; it appears that some compounds of fungal origin can act as feeding stimulants or deterrents for wood-feeding insect species (Becker 1971).

Snag diameter was reported in several cases as influencing species richness and abundance. Lindhe and Lindelöw (2004) found a positive relationship between species richness and diameter; however, the relationship was negative when number of species per unit of area was the response variable. In a study of wood-feeding Coleoptera attacking mechanically-killed high stumps of Norway spruce, Schroeder *et al*. (1999) showed that the bark beetle *Ips typographus* (L.) preferred stumps with higher diameters, while *Hylurgops palliatius* (Gyllenhall) and *Trypodendron lineatum* (Olivier) showed opposite trends. In fire-killed black spruce, all Coleoptera species emerged at higher densities from snags of an 18-21 cm diameter at breast height class than from the 8-11 cm class (Saint-Germain *et al*. 2004c). However, this preference for larger diameters may have been due to greater dessication in small trees during the fire, and thus not related directly to diameter *per se*. Despite the fact that diameter does influence to some extent saproxylic insect host choice, it is rarely, if ever, selected as the most important variable in designs considering multiple variables such as exposure, decay stage and wood-decay fungi (Saint-Germain *et al*. 2004a, Jonsell *et al*. 2005, Lindhe *et al*. 2005).

Again, as in studies conducted at stand scale, most of the studies published thus far at the host scale consider the whole saproxylic assemblages in their analysis. However, members of different trophic guilds are likely to respond differently to some environmental factors. Because most of the time assemblages captured with trunk-window traps (the method of choice for most of the above-mentioned studies) are dominated by fungivores and saprophage species, factors enumerated on Table 2.1 are more likely to reflect the preferences of these trophic groups, and not necessarily the ones of others, especially wood-borers, which are always under-sampled by most types of flight-intercept traps.

2.4 Colonization dynamics of saproxylic wood-feeding Coleoptera

Colonization dynamics of saproxylic wood-feeders are directly influenced by the type of substrate required by the larvae. Cerambycidae and Scolytidae have been classified according to the type of substrate on which they oviposit, and types of host-selection behaviour generally correspond well with this classification. Hanks (1999) identified two behavioural guilds among saproxylic Cerambycidae: stressed-host species and dead-host species. Stressed-host species oviposit on hosts severely stressed or recently dead. In this physiological state, hosts offer their highest nutritional value, as the metabolism of individual cells continue for some time, while defense mechanisms are severily compromised. However, the window of opportunity for colonization is short: Alya and Hain (1985) determined that freshly-killed pine logs remained attractive to females of *Monochamus carolinensis* (Olivier) and *M. titillator* (F.) for an average of 42 days. Because of this, a single host will usually only be attacked by a single generation of these

species. Stressed-host species are thus dependent on strong host-location and dispersal capabilities. The availability of stressed or recently dead hosts is highly unpredictable in most ecosystems; behaviours necessary to successfully cope with such conditions lead to extreme scramble competion in such substrates when insect population levels are relatively high (Hanks *et al*. 1993). In a study looking at snow-broken Norway spruce and Scots pine in Sweden, Schroeder and Eidmann (1993) reported that all stumps with no remaining living branches had been intensively colonized during the first summer. In another study, 95% of mechanically-created Norway spruce high stumps were colonized during the first summer by several species of Scolytidae and cerambycids *Monochamus sutor* (L.) and *Tetropium* spp. (Schroeder *et al*. 1999). Saint-Germain *et al*. (2004a) observed average densities of *Monochamus* sp. entry holes of 92.8/m^2 and up to as high as 378.2/m^2 in fire-killed black spruce. In such conditions, intra- and inter-specific competition have been well documented and plays an important role in the population dynamics of these species (Coulson *et al*. 1980, Victorsson and Wikars 1996, Schroeder 1997).

To locate their hosts, stressed-host species rely mainly on host-produced volatiles, but also use intra-guild kairomones. The use of volatiles, as other aspects of host-selection behaviour, has mainly been studied in coniferophagous species in Cerambycidae (review by Allison *et al*. 2004). Most coniferophagous cerambycid stressed-host species respond to some degree to host-produced monoterpenes and ethanol. Monoterpenes are defensive secondary compounds produced throughout the life of most coniferous trees, usually at higher concentrations when stressed or damaged (Trapp and Croteau 2001, Allison *et al*. 2004). Ethanol is a product of fermentation occuring in dying cells of stressed or dead

trees (Kelsey 1994, Kelsey and Joseph 2003). Several studies, either conducted in the field or in laboratory, showed that the response to these two compounds is usually synergetic (Montgomery and Wargo 1983, Chénier and Philogène 1989b, Schroeder and Weslien 1994, Brattli *et al*. 1998, Allison *et al*. 2001, Suckling *et al*. 2001). Response of cerambycids to scolytid-produced aggregation pheromones has also been documented, mostly in the genus *Monochamus* (Billings and Cameron 1984, Allison *et al*. 2001, Allison *et al*. 2003). Some short-range pheromones have been identified in stressed-host cerambycids (Lacey *et al*. 2004, Ray *et al*. 2006), but host-produced volatiles remain the most probable drivers of long-range host location (Hanks 1999).

The ecology of cerambycid dead-host species has not been the object of intensive research like stressed-host species have been. This group is defined as insects that oviposit on wood that is no longer green (Hanks 1999). It thus includes species found in a large array of conditions, i.e., from snags that have been dead for only a few months to highly decayed logs. How these insects locate their hosts has not been intensively researched; however they may be attracted to some degree by ethanol and possibly volatiles produced by wood-decay fungi. In most dead-host species, adults will feed on different hosts than their progeny, so males and females are known to encounter one another on the adult food plant (Michelsen 1966 and Heintze 1925, *in* Hanks 1999). In a limited number of species, especially those in which adults do not feed and usually do not disperse over long distances, long-range pheromones assisting mate location have been identified (Fettköther *et al*. 1995). Because physical and nutritional qualities of dead hosts change at a slow pace, several successive generations of dead-host species can breed in a single host (Hanks 1999).

The classification of Scolytidae proposed by Wood (1982) is similar to Hanks' (1999) classification of Cerambycidae. Some species typically colonize recently fallen or broken trees (e.g., *Ips*, *Pseudohylesinus*, *Pityogenes*); they can be seen as the equivalent of stressed-host species in Cerambycidae. Others (e.g. *Hylastes*, *Hylurgops*) prefer hosts in more advanced degree of deterioration (i.e., fermentation of the phloem) (Wood 1982), and correspond to early dead-host cerambycid species. The colonization dynamics of Scolytidae is more complex than the one seen in Cerambycidae, mostly because of the widespread use of long-range pheromones, mostly used for aggregation. Aggregation allows some species of Scolytidae to attack healthy trees, which they eventually kill if enough individuals colonize it to overcome their defense mechanisms. The typical colonization process of bark beetles can be divided into four phases (Wood 1982). The *dispersal* phase consists of the emergence of the adult and random flight until the insect detects host-produced volatiles or appropriate pheromones. The *selection* phase includes all pre-landing selection behaviours and ends with sustained feeding on a selected host's subcortical tissues. The *concentration* phase covers the whole period during which aggregation pheromones are released; this phase usually overlaps with the subsequent *establishment* phase. This last phase starts the moment the host's defences are overwhelmed (Wood 1982, Byers 1995). Depending on the physiological state of the species' preferred hosts, the concentration phase may or may not take place (i.e., in dead-host species or in ambrosia beetles). Unfortunately, little is known about the colonization dynamics of less-diverse or innocuous families of wood-borers.

2.5 Changes in substrate physical and nutritional status as wood decays

The decay process of dead wood has been mostly studied in the context of nutrient cycling and its role in geochemical cycles. Because of this, most studies of decomposition considered logs only, including snags only rarely (e.g., Yatskov *et al*. 2003). Changes in the physical characteristics of dead wood are the most obvious. As decay proceeds, wood density (g/cm^3) decreases more or less steadily. During most of the process, the woody material retains its volume and shape, but its porosity increases (Yoneda 1975). Decay rates vary between tree species and habitats. Lambert *et al*. (1980) estimated that boles of Balsam fir (*Abies balsamea* (L.) lost 50% of their mass in 23 years, and 90% of their mass in 70 years. In most cases, decomposition constants (*k*) are higher in deciduous species when compared to coniferous species (Alban and Pastor 1993, Yatskov *et al*. 2003). Differences have also been found within each group. Decay rates of most pine species are always among the lowest of coniferous species, while classification of other species varies between studies (Alban and Pastor 1993, Yatskov *et al*. 2003, Lahio and Prescott 2004). In deciduous trees, aspen, maple (*Acer* sp.) and beech (*Fagus* sp.) seem to decay faster than birch and ash (*Fraxinus* sp.) (Alban and Pastor 1993, Arthur *et al*. 1993, Yatskov *et al*. 2003). Decay rates also appear to vary according to diameter, bigger pieces of dead wood decaying more slowly than smaller ones (Janisch *et al*. 2005), and one study found within-log variation of decay in oak, especially at the middle of the decay sequence (Pyle and Brown 1999). In all cases, water content (ml/g or ml/cm^3) always increases along the decay gradient (Yoneda 1975, Lambert *et al*. 1980, Fraver *et al*. 2002). Yoneda (1975) also noted that the dessication rate of coarse woody debris in stable

conditions was higher in dead wood of lower density. More decayed wood could thus be considered as a less stable environment for saproxylic organisms.

Again in the context of nutrient cycling studies, changes in the chemical contents of dead wood along the decay gradient have received considerable attention, especially concerning nutrients important for plant growth, such as N, P, K, Ca and Mg. Some of these nutrients usually increase in concentration during the decay process, while others decrease or remain stable. In almost all studies, total nitrogen concentrations increase, especially in advanced decay stages (Lambert *et al*. 1980, Alban and Pastor 1993, Busse 1994, Krankina *et al*. 1999, Lahio and Prescott 2004). This increase in nitrogen can be partially explained by the significant nitrogenase activity detected in dead wood. Bacteria fixing atmospheric nitrogen are widespread in dead wood, and their activity is directly correlated with water content (Hendrickson 1991, Brunner and Kimmins 2003). Hendrickson (1991) also detected differences in bacterial activity levels between tree species, as moderately decayed aspen and birch logs had higher populations of bacteria than similar coarse woody material of red maple (*Acer rubrum* L.), balsam fir and jack pine (*Pinus banksiana* Lambert). Also, losses of nitrogen through formation of fungal sporocarps were less important than those seen for other major nutrients (Harmon *et al*. 1994). Other nutrients that increase in concentration with decay are phosphorus, calcium and magnesium, regardless of tree species (Lambert *et al*. 1980, Alban and Pastor 1993, Busse 1994, Krankina *et al*. 1999, Lahio and Prescott 2004). Potassium concentrations decrease with decay in most studies (Lambert *et al*. 1980, Keenan *et al*. 1993, Busse 1994, Lahio and Prescott 2004).

Because wood decomposition has not been studied in the context of insect nutrition, we have very little information on how other compounds important for insect growth, but irrelevant to plants, vary during the decay process. Thus, the influence of decay on non-structural carbohydrates, lipids and secondary compounds, among others phenolic compounds, is mostly unknown. Chararas (1981a) reports results on the decrease of simple sugars following the death of *Pinus pinaster* Aiton. Concentrations of non-structural carbohydrates in the phloem decreased rapidly after the trees had been felled, going from 5.6 g/100 ml of extracts in vigorous trees to 3.4 g/100 ml after 42 days, and 0.2 g/100 ml after 148 days. This drop during the few months following the death of the tree may be associated with the shift in colonizing wood-feeders from stressed-host species to dead-host species (Graham 1925, Hanks 1999). Among other compounds potentially having some biological significance, Becker (1971) investigated substances produced by wood-decaying microorganisms and their effects on wood-feeding insects. Some compounds clearly acted as feeding stimulants; however these effects were mostly studied on termites (Isoptera). Some other compounds have been suspected of having deleterious effects on larval growth, but the evidence has rarely been conclusive (reviewed by Becker, 1971). Since there are clear successional patterns among wood-decaying fungi along the decay process (Lindhe *et al*. 2004), the concentrations of such compounds are expected to vary along that same gradient.

2.6 Influence of substrate physical and nutritional status on insect performance

The effects of physical and nutritional parameters on the performance of wood-feeding larvae are difficult to assess experimentally, mostly because of the nature of the substrate

in question. Most studies focusing on these issues have used artificial diets, or more rarely natural host material manipulated in controlled conditions. Significant correlations were found in some species of wood-borers between larval growth or survivorship and water content, concentrations of soluble sugars and nitrogen. Chararas (1981a) tested larval survivorship of several *Arhopalus* species and *Ergates faber* (L.) along a range of substrate water content. All species exhibited better survivorship in substrate with high water content. In another study (Shibata 1998), larvae of *Semanotus japonicus* Lacordaire also performed better (higher weight gain) in hosts with higher water content. However, high water content can be deleterious to some species in specific conditions. Hanks *et al*. (1999) studied the establishment of cerambycid *Phoracantha semipunctata* F. on eucalypt trees in relation to host plant water potential. Larvae were unable to colonize the cambium of hosts with high water potential, and instead developed poorly in the less-suitable outer bark. *P. semipunctata* is considered a stressed-host species, and hosts with lower water potential, which indicate heavy stress, may be more suitable for this species. Whether larval development was hindered by the water potential *per se*, or another factor not measured correlated with stress level (e.g., secondary compounds) was left undetermined in that study.

Some studies suggested links between insect performance and concentrations of soluble sugars. In another study involving *Phoracantha semipunctata* and eucalypt hosts under different levels of stress, Caldeira *et al*. (2002) showed that concentrations of soluble sugars were higher in the inner bark of water-deprived hosts, in which larvae showed better survivorship and growth. However, other compounds whose concentrations can vary with stress level, e.g., secondary compounds, were not measured. Muryiri and

Ishikawa (2005) and Muryiri *et al*. (2003) demonstrated the importance of glucose and sucrose in the diet of cerambycid *Psacothea hilaris* (Pascoe) in a different way. Larvae of this species usually pupate following 5 instars, but in media with lower levels of soluble sugars, individuals have shown the capability of pupating following a shortened 4^{th} instar and form morphologically complete adults, suggesting that these compounds are important to the growth of immatures. Examples of such dependence on non-structural carbohydrates are few in cerambycids, as most species investigated possess to some degree endogenous enzymes hydrolizing structural carbohydrates (Chararas 1981b, Breznak 1982, Kukor *et al*. 1988, Rouland and Lenoir-Labé 1998, Zverlov *et al*. 2003). Several species thus have the capacity to digest cellulose and hemicellulose, and acquire a large proportion of their energy through these compounds. Some other groups of wood-feeding insects are known to be deprived of such enzymes. Species of the family Lyctidae are thus highly dependant on starch content of their substrate for their growth and survival (Haack and Slansky 1987).

Although some species of cerambycids can complete their development in substrates with nitrogen concentrations as low as 0.03% (Haack and Slansky 1987), some studies have suggested links between nitrogen content and larval growth rates. Larvae of *Semanotus japonicus* gained more weight in hosts with higher nitrogen concentrations (Shibata 1998). Hosking and Hutcheson (1979) showed a similar response in larvae of *Arhopalus ferus* Mulsant. However, no links with survivorship were established. Even in the best conditions, wood-feeding beetles are faced with especially nitrogen-poor substrates, as concentrations of nitrogen usually differ by two orders of magnitude between the larva's tissues and its feeding substrate. Some species have been shown to rely on endosymbionts

to acquire more nitrogen, as nitrogen-fixing bacteria have been found in their gut. These endosymbionts can in some cases provide 50% of the insect's nitrogen uptake (Rouland and Lenoir-Labé 1998). Elaborate mechanisms of nitrogenous metabolic waste recycling have also been described in termites, but have not been researched thus far in other wood-feeding taxa (Breznak 1982, Rouland and Lenoir-Labé 1998). In species with such adaptations, higher nitrogen contents in the substrate could allow faster larval growth but whether or not nitrogen can reach limiting levels remains to be determined.

Most of the aformentioned studies are correlative in their approach, and few conclusions can be reached regarding any limiting nutritional factors for wood-feeding species. It seems probable that concentrations of some compounds like nitrogen and soluble sugars will affect larval growth rates, and the sharp decrease in soluble sugars in the few months following tree death may very well be one of the mechanisms underlying the shift from stressed-host to dead-host species of the Cerambycidae. However, the cellulolytic potential of stressed-host species has not been experimentally assessed thus far. Also, whether or not nutrient concentrations play a role in host acceptance remains unknown beyond vague indications that some lyctid beetles appear to 'taste' the substrate before oviposition (Becker 1971). It is thus obvious that we do not understand fully the mechanisms at play in host selection of wood-feeding insects, especially in dead-host species.

3. Sampling saproxylic Coleoptera: Scale issues and the importance of behaviour.

Michel Saint-Germain[1,2], Christopher M. Buddle[1,2] and Pierre Drapeau[2].

[1]Department of Natural Resource Sciences, McGill University, 21,111 Lakeshore Road, Saint-Anne-de-Bellevue, Québec, Canada, H9X 3V9

[2]Groupe de Recherche en Écologie Forestière interuniversitaire, Département des sciences biologiques, Université du Québec à Montréal, CP 8888, succ. Centre-Ville, Montréal, Québec, Canada, H3C 3P8

Published in *Environmental Entomology*, 35: 478-487 (2006)

3.1 Preface

Pre-landing host-selection behaviours, including primary attraction, are commonly viewed as a predominant component of the overall host-selection behaviour of saproxylic insects, expecially in wood-feeding guilds. Distinctiveness of volatile profiles produced by different host types and their influence on subsequent host-selection behaviour could thus be a major driver of the host-use patterns seen in these insects. This paper investigates the importance of pre-landing host-selection behaviours by comparing landing rates of saproxylic species on contrasting snag types and stovepipe controls. Many aspects of the sampling design used contribute at making this paper an original advancement of knowleged in the field. First, pre-landing host-selection behaviours have mostly been studied in Scolytidae, and in a limited number of papers in Cerambycidae and Curculionidae. In this paper, whole saproxylic assemblages including several trophic guilds are considered. Also, sticky traps, the sampling technique used in this paper, are rarely seen in saproxylic insect research. This technique directly captures insects landing on a potential host, and is thus especially appropriate to tackle the types of questions asked within this part of the thesis. The information presented within this chapter should thus be considered unprecendented particularly because of the combination of the methods used and the taxa considered.

3.2 Abstract

Some currently used tree-scale sampling techniques targeting saproxylic insects capture individuals that are attracted to or landing on specific potential hosts. The success of such techniques is entirely dependant on strong primary attraction in targeted insects. However, up to this point, field experiments testing the primary attraction hypothesis have produced contradictory results. To test the efficiency of such techniques, and consequently the strength of primary attraction for saproxylic Coleoptera, we sampled insects landing on contrasting snag types including new and old snags of 5 different tree species using sticky traps in a single mixed 135-year-old boreal stand in western Quebec, Canada. Ordination analyses showed homogenous assemblages among the different snag types and stovepipe controls, when considering either all species captured or only targeted functional groups, and very few species showed strong affinities to specific snag types. Species composition of assemblages was in several cases correlated with the species and status of trees neighbouring the sampling units, which suggest that pre-landing host-selection mechanisms do not allow insects to single out a potential host while in flight. Our results suggest that primary attraction may play a role at larger spatial scales and help insects identify potential habitat patches, while selection of a single host at the local scale is done by trial-and-error through random landing. In such a context, future studies aiming at describing precise host-use patterns of saproxylic insects should rely on methods targeting larvae or emerging adults such as wood dissection and rearing.

Keywords: host-selection behaviour, primary attraction, random attack, saproxylic Coleoptera, tree-scale sampling.

3.3 Introduction

Many holometabolous insects can be characterized as living a «double life», in that larvae and adults can belong to different trophic guilds and may use very different habitats. This is the case for most saproxylic beetles, especially in phloeophagous, xylophagous and xylomycetophagous groups. While larvae are restricted to a single piece of decaying wood and can live as such for several years, adults are generally mobile, short-lived and often feed only during a short maturation phase, when feeding at all (Haack and Slansky 1987, Hanks 1999). For these insects, larvae are definitely the dominant life stage, with adults being generally reduced to play a dispersal role besides reproduction. Thus, larval habitat requirements are generally much more definite and constraining and are likely to be more relevant to the persistence of the species at the local scale.

There is a growing interest in understanding the habitat requirements of saproxylic insects (Grove and Stork 1999, Grove 2002a), as they are sensitive to many forest management practices (Berg *et al*. 1994, Martikainen *et al*. 2000, Siitonen 2001, Grove 2002b, Maeto *et al*. 2002). Most of the work on saproxylic insects has focused thus far at describing and comparing assemblages at the stand scale, using different sampling techniques that target adults such as flight-intercept traps (Similä *et al*. 2003, Saint-Germain *et al*. 2004a), trunk-window traps (Martikainen *et al*. 1998, Ranius and Jansson 2000), Lindgren multiple funnels (Chénier and Philogène 1989a) and even mass rearing (Grohmann *et al*. 2004). Most of these approaches have limitations, since the adults caught are, for a high proportion of species, actively dispersing, and thus not necessarily closely tied to the habitat in which they were captured. The assumption that an adult caught flying will

oviposit on some substrate present in the stand is not justified. However, one can try to sample adults as close as possible to oviposition, and thus be able to make inferences about actual host use.

Some studies have attempted to sample at the tree scale, using either trunk-window traps (Kaila *et al*. 1994, Økland 1996; Ranius and Jansson 2002, Hammond *et al*. 2003), sticky traps (Schroeder 1987, Shepherd and Goyer 2003), or logistically-demanding rearing (Hammond *et al*. 2001, Hammond *et al*. 2003, Hövemeyer and Schauermann 2003, Kappes and Topp 2004, Lindhe and Lindelöw 2004, Saint-Germain *et al*. 2004b) and bark dissection (Jonsell and Weslien 2003, Jonsell *et al*. 2004). Rearing and woody debris dissection give precise information about host use, but usually require a lot of space (i.e., for *ex-situ* rearing) and/or a lot of time, and they usually do not produce many specimens. It would therefore be worthwhile to refine passive techniques to allow for reliable sampling at the tree scale.

Passive techniques used to sample at tree scale (trunk-window and sticky traps) capture individuals that are attracted to or landing on specific potential hosts. The success of such techniques is entirely dependant on strong primary attraction in targeted insects, since it is assumed that they are able to discriminate between suitable and unsuitable hosts while in flight. The primary attraction hypothesis (Person 1931) states that selection is host-induced by chemical and/or visual cues while the beetle is still in flight. While several groups of insects have been shown to react physiologically to host and non-host volatiles (Mustaparta *et al*. 1979, Tunset *et al*. 1993, Brattli *et al*. 1998, Huber *et al*. 2000, Belmain *et al*. 2002, Allison *et al*. 2004), other studies have shown random landing patterns in

field experiments among hosts of contrasting quality (Goeden and Norris 1964, Berryman and Ashraf 1970, Moeck *et al*. 1981). Thus, actual support for a generalized and dominant primary attraction in the overall host-selection process of saproxylic insects is at best equivocal. There is evidence, at least for some groups, that insects may reject a high proportion of potential hosts after having landed (Berryman and Ashraf 1970). Therefore, we must question whether currently-used passive tree-scale sampling techniques targeting adults prior to oviposition can provide precise information about actual host use.

In this study, we used sticky traps to sample saproxylic Coleoptera landing on different types of snags and on stovepipe controls in a boreal mixed-wood forest of western Quebec, Canada. Among sampling techniques, sticky traps capture insects closest to oviposition; captures obtained are thus more likely to reflect actual host use. Snags sampled included heavily-decayed snags and new, mechanically-killed snags of five different tree species (two deciduous and three coniferous). Coleoptera assemblages using such contrasting snag types were expected to be very different, as species are usually much more specialized at the beginning of the decay gradient than at the end, and the barrier between coniferous and deciduous hosts is very rarely crossed (Heliövaara and Väisänen 1984, Haack and Slansky 1987, Dajoz 2000). Our main objective was to compare saproxylic Coleoptera assemblages landing on these contrasting snag types and to use this data to determine if such passive pre-oviposition sampling techniques can be used to sample saproxylic Coleoptera at tree-scale.

3.4 Material and Methods

3.4.1 Study area

The study was conducted in Aiguebelle Provincial Park in western Quebec, Canada (48° 32' N, 78° 39' W). We chose a single ~10-ha 135 year-old mixed stand of which the living basal area consists of 30.8% black spruce *Picea mariana* (Miller), 28.0% balsam fir *Abies balsamea* (L.), 15.6% paper birch *Betula papyrifera* Marshall, 9.6% trembling aspen *Populus tremuloides* Michaux, 9.6% white spruce *Picea glauca* (Moench), 4.8% jack pine *Pinus banksiana* Lambert and 1.5% eastern white-cedar *Thuya occidentalis* L.. The density of snags over 10 cm in diameter at breast height (DBH) and over 1.5 m in height was estimated at 180.5/ha, and total snag basal area is distributed as follow: 39.1% jack pine, 28.3% paper birch, 18.8% balsam fir, 11.1% aspen and 2.7% black spruce. Compositional data suggest that this stand is currently shifting from a jack pine/paper birch dominance to a black spruce/balsam fir dominance. Aiguebelle Park is 268.3 km² in area and is nested in a moderately fragmented aspen-dominated landscape.

3.4.2 Sampling design

Saproxylic insects were sampled on snags of five tree species, two deciduous (trembling aspen and paper birch) and three coniferous (black spruce, jack pine and balsam fir). Snags were selected along six parallel transects going through the stand, each 40 m apart. For each species except black spruce, of which old snags were almost absent, we selected four heavily decayed snags having a DBH over 16 cm. We also selected four healthy trees

using the same DBH criterion, which were mechanically killed by girdling on the first day of sampling to create «new» snags. «Old» and «new» snags totalled 36 snags. In addition, we set up four 1.5-m-high stovepipes painted black to serve as inert controls (see Chénier and Philogène 1989b). Unbaited stovepipes are thought to have a vertical shape reminiscent of snags (i.e., to beetles), without emitting any potentially attractant or repellent semiochemical. On each of these 40 sampling units, we pinned between 1.1 and 1.7 m a 0.25-m^2 (~60×40 cm) polyethylene sheet coated with Tree Tanglefoot™ Pest Barrier (The Tanglefoot Company, Grand Rapids, MI, USA), centered on their southern aspect. Tree Tanglefoot™ is mainly composed of manila copal rosin, castor oil and carnauba wax. Manila copal rosin is the non-volatile fraction left after the distillation of turpentine from the resin of the tropical conifer genus *Agathis* Salisb., while carnauba wax comes from the tropical palm *Copernicia prunifera* (Mill.). Since none of its key components are volatile, Tree Tanglefoot™ does not interfere with primary attraction. Sticky traps were active for three 2-week sessions during the summer. Session 1 spanned from 6 June to 20 June, session 2 from 28 June to 12 July and session 3 from 15 July to 30 July 2004. At the end of each session, the polyethylene sheets were covered with a plastic film, folded and brought to the laboratory. All Coleoptera were removed from the resin and cleaned using the Histo-Clear® histological clearing agent (National Diagnostics, Atlanta, GA, USA). Polyethylene sheets were replaced by new ones at the beginning of each session. Coleoptera were identified to species, or morphospecies for some families. Vouchers will be deposited at the Lyman Entomological Museum (McGill University, Montreal, Canada).

3.4.3 Statistical analyses

Mean number of captures and mean species richness were compared among the 10 snag types using one-way ANOVAs. Normality was confirmed using a Shapiro-Wilk test. Two-way ANOVAs could not be used because of the missing «old» black spruce snag type and to include the stovepipe controls. Individual-based rarefaction curves were used to compare species richness. Rarefaction curves provide more reliable estimates of species richness, as they remove the effect of differing sample sizes. Individual-based rarefaction is also useful to correct for sampling effort, in cases where frequent trap disturbance may have occurred (Buddle *et al*. 2005). Detrended correspondence analysis (DCA) was used to compare species composition among snag types. DCA is an eigenanalysis-based multivariate analysis that arranges sites along axes on the basis of data on species composition (ter Braak 1987). DCA ordination does not suffer from the major problems found in correspondence analysis, i.e., arch effects and compression of the ends of the gradients (Hill and Gauch 1980), and is widely used for analyzing ecological data sets. To investigate the specific response of targeted functional groups, species and morphospecies were subdivided into wood-feeders, fungivores and predators whenever published information about the taxon was available (wood-feeders: 37 species, 213 individuals; fungivores: 44 species, 5033 individuals; predators: 29 species, 458 individuals). These sub-matrices were analyzed with DCA ordinations to compare percentages of the explained species data variance and gradient lengths. Gradient length of the first DCA axis is a good estimator of species turnover between samples (Eilersten *et al*. 1990, Drapeau *et al*. 2000), and was used to quantify the homogeneity of assemblages between snag types for each functional group. To look at the influence of the

immediate neighbours on sample composition, sample scores along axes 1 and 2 of all DCAs were correlated with the basal area (BA) of live and dead coniferous trees, BA of live and dead deciduous trees and a total coniferous/deciduous BA ratio of trees found within a 3 m radius around the sample unit. Indicator species analyses (Dufrêne and Legendre 1997) were also used to identify species that were more or less restricted to specific types of snags, classified as coniferous vs. deciduous, new vs. old, by tree species and by treatment (all species per snag stage plus stovepipes). ANOVAs and correlations were performed using SPSS 10.0.5 for Windows (SPSS Inc., Chicago, IL, USA). Rarefaction curves were calculated with the software Ecosim (Acquired Intelligence Inc. & Kesey-Bear. Burlington, VT, USA). Detrended correspondence analyses were performed using CANOCO for Windows 4.0.2 (Microcomputer Power, Ithaca, NY, USA) and indicator species analyses were done using PCOrd 4.17 (MJM Software Design Inc., Gleneden Beach, OR, USA).

3.5 Results

During the course of our experiment, a total of 7194 beetles were captured, belonging to 207 species and morphospecies. Main families found in terms of abundance and species richness are summarized in Table 3.1. A single lathridiid morphospecies (*Corticaria* sp.) accounted for 51.8% of total abundance, and was captured on all sampling units. No significant differences were found either in abundance ($F_{9,26}$=1.842; P=0.108) or species richness ($F_{9,26}$=2.108; P=0.067) between the snag types when analyzed with one-way ANOVAs (Table 3.2). Rarefied estimates of species richness, when standardized to 476

individuals (total captures for new aspen), was highest for the stovepipe controls, and lowest in old balsam fir, new paper birch and new black spruce (Table 3.2).

The DCA run for the full data matrix explained relatively little species data variance (Table 3.3). We were unable to discriminate clearly, using the graphical output of the DCA, between insect assemblages that landed on coniferous vs. deciduous snags (Figure 3.1a), on old vs. new snags (Figure 3.1b), on any of the sampled tree species (Figure 3.1c) or either snag types (all combinations, not shown), as the overlap between all groups was in most cases almost complete. The stovepipe controls had assemblages very similar to those of natural snags (Figure 3.1). This total lack of specificity in captured assemblages was reflected in the indicator species analyses, as only 1 of the species captured more than 10 times obtained a significant indicator value over 50 [*Pissodes fiskei* Hopkins; IndVal: 54.3 for coniferous snags; P=0.026]. Figure 3.2 shows species rank-abundance graphs based on species rank from all snag types combined (50 most abundant while captured on at least 3 snags) among contrasting treatment groups between which assemblages should differ the most according to our predictions. Again here the lack of specificity is explicit, as very few species among the 50 most abundant are totally absent from any of the treatment groups. The identity of these species and the number captured on each snag type is presented in Appendix 3.1.

The DCAs run on the matrices for different functional groups explained little more variance of the species data (Table 3.3). Gradient lengths of the first axes of each of these DCAs show that fungivore assemblages were much more homogenous than those of predators and wood-feeders (Table 3.3). Although species turnover was higher in

assemblages of predators and wood-feeders, we were still unable to discriminate between assemblages having landed on any snag types (DCA graph for wood-feeders shown on Figure 3.3).

Sample scores of some DCA ordinations were significantly correlated to species composition, basal area and physiological status of neighbouring trees. Axis 2 of the DCA involving all species was positively correlated with dead deciduous trees basal area (R^2=0.174; P=0.007). Axis 1 of the predators DCA was positively correlated with dead deciduous trees basal area within a 3-m radius (R^2=0.279; P=0.001) while axis 2 was positively correlated with dead coniferous trees basal area (R^2=0.154; P=0.014) (Table 3.3).

3.6 Discussion

We found a high degree of similarity in Coleoptera assemblages of different snag types, in spite of having sampled both extremes of the decay gradient and numerous tree species, including both deciduous and coniferous snags. Pissodes fiskei was the only taxon to show some degree of specificity to a single snag type (coniferous). Based on the variety of snag types sampled in our study, we expected to obtain at least in some cases very different saproxylic beetle assemblages. Our expectations were well supported by current knowledge on saproxylic insect host use. Models of insect host-use patterns along the decay gradient based on empirical data from other systems show a clear succession in assemblages, suggesting very different communities at both extremes of the gradient

(Heliövaara and Väisänen 1984, Dajoz 2000). There is also a clear distinction between wood-feeding species using recently dead trees (stressed-host species) and others using the same host in the following years (dead-host species) (Wood 1982, Hanks 1999). Saproxylic insects using less decayed wood are generally more specialized than species using older, more decayed hosts, but the barrier between deciduous and coniferous hosts is rarely crossed even in highly-decayed log stages (Haack and Slansky 1987). None of these well-known patterns was reflected in our results. In this context, it is clear that the assemblages obtained through our sampling did not closely reflect actual host use, either when using all species in the analyses or when targeting specific functional groups such as wood-feeders.

The potential success of a sampling approach targeting landing adults rests on strong and determinant pre-landing host-selection behaviours. Two main hypotheses concerning pre-landing host selection are still debated in the literature. The primary attraction hypothesis (Person 1931) states that selection is host-induced by chemical and/or visual cues while the beetle is still in flight. In contrast, the random landing hypothesis states that the insect lands randomly on a host and then can evaluate its quality. These two hypotheses are not necessarily mutually exclusive, and either could be predominant in a particular species (Byers 1995). Studies have showed that numerous species of several beetle families are attracted in some way to host volatiles [Curculionidae (Tunset *et al*. 1993, Brattli *et al*. 1998); Cerambycidae (Chénier and Philogène 1989a, Brattli *et al*. 1998, Allison *et al*. 2004, Pajares *et al*. 2004); Scolytidae (Borden *et al*. 1987, Chénier and Philogène 1989b, Tunset *et al*. 1993, Brattli *et al*. 1998, Macias-Samano *et al*. 1998, Fletchmann *et al*. 1999)], apparently giving support to the primary attraction hypothesis. Some evidence

also supports some sort of primary attraction for fungivores (Belmain *et al*. 2002) and some predators (Cleridae; Chénier and Philogène 1989b). However, there is a body of literature reporting equivalent landing rates on both high-quality and inappropriate hosts for several species of Scolytidae (Goeden and Norris 1964, Berryman and Ashraf 1970, Moeck *et al*. 1981), and thus supporting the random landing hypothesis.

Although at least some species of wood-feeders respond physiologically to host volatiles, it is not clear if this attraction helps the beetle to target a single host or rather to orient towards a habitat patch containing the potential host. Most studies focusing on primary attraction were not designed to make such a distinction. It would be expected that neighbouring trees all contribute to a common pool of volatiles. It is far from clear if the olfactive signal emitted by a single tree is clear enough in this mixture of contradictory chemical cues to allow the insect to target a single host while still in flight. Such a conception of the host-selection process is to some degree invalidated in our study by the fact that the species composition and status of neighbouring trees had a significant influence on the insect assemblages caught on specific snags, an influence that seems to be greater than the identity of the sampled snag itself. The importance of neighbouring trees, the lack of specificity showed in the ordination analyses and the ability of stovepipe controls to collect assemblages very similar to the ones caught on natural snags without emitting any potentially attractant semiochemicals all support that beetles in flight might orient themselves toward a promising habitat patch using host volatiles, but, at smaller scale, land randomly on trees to perform post-landing host-selection steps in a trial-and-error fashion. Primary attraction would thus play a role in orienting long-range dispersal, while host selection at short range would be the result of random landing. The fact that

only one species showed specificity to some snag type in our results suggest that primary attraction plays a role at short range for a very limited number of species.

Although some studies show that predators and fungivores can be attracted by host volatiles (Chénier and Philogène 1989b, Belmain *et al*. 2002), most of the evidence for such a behaviour concerns wood-feeders. Hence, we analyzed wood-feeder data separately, but did not observe any more patterns in results from this functional group (Figure 3.3). Since the number of captures for this functional group was relatively low (37 species with 213 individuals), it may be necessary to sample this group with an active area larger than 0.25 m^2 to catch sufficient specimens. However, even with a small sample size, the almost total absence of patterns in wood-feeder distribution still goes against our initial predictions. We can also point out that the stand in which the experiment was performed is exceptionally mixed; a higher proportion of non-host volatiles in the environment can possibly obscure chemical signals, and thus result in such random landing patterns. Several behavioural experiments have shown that some green-leaf volatiles (C-6 alcohols) produced by angiosperm trees disrupt the attraction of some coniferophagous bark beetles and cerambycids to host volatiles and pheromones (Huber *et al*. 2000, Huber and Borden 2001, Morewood *et al*. 2003, Zhang and Schlyter 2004). In such a mixed forest, several non-host volatiles were most probably present in the environment for both coniferous- and deciduous-using saproxylic beetles and they may have in some way influenced the behaviour of these insects. Wood-feeder assemblages sampled with sticky traps could possibly have been more structured in purely coniferous or deciduous stands, without the interference of an array of non-host volatiles.

These results force us to reconsider how we should sample saproxylic insects depending on the scale of interest (Figure 3.4). Flight-intercept and multiple-funnel traps are convenient ways to sample at a stand scale, even if they are likely to catch, at least for some insect groups dispersing over long distances, some proportion of transient individuals having no real affinity with the immediate environment in which they are caught. They paint in some cases a somewhat blurred portrait of the local communities, but can give valuable information on regional diversity. Trunk-window traps and sticky traps suffer to a larger degree from the same problem, as the composition of their catches is tainted by both stand- and tree-scale influences. Our study even shows that, at least in some cases when using such techniques, the tree-scale influence can be minimal. In a recent study characterizing saproxylic beetles using aspen in old-growth boreal forests and clear-cuts using trunk-window traps (Martikainen 2001), over 40% of individuals and 65% of species caught were confirmed transient, as they were either not saproxylic, or were dependant on coniferous tree species. Caution must be taken when interpreting results gathered using either of these techniques, as they are bound to produce, at best, weak patterns. Rearing and dissection are still the most appropriate ways to sample at tree scale, since they cannot produce, when properly used, significant numbers of transient individuals.

Insect assemblages landing on a specific snag could not be used in our study to obtain precise information on actual host use patterns. Our results also suggest that the relative importance of pre-landing host-selection steps is low. Extreme caution must be taken when interpreting results gathered using methods targeting adults at the tree scale. More time-costly and possibly destructive methods such as in-situ or ex-situ rearing and wood

dissections will have to be used in future research aiming at explaining host-use patterns of saproxylic insects at tree scale. This study also demonstrates that post-landing host-selection steps are crucial in the overall host-selection behaviour, and should be a focus of future behavioural research.

3.7 Acknowledgements

We would like to thank Aiguebelle Provincial Park for facilitating our research within the park boundaries and Elise Bolduc, Christopher Cloutier, Maxim Larrivée and Matthew Wild for field work. This project was funded by Action Concertées - Fonds forestiers (P. Drapeau and C. Buddle) and new researcher grants (C. Buddle) from the Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT) and a Discovery grant to C. Buddle from the Natural Science and Engineering Research Council of Canada (NSERC).

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Table 3.1 Beetle families representing at least 1% of total captures from all sticky traps. A total of 7194 individuals was captured.

Family	Species	Individuals	% of total captures
Lathridiidae	11	4508	62.6
Melandryidae	6	440	6.1
Elateridae	19	378	5.3
Cantharidae	10	287	4.0
Staphylinidae	19	278	3.9
Mordellidae	7	133	1.9
Leiodidae	4	116	1.6
Alleculidae	1	107	1.5
Scolytidae	14	88	1.2
Curculionidae	15	88	1.2
Melyridae	4	73	1.0

Table 3.2 Mean number of captures, mean species richness per snag (n=4 per treatment) and individual-based rarefied richness for all taxa caught on each snag types ± 1 standard deviation (N – new snag; O – old snag; Asp – aspen; PBi – paper birch; BSp – black spruce; JPi – jack pine; BFi – balsam fir; Stv – stovepipe). No significant differences were detected.

	NAsp	OAsp	NPbi	OPbi	NBsp	NJpi	OJpi	NBfi	OBfi	Stove
Abundance	194.0 ± 36.8	185.3 ± 73.8	167.0 ± 48.0	141.0 ± 32.1	276.7 ± 12.0	224.0 ± 22.7	166.5 ± 47.4	228.8 ± 102.6	161.8 ± 53.1	192.8 ± 36.7
Species richness	38.5 ± 13.4	36.5 ± 9.5	32.7 ± 6.0	32.8 ± 1.3	36.0 ± 3.6	42.8 ± 5.4	35.8 ± 8.9	44.5 ± 13.1	31.8 ± 6.7	49.0 ± 2.9
Rarefied species richness	72.0 ±0.0	74.0 ± 7.0	61.6 ± 5.5	71.7 ± 4.3	56.9 ± 6.1	66.7 ± 6.3	71.0 ± 6.0	71.5 ± 7.5	59.5 ± 4.5	86.0 ± 7.0

Table 3.3 Results from detrended correspondence analyses performed on all species and on sub-matrices restricted to individual functional groups, and significant correlations of DCA sample scores with species composition and status of trees neighbouring the sampled snag (BA – basal area). Gradient lengths are used to estimate species turnovers among samples.

Trophic guild	% variance of species data explained	Length of gradient 1	Correlations of DCA axes with environmental factors
All	21.1	1.956	Axis 2 – dead deciduous BA; P=0.007
Wood feeders	26.5	6.740	None
Fungivores	29.3	0.891	None
Predators	31.2	2.632	Axis 1 – dead deciduous BA; P=0.001 Axis 2 – dead coniferous BA; P=0.014

List of figures

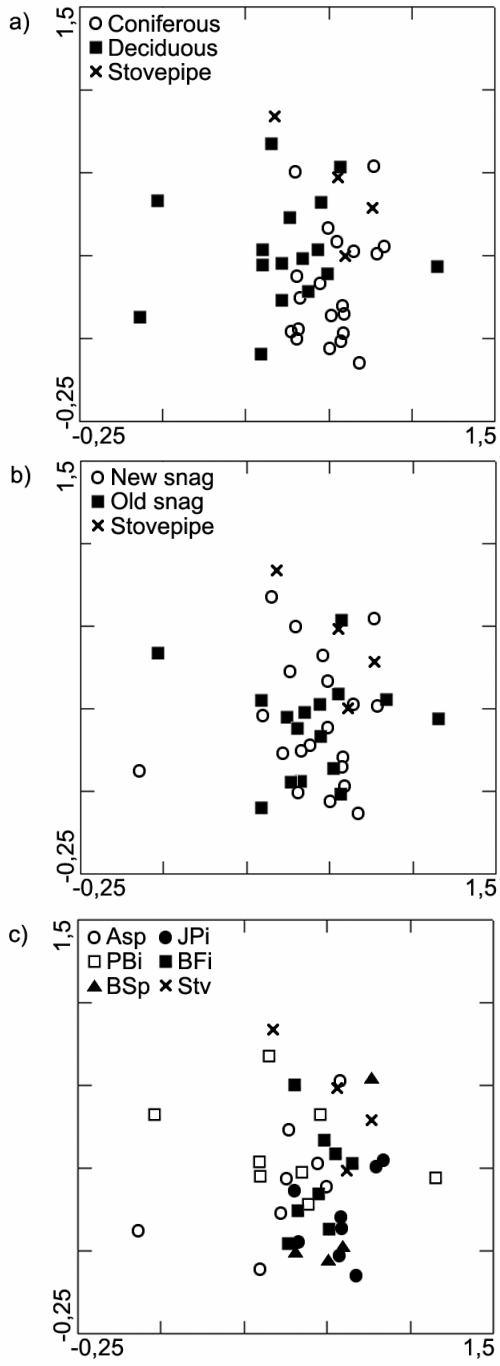
a)
Coniferous
Deciduous
Stovepipe
1,5
-0,25
-0,25
1,5
b)
New snag
Old snag
Stovepipe
1,5
-0,25
-0,25
1,5
c)
Asp
JPi
PBi
BFi
BSp
Stv
1,5
-0,25
-0,25
1,5

Figure 3.1

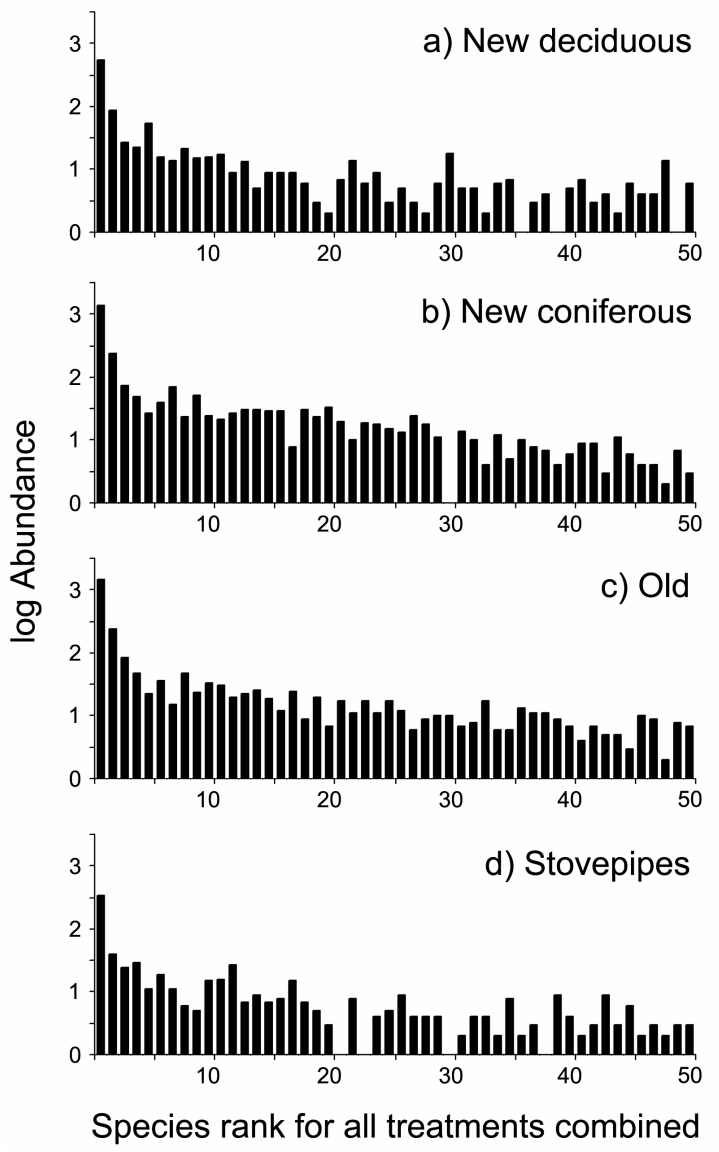
a) New deciduous
b) New coniferous
c) Old
d) Stovepipes
log Abundance
Species rank for all treatments combined
0
1
2
3
10
20
30
40
50

Figure 3.2

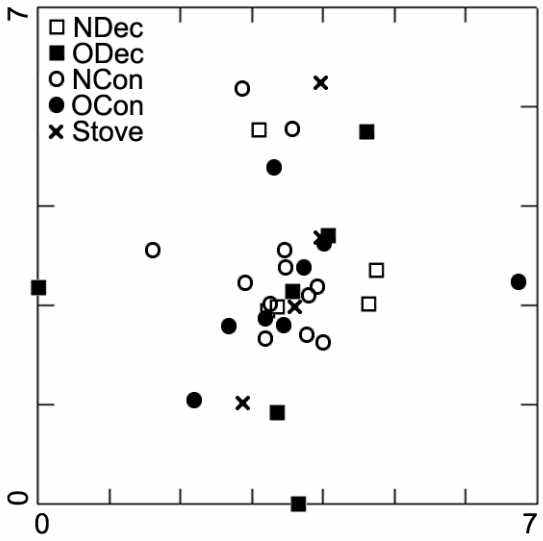

Figure 3.3

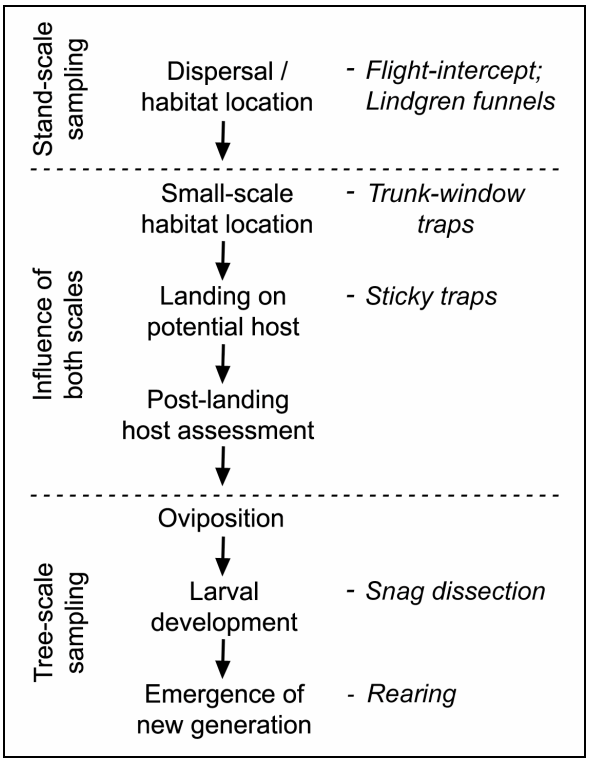
Stand-scale sampling
Dispersal / habitat location
- Flight-intercept; Lindgren funnels
Influence of both scales
Small-scale habitat location
- Trunk-window traps
Landing on potential host
- Sticky traps
Post-landing host assessment
Tree-scale sampling
Oviposition
Larval development
- Snag dissection
Emergence of new generation
- Rearing

Figure 3.4

Appendix 3.1 Mean abundance ± 1 standard deviation for each snag type of the 50 most abundant species (all snag types combined).

Rank	*Species*	NAsp	OAsp	NPbi	OPbi	NBsp	NJpi	OJpi	NBfi	OBfi	Stove
1	*Corticaria* sp. (Lathridiidae)	65.5 ± 51.1	106.0 ± 56.2	72.8 ± 38.9	77.3 ± 23.8	123.8 ± 68.8	113.3 ± 29.3	84.3 ± 32.4	89.5 ± 50.0	89.5 ± 31.4	85.0 ± 21.0
2	*Melanophthal*ma sp. (Lathridiidae)	9.8 ± 6.1	15.0 ± 4.1	12.3 ± 7.6	9.8 ± 6.1	22.8 ± 14.8	22.5 ± 9.3	18.0 ± 9.2	15.0 ± 7.2	17.8 ± 2.5	9.5 ± 7.2
3	*Scraptia sericea* Melsheimer (Melandryidae)	2.0 ± 1.6	4.0 ± 1.6	4.5 ± 3.4	2.0 ± 1.6	6.5 ± 4.7	6.8 ± 1.7	9.0 ± 2.4	4.5 ± 2.4	6.0 ± 3.2	6.0 ± 3.5
4	*Ctenicera triundulata* (Randall) (Elateridae)	1.3 ± 1.0	3.8 ± 3.3	4.0 ± 3.3	3.8 ± 3.1	4.3 ± 3.9	4.8 ± 2.6	1.0 ± 1.4	3.0 ± 2.2	3.3 ± 2.9	7.0 ± 5.8
5	Nitidulidae sp.#1 (Nitidulidae)	1.3 ± 1.9	1.8 ± 3.5	12.3 ± 15.3	0.8 ± 1.0	1.0 ± 2.0	0.8 ± 1.0	1.3 ± 1.3	4.8 ± 4.3	1.5 ± 1.7	2.5 ± 3.7
6	*Isomira quadristriata* Couper (Alleculidae)	0.5 ± 1.0	2.5 ± 2.4	3.3 ± 2.5	0.8 ± 1.0	5.0 ± 1.6	1.3 ± 1.3	2.5 ± 2.1	3.3 ± 2.6	3.3 ± 3.3	4.5 ± 3.7
7	*Serropalpus coxalis* Mank (Melandryidae)	0	0.3 ± 0.5	3.3 ± 5.9	1.0 ± 2.0	4.3 ± 3.3	3.8 ± 1.3	0.3 ± 0.5	9.0 ± 7.3	2.0 ± 2.8	2.5 ± 3.7
8	*Podabrus* sp.#1 (Cantharidae)	1.8 ± 2.1	1.5 ± 0.6	3.3 ± 2.2	4.5 ± 3.9	2.5 ± 2.1	1.3 ± 1.3	2.5 ± 2.9	1.8 ± 2.4	3.0 ± 1.2	1.3 ± 1.3
9	*Mordellistena* sp. (Mordellidae)	0.8 ± 1.0	0.5 ± 1.0	2.8 ± 2.4	1.8 ± 0.5	2.3 ± 0.5	6.8 ± 8.3	2.3 ± 1.0	3.5 ± 2.4	1.0 ± 0.8	1.0 ± 1.4
10	*Melandrya connectens* (Newman) (Melandryidae)	1.0 ± 1.2	2.3 ± 2.5	2.8 ± 0.5	2.5 ± 1.7	0.8 ± 1.0	0.5 ± 0.6	1.3 ± 1.0	4.8 ± 5.7	2.0 ± 1.4	3.5 ± 3.4
11	Leiodidae sp.#1 (Leiodidae)	1.3 ± 1.5	3.0 ± 1.4	2.8 ± 2.6	1.0 ± 0.8	0.8 ± 1.0	1.8 ± 1.0	2.3 ± 1.9	2.5 ± 3.3	1.3 ± 1.5	3.8 ± 3.3
12	*Lathridius* sp. (Lathridiidae)	0.5 ± 0.6	1.5 ± 2.4	1.5 ± 1.3	1.0 ± 0.0	2.8 ± 3.6	1.8 ± 0.5	1.3 ± 1.0	2.0 ± 2.2	1.0 ± 0.8	6.5 ± 6.9
13	*Podabrus* sp.#2 (Cantharidae)	0.8 ± 1.5	1.8 ± 1.5	2.3 ± 1.3	1.5 ± 0.6	4.0 ± 4.1	0.8 ± 1.0	1.3 ± 1.0	2.8 ± 2.1	0.8 ± 1.0	1.5 ± 1.3

Appendix 3.1 *(continued)*

Rank	*Species*	NAsp	OAsp	NPbi	OPbi	NBsp	NJpi	OJpi	NBfi	OBfi	Stove
14	Staphylinidae sp.#1 (Staphylinidae)	0.8 ± 1.0	1.5 ± 1.3	0.3 ± 0.5	1.5 ± 0.6	2.5 ± 2.6	1.5 ± 1.7	2.3 ± 3.2	3.3 ± 1.7	1.0 ± 0.8	2.0 ± 1.2
15	Staphylinidae sp.#2 (Staphylinidae)	0.8 ± 1.0	1.8 ± 2.9	1.3 ± 1.0	1.5 ± 1.3	1.5 ± 1.3	3.5 ± 2.5	0.3 ± 0.5	2.0 ± 2.2	1.0 ± 2.0	1.5 ± 1.3
16	Staphylinidae sp.#3 (Staphylinidae)	0.5 ± 0.6	1.5 ± 1.3	1.5 ± 1.7	1.0 ± 1.2	0.8 ± 1.5	5.0 ± 3.6	0.3 ± 0.5	1.3 ± 1.9	0	1.8 ± 1.0
17	Lathridiidae sp.#1 (Lathridiidae)	1.0 ± 1.2	0.5 ± 0.6	1.0 ± 1.4	2.5 ± 1.0	0	0.3 ± 0.5	1.5 ± 1.9	1.5 ± 1.3	1.5 ± 1.0	3.5 ± 3.3
18	*Polygraphus rufipennis* (Kirby) (Scolytidae)	1.0 ± 1.4	0.8 ± 1.0	0.3 ± 0.5	0.3 ± 0.5	2.5 ± 2.1	2.8 ± 2.4	0.3 ± 0.5	2.3 ± 2.6	0.8 ± 0.5	1.5 ± 1.3
19	Ciidae sp.#1 (Ciidae)	0	0.5 ± 0.6	0.5 ± 1.0	1.0 ± 1.2	3.8 ± 5.2	1.8 ± 1.3	0.8 ± 1.5	0	2.5 ± 5.0	1.0 ± 1.4
20	*Pissodes fiskei* Hopkins (Curculionidae)	0.3 ± 0.5	0.3 ± 0.5	0	0.3 ± 0.5	4.0 ± 3.9	2.0 ± 1.2	0.5 ± 0.6	2.0 ± 1.4	0.5 ± 0.6	0.5 ± 0.6
21	*Mulsantina hudsonica* (Casey) (Coccinellidae)	0.5 ± 0.6	0.5 ± 1.0	1.0 ± 0.8	0.3 ± 0.5	2.3 ± 2.2	1.8 ± 1.7	2.3 ± 1.7	0.8 ± 1.0	1.0 ± 1.2	0
22	*Limonius aeger* LeConte (Elateridae)	0.5 ± 1.0	1.3 ± 1.0	2.8 ± 1.3	0	0	1.8 ± 2.4	1.0 ± 1.2	0.5 ± 0.6	0.3 ± 0.5	1.8 ± 1.5
23	*Attalus nigrellus* LeConte (Melyridae)	0.5 ± 1.0	1.3 ± 1.9	0.8 ± 1.0	0	1.8 ± 2.2	0.8 ± 1.0	1.5 ± 1.7	2.0 ± 0.8	1.3 ± 1.9	0
24	*Dalopius sp.* (Elateridae)	0	0.3 ± 0.5	2.0 ± 4.0	1.3 ± 1.9	1.0 ± 1.4	1.3 ± 1.5	1.0 ± 1.2	2.0 ± 4.0	0	0.8 ± 1.0
25	*Podabrus* sp.*#3* (Cantharidae)	0.3 ± 0.5	0	0.3 ± 0.5	0.5 ± 0.6	2.5 ± 5.0	1.0 ± 1.4	2.8 ± 2.2	0	0.8 ± 1.0	1.0 ± 1.4
26	Elateridae sp.#1 (Elateridae)	0.3 ± 0.5	0.3 ± 0.5	0.8 ± 0.5	0.5 ± 0.6	0.5 ± 0.6	1.3 ± 1.9	1.0 ± 1.4	1.3 ± 1.0	1.0 ± 0.8	2.0 ± 1.6
27	Staphylinidae sp.#4 (Staphylinidae)	0	0.3 ± 0.5	0.5 ± 0.6	0.3 ± 0.5	0.8 ± 1.5	4.5 ± 4.2	0.5 ± 1.0	0.5± 0.6	0.3 ± 0.5	0.8 ± 1.0

Appendix 3.1 *(continued)*

Rank	*Species*	NAsp	OAsp	NPbi	OPbi	NBsp	NJpi	OJpi	NBfi	OBfi	Stove
28	Melyridae sp.#1 (Melyridae)	0	0.3 ± 0.5	0.3 ± 0.5	0	0.8 ± 0.5	1.0 ± 0.8	0.5 ± 1.0	2.5 ± 3.7	1.3 ± 2.5	0.8 ± 1.0
29	Mordellidae sp.#1 (Mordellidae)	1.0 ± 1.4	0.8 ± 1.5	0.3 ± 0.5	0.8 ± 0.5	1.0 ± 1.4	0.8 ± 1.0	0.8 ± 0.5	0.8 ± 1.0	0	0.8 ± 1.0
30	Tenebrionidae sp.#1 (Tenebrionidae)	4.0 ± 8.0	0.3 ± 0.5	0.3 ± 0.5	2.0 ± 4.0	0	0	0	0	0	0
31	*Limonius* sp. (Elateridae)	0	0.3 ± 0.5	1.0 ± 1.4	0.3 ± 0.5	1.0 ± 1.4	2.3 ± 1.7	0.3 ± 0.5	0	0.8 ± 1.0	0.3 ± 0.5
32	*Orchesia ovata* Laliberté (Melandryidae)	0.5 ± 1.0	0.3 ± 0.5	0.5 ± 0.6	0.5 ± 1.0	0.5 ± 1.0	0.8 ± 1.0	1.0 ± 0.0	1.0 ± 0.8	0	0.8 ± 0.5
33	*Eucinetus morio* LeConte (Eucinetidae)	0	2.5 ± 2.9	0.3 ± 0.5	0.8 ± 1.0	0.3 ± 0.5	0	0.3 ± 0.5	0.5 ± 0.6	0.5 ± 0.6	0.8 ± 1.0
34	*Celetes basalis* LeConte (Lycidae)	0.5 ± 1.0	0	0.8 ± 1.0	0.3 ± 0.5	1.3 ± 1.5	0	0.3 ± 0.5	1.5 ± 1.3	0.8 ± 0.5	0.3 ± 0.5
35	Leiodidae sp.#2 (Leiodidae)	1.5 ± 1.3	0.8 ± 1.5	0	0	0	0	0	1.0 ± 2.0	0.5 ± 0.6	1.8 ± 1.7
36	*Ampedus pedalis* Germar (Elateridae)	0	0.8 ± 1.5	0	2.0 ± 4.0	0	0	0.3 ± 0.5	2.3 ± 4.5	0	0.3 ± 0.5
37	*Phymaphora pulchella* Newman (Endomychidae)	0.3 ± 0.5	1.3 ± 1.3	0.3 ± 0.5	0.8 ± 1.0	0.3 ± 0.5	0	0.3 ± 0.5	1.5 ± 1.3	0.3 ± 0.5	0.5 ± 0.6
38	*Podabrus* sp.#4 (Cantharidae)	0.5 ± 1.0	0.8 ± 1.0	0.3 ± 0.5	0	0.3 ± 0.5	0.8 ± 0.5	0.8 ± 1.0	0.5 ± 1.0	1.0 ± 1.2	0
39	Tenebrionidae sp.#2 (Tenebrionidae)	0	0.3 ± 0.5	0	0	0.3 ± 0.5	0	1.0 ± 1.4	0.5 ± 1.0	0.8 ± 0.5	2.0 ± 2.3
40	*Dictyopterus aurora* Herbst (Lycidae)	0.3 ± 0.5	0	0.8 ± 1.0	0	0.3 ± 0.5	0.5 ± 0.6	0.5 ± 0.6	0.5 ± 0.6	1.0 ± 0.8	0.8 ± 0.5
41	*Ellychnia corrusca* LeConte (Lampyridae)	0	0.5 ± 0.6	1.5 ± 1.7	0	0	0	0.3 ± 0.5	2.0 ± 1.2	0	0.3 ± 0.5

Appendix 3.1 *(continued)*

Rank	*Species*	NAsp	OAsp	NPbi	OPbi	NBsp	NJpi	OJpi	NBfi	OBfi	Stove
42	Anobiidae sp.#1 (Anobiidae)	0.3 ± 0.5	0	0.3 ± 0.5	0.8 ± 1.0	0.5 ± 0.6	0.8 ± 1.0	0.3 ± 0.5	0.8 ± 1.0	0.5 ± 0.6	0.5 ± 1.0
43	*Denticollis denticornis* (Kirby) (Elateridae)	0.3 ± 0.5	0.5 ± 0.6	0.5 ± 1.0	0.5 ± 1.0	0	0	0	0.5 ± 1.0	0	2.0 ± 4.0
44	*Epuraea sp.* (Nitidulidae)	0.3 ± 0.5	0.3 ± 0.5	0	0.3 ± 0.5	0.5 ± 1.0	2.0 ± 1.6	0.3 ± 0.5	0	0.3 ± 0.5	0.5 ± 0.6
45	Staphylinidae sp.#5 (Staphylinidae)	1.3 ± 1.9	0	0	0	0.3 ± 0.5	0.5 ± 1.0	0	0.5 ± 1.0	0.5 ± 0.6	1.3 ± 1.0
46	*Atomaria pumilio* Casey (Cryptophagidae)	0.3 ± 0.5	0.8 ± 1.0	0.5 ± 0.6	0	0.3 ± 0.5	0	0.5 ± 0.6	0.5 ± 0.6	1.0 ± 0.0	0.3 ± 0.5
47	Cryptophagidae sp.#1 (Cryptophagidae)	0.8 ± 1.5	1.0 ± 0.5	0	0.8 ± 0.5	0	0	0.3 ± 0.5	0.8 ± 0.5	0	0.5 ± 0.6
48	Helodidae sp.#1 (Helodidae)	2.3 ± 4.5	0	1.0 ± 1.2	0	0	0	0	0.3 ± 0.5	0.3 ± 0.5	0.3 ± 0.5
49	*Ips latidens* (LeConte) (Scolytidae)	0	0.3 ± 0.5	0	0	0	0.8 ± 1.5	1.5 ± 2.4	0.8 ± 1.5	0	0.5 ± 1.0
50	*Endomychus biguttatus* Say (Endomychidae)	0.5 ± 1.0	0.3 ± 0.5	0.8 ± 0.5	0.3 ± 0.5	0.3 ± 0.5	0	0.8 ± 1.0	0.3 ± 0.5	0.3 ± 0.5	0.5 ± 0.6

4. Primary attraction and random landing in host selection by wood-feeding insects: A matter of scale?

Michel Saint-Germain[1,2], Christopher M. Buddle[1] and Pierre Drapeau[2]

[1]Department of Natural Resource Sciences, McGill University, 21111 Lakeshore Road, Saint-Anne-de-Bellevue, Québec, Canada, H9X 3V9

[2]Groupe de Recherche en Écologie Forestière interuniversitaire, Département des sciences biologiques, Université du Québec à Montréal, CP 8888, succ. Centre-ville, Montréal, Québec, Canada, H3C 3P8

4.1 Preface

Results from chapter 3 suggested that pre-landing host-selection mechanisms were weak or absent in most species. However, some finer results hinted that this may be true at a fine scale, but not necessarily at larger scale. Chapter 4 is a direct follow-up of these findings. In this paper, pre-landing host-selection mechanisms are investigated at fine and large scale simultaneously, mainly in wood-feeding taxa. Such a multiple-scale effort to investigate primary attraction is unprecedented in the literature. Results from this research project show that primary attraction and random landing, two mechanisms of pre-landing host selection often seen as mutually exclusive in the literature, can occur within a single taxa when multiple scales are considered.

4.2 Abstract

Most plant-feeding insects show some degree of specialization and will use a various cues to locate their host. Two mechanisms of host-finding, primary attraction and random landing, have been proposed for such insects. Multiple studies have come to contradictory conclusions about those hypotheses, especially for wood-feeding insects; however, recent studies suggest that both mechanisms may take place in a single taxon but at different scales. We developed a field experiment to test the hypothesis that primary attraction occurs at larger scale and random landing at finer scale in wood-feeding insects. Landing rates, measured using sticky traps, were compared first between patches and then between individual trees according to their distance to a baited central tree in jack pine stands in the boreal forest (Quebec, Canada). Polynomial functions describing landing rate to distance relationships were then compared to a function produced by a null model describing what should occur under the random landing hypothesis. Beetles in the families Scolytidae (bark beetles) and Cerambycidae responded to volatiles at the patch scale, supporting the primary attraction hypothesis. However, the landing patterns of cerambycids at a finer scale matched closely the predictions of our null model, giving support to the random landing hypothesis. Bark beetles were more efficient at locating the source of volatiles, but still showed a non-negligible proportion of random landing. Our results show that primary attraction and random landing hypotheses are not mutually exclusive and that scale considerations should be included in the study of pre-landing host-selection of wood-feeding insects.

Key words: Cerambycidae, host volatiles, kairomones, Scolytidae, semiochemicals.

4.3 Introduction

Most plant-feeding insects show some degree of specialization in their host preferences. In most cases, a dispersal phase is necessary, and insects will use a variety of cues to locate their host, most frequently either visual or olfactive (Bernays and Chapman, 1994). The use of volatiles produced and released by plants as attractants has received much attention in the literature, as reviewed by Metcalf (1987).

Several species of wood-feeding insects lay their eggs exclusively on heavily stressed or recently dead trees (i.e., secondary, or stressed-host insects), taking advantage of the weakened defense mechanisms and of the nutritional quality of the woody tissues, which at this point has not yet declined significantly (Wood, 1982; Hanks, 1999). Such resources are ephemeral and of unpredictable availability; stressed-host insects have thus evolved particularly efficient mechanisms helping them locating potential hosts. Numerous papers have been published on the use of volatiles by bark beetles in particular (Coleoptera: Scolytidae) (Person, 1931; reviews in McMullen & Atkins, 1962; Miller and Strickler, 1984; Raffa *et al*., 1993; Byers, 1995; Pureswaran *et al*., 2004). This is largely because species of this family can reach epidemic population levels and kill healthy trees over large areas (Wallin and Raffa, 2004).

The importance of volatiles in host selection is generally acknowledged, but in which context(s) these volatiles convey usable information during pre-landing location processes is still unclear. Numerous laboratory experiments demonstrated that host volatiles do play a role at some point in host selection by showing physiological

responses to host volatiles in several species of bark beetles (Mustaparta *et al*., 1979; Huber *et al*., 2000; Pureswaran *et al*., 2004) and longhorn beetles (Coleoptera: Cerambycidae) (review in Allison *et al*., 2004). Field experiments comparing capture rates of baited traps to controls usually show strong responses of beetles to host-produced volatiles (Chénier and Philogène, 1989; Tunset *et al*., 1993; Brattli *et al*., 1998; Pureswaran and Borden 2003), suggesting primary attraction (i.e., positive response of insects to host-produced volatiles in the orientation of their flight; Person, 1931) as being an important contributor in pre-landing steps of host selection. However, other field studies have shown equivalent landing rates of bark beetles on neighbouring hosts and non-hosts trees (Goeden and Norris, 1965; Berryman and Ashraf, 1970; Moeck *et al*., 1981; Wood, 1982; Byers, 1995), and such studies are sometimes interpreted as suggesting random landing as the principal mechanism of host-finding. The random landing hypothesis states that insects fly and land on trees at random and then assess their quality as potential hosts using short-range olfactory and gustatory cues.

However, we should interpret these apparently contradictory results in the context of a multi-stepped host location sequence. At each of these steps, the relative importance of primary attraction and more random mechanisms may vary, and results supporting either of the two hypotheses could be seen for the same insect species depending on the scale at which host selection is considered. In a recent study, Saint-Germain *et al*. (2006) compared insect assemblages landing on contrasting snag types and stovepipes controls using sticky traps. Despite sampling 5 tree species and aluminium pipes painted black, no major differences in captured assemblage species composition were detected between the different treatments. However, the species and physiological state of neighbouring trees

(within a 3-m radius) had a significant influence on the captured assemblages. These results suggest that habitat patches may be located using host volatiles, but that individual potential hosts are then explored and assessed through random landing. Thus, in such cases, volatiles may be usable to locate habitat patches but not to identify precise sources of volatiles at a finer scale.

Few field studies were appropriately conceived to actually test primary attraction concurrently at more than one of the pre-landing host selection steps. Hynum and Berryman (1980) and Moeck *et al*. (1981) did compare landing rates on suitable hosts and neighbouring non-hosts and found no differences. However, they did not consider whether primary attraction occurred concurrently at a larger scale. To fully understand the role of host-produced volatiles in pre-landing host location processes, these multiple steps must be considered together for the same taxa in a single study. Understanding pre-landing host selection processes of wood-feeding insects is of primary importance, as volatiles are commonly used in monitoring and mass-trapping procedures in the management of economically important bark beetle species (Borden *et al.*, 2003; Wermelinger, 2004; Progar, 2005; Faccoli and Stergulc, 2006).

This study was designed to test primary attraction at two scales relevant to pre-landing host location. We first compared landing rates of secondary wood-feeding insects between patches (~400m^2) including control patches, patches with a mechanically-killed tree in their center (natural volatiles), and patches with a tree baited with a high-release commercial blend of ethanol and α–pinene in its center. For this part of the study, we predicted, in accordance with the primary attraction hypothesis, higher landing rates in

baited patches and lower rates in controls. In the second part of the study, we looked at landing rates of selected taxa at a finer scale. In the same patches, we looked at landing rates occurring on several healthy (non-hosts) trees in relation to their distance to the baited central tree. Here we predicted significant landing rates on non-host trees, in accordance to the random landing hypothesis.

4.4 Material and Methods

4.4.1 Study site

For this study, nine jack pine (*Pinus banksiana* Lambert)-dominated sites were selected in the Lake Duparquet Research and Teaching Forest (Université du Québec en Abitibi-Témiscamingue, 48° 28' N, 79° 16' W), Canada. This forest is situated in the boreal mixed-wood domain, and is dominated by trembling aspen (*Populus tremuloides* Michaux) and black spruce [*Picea mariana* (Miller)]. Most of the nine sites were 4-10 ha stands isolated within an aspen-dominated matrix. Two sites were located in the same >35 ha stand. All of the 9 sites originated from the same 1923 fire (Bergeron *et al.* 2004) and are of comparable structure, with some marginal components of trembling aspen and black spruce. The average jack pine stem density was estimated at 585.0/ha using the point-centered quarter method (Pollard 1971).

4.4.2 Sampling

In each of the nine plots, a tree was selected near the middle of the stand. In the four cardinal directions, distances of 2, 5 and 10 m were measured from the central tree (Figure 4.1). For 10 of these 12 points, the closest tree with a diameter at breast height (DBH) ≥ 20 cm was selected. All selected trees were apparently healthy jack pines. Plots were not established at proximity of dying or recently dead pines. The exact distance between each tree and the central one was measured. When all of the nine plots had been established, each was randomly assigned a treatment. The treatments were as follows: 1) controls; with nothing added to the plots; 2) CB (commercial bait); a high-release commercial blend of ethanol and α-pinene (Phero Tech Inc., Delta, BC, Canada) was fixed to the central tree; 3) MK (mechanically-killed); a healthy jack pine was cut outside our sampling area the day before we started sampling and a 1.2-m bole segment was suspended in the middle of each plot. Each treatment was replicated three times (n=3). Ethanol and α-pinene have been shown to act as attractant to a large number of wood-feeding species and often act synergistically (Chénier and Philogène 1989, Kelsey and Joseph 1997, Czokajlo and Teale 1999, Sweeney *et al.* 2004). The CB and MK treatments differ both in their release rates of volatiles (higher in CB) and in the spectrum of volatiles emitted (wider in MK). No attractants derived from bark beetle pheromones were added to CB because this study was intended to focus on primary attraction without as little interference as possible from secondary attraction (insect-produced kairomones).

For all nine plots, a 0.25-m^2 (~60×40 cm) polyethylene sheet coated with Tree Tanglefoot™ Pest Barrier (The Tanglefoot Company, Grand Rapids, MI, USA) was pinned between hips and shoulders height on each tree, including the central one, facing outward of the plot. Tree Tanglefoot™ is a substance designed to intercept crawling insects, and since none of its key components are volatile, Tree Tanglefoot™ does not interfere with primary attraction. Such sticky traps are appropriate to sample insects as they land on a potential host, hence between pre-landing and post-landing host assessment (Saint-Germain *et al*. 2006). Sampling took place for 58 days from June 19th to August 15th 2005. Polyethylene sheets were replaced once during the sampling period. Sheets were taken to the laboratory and specimens were cleaned using Histo-Clear® (histological cleaning agent; National Diagnostics, Atlanta, GA, USA). All Coleoptera were identified to family, and wood-feeding individuals to species. Voucher specimens are deposited at the Lyman Entomological Museum (McGill University, Montreal, Canada).

4.4.3 Statistical analyses

For analytical purposes, number of captures was standardized as landing rates (number of insects per m^2 per week) for each tree. To address our first objective (compare landing rates between patches), the tree-scale landing rates were pooled by patch. Pooled landing rates were compared for selected taxa between treatments with one-way analyses of variance (ANOVA). Tukey's Honestly Significant Difference tests were used for post-hoc multiple comparisons (α=0.05). For the second part of the study, we used polynomial linear regressions to correlate individual landing rates to distance of the trap to the central

tree, but only for relevant taxa as identified from the first part of the study. For these regressions, the 33 trees of the appropriate treatment were used. ANOVA and regressions were performed using SPSS 10.0.5 (SPSS Inc., Chicago, IL, USA).

4.4.4 Null model

If we assume that beetles attracted to volatiles converge from all directions towards the central tree and potentially land on any encountered tree before reaching the true source of volatiles (i.e., random landing at fine scale), then we must expect a concentration effect. Incoming beetles, as they get closer to the center, are restricted to fewer trees acting as potential hosts. We thus expect to have higher landing rates on trees near the center when compared to trees on the periphery of the plot. To account for this concentration effect, we created a null model that we calculated for selected taxa presented in the results to which we compared the polynomial function obtained from real data and their 95% confidence intervals. A predicted landing rate was calculated for each sampled tree by dividing the total number of beetles (average landing rate found on central trees per treatment) by the average number of trees found in a 2-m wide circular band centered at the radius of the tree (Figure 4.2a). The predicted landing rate (LR_{pred}) is calculated as follows for each sampled tree:

$$LR_{pred} = \frac{\bar{x}LR_{center}}{\left(\frac{((\pi(d+1)^2)-(\pi(d-1)^2))}{10000}\times D\right)}$$

were *LR* stands for landing rate, *d* the distance between the sampled tree and the central tree (in meters) and *D* jack pine stem density (per hectare). If we calculate this null model for a central *LR* of 20 beetles, we obtain the relationship shown on Figure 4.2b (cubic polynomial function). Differences between the predicted and observed functions would indicate higher efficiency on the part of the insect if the observed function fall below the predicted one, and lower efficiency (sometimes getting away from the source during random landing) if the observed function is above the predicted one.

4.5 Results

4.5.1 Analysis of plot-level landing rates

All families with sufficient landing rates (over 2/m^2/week in at least one treatment) were compared between treatments with one-way analyses of variance (Table 4.1). Among wood-feeding families, landing rates of Cerambycidae were significantly higher in CB and MK plots than in controls ($F_{2,6}$=5.66; P=0.0415), while rates of Scolytidae were significantly higher only in CB ($F_{2,6}$=16.95; P=0.0034) (Table 4.1; Figure 4.3). Among those two families, cerambycid *Xylotrechus undulatus* ($F_{2,6}$=6.25; P=0.0341), and scolytids *Dryocoetes autographus* ($F_{2,6}$=24.14; P=0.0014) and *Hylurgops pinifex* ($F_{2,6}$=5.86; P=0.0389; Figure 4.3) all had significantly higher landing rates in CB plots (Table 4.1). For families belonging to other trophic groups, only predatory Lycidae ($F_{2,6}$=7.08; P=0.0264; higher in controls), Nitidulidae of the genus *Epuraea* ($F_{2,6}$=12.42; P=0.0074; higher in MK; Figure 4.3) and detritus-feeding *Scraptia sericea* ($F_{2,6}$=15.14;

P=0.0045; higher in MK; Figure 4.3) showed significant differences between treatments (Table 4.1). Landing rates of other groups showed no response to treatments (e.g., Elateridae, Figure 4.3).

4.5.2 Analysis of tree-level landing rates

Analysis at tree-scale was performed for Scolytidae (CB), Cerambycidae (CB), Melandryids *Serropalpus coxalis* (CB) and *Scraptia sericea* (MK), and *Epuraea* Nitidulid (MK) (Figure 4.4). We opted to settle with family-level analyses in several cases because of insufficient landing rates from individual species. Relationships between tree-specific landing rates and distance to the center were best described in all cases (except for *Scraptia* with non-significant relationships) with cubic polynomial functions. Scolytidae landing rates were highest in the first 3 m (polynomial function: $F_{3,29}$=28.60; P<0.001; R^2=0.747), and the observed function falls below the function predicted by the null model (not included in the 95% confidence intervals) (Figure 4.4a). For Cerambycidae and *Serropalpus*, the observed functions were significant (Cerambycidae: $F_{3,29}$=10.15; P<0.001; R^2=0.512; *Serropalpus*: $F_{3,29}$=11.94; P<0.001; R^2=0.553) but were closely fitted with the predicted functions (Figures 4.4b and 4.4c). Nitidulidae showed a response similar to the Scolytidae, the observed function being distinct and below the predicted function ($F_{3,29}$=13.14; P<0.001; R^2=0.576; Figure 4.4d). For *Scraptia sericea*, all relationships were non-significant (Figure 4.4e).

4.6 Discussion

Our study brings support for both the primary attraction and random landing hypotheses within single taxa as host-selection is considered at multiple scales. Furthermore, the efficiency with which insects were able to locate the source of volatiles within a patch varied between taxa of the same functional group.

Wood-feeding insects did respond to host-produced volatiles at the patch scale in our study, as higher landing rates were observed in patches baited with host-produced semiochemicals in major groups of wood-feeding insects and several individual species. Scolytidae were significantly attracted to the 'commercial bait' patches, while Cerambycidae were attracted to both 'commercial bait' and 'mechanically-killed tree' patches. A difference in release rate between the two treatments could explain the different responses of two groups which are otherwise frequently found together in recently dead trees (i.e., *Xylotrechus undulatus* and *Dryocoetes affaber*). The high-release commercial bait is expected to produce a stronger volatile concentration gradient, on which some Scolytidae may be more dependant than Cerambycidae. Byers *et al.* (1989) showed that the effective attraction radius of a baited trap varies considerably depending on the release rate of the attractants and on the identity of the insect species considered. Some non-wood-feeding groups were also attracted to the 'mechanically-killed tree' patches. Nitidulidae of the genus *Epuraea* were probably attracted to volatiles not contained in the commercial blend but produced by the mechanically-killed tree. *Epuraea* is a species-rich genus within which differences in behaviour can be expected; however, Schröeder and Lindelöw (1989) have shown that species of *Epuraea* respond to the same

compounds as some bark beetles do, suggesting that they may be predatory on these beetles. As very little information is available on the ecology of *Scraptia*, it is difficult at this point to explain its attraction for the 'mechanically-killed tree' patches.

Results from the second part of our study shows that all taxa for which the primary attraction hypothesis was supported at patch-scale landed to varying degrees on non-host trees, at higher rates than landings observed in control patches, showing some degree of random landing within patches. The observed landing rate to distance function for Cerambycidae fitted closely the function predicted by our null model. This suggests that cerambycids are rather inefficient at locating the source of volatiles in a within-patch context. This result clearly indicates that these insects cannot rely on host volatiles to discriminate before landing between several potential hosts, even if primary attraction was shown in the same group at a larger scale. The Melandryid *Serropalpus*, for which trends but no significant differences were observed in analyses at the patch level, had a significant polynomial landing rate to distance function, and showed the same pattern as the Cerambycidae. Scolytidae, and to a larger degree Nitidulidae had an observed function below the predicted function and were thus more efficient at locating the source of volatiles than Cerambycidae, although a non-negligible proportion of landing on non-hosts was still observed.

These findings bring us back to the contradictory results often reported from laboratory and field experiments dealing with primary attraction and random landing. Such contradictions are reported in the literature within single species. Examples of this can be found for the bark beetles *Scolytus ventralis* LeConte and *Dendroctonus ponderosae*

Hopkins. In laboratory bioassays, *S. ventralis* has been found to respond physiologically to 19 compounds released by its host (*Abies grandis* Lindley) when under heavy stress, thus showing some form of primary attraction (Macias-Samano *et al*. 1998). However, in field surveys during which both healthy and stressed trees were examined, 74% of the trees examined showed signs of post-landing host assessment (gallery initiation), while completed galleries, and thus host selection, were found on only 3,5% of the trees (Berryman and Ashraf 1970). The authors thus concluded that host selection in *S. ventralis* was random prior to the aggregation phase. The same scenario can be seen for *D. ponderosae*. Again, this species has been shown to react to several host-produced monoterpenes (Pureswaran *et al*. 2004), but a field study using baited traps showed no significant response to host volatiles in this species (Pureswaran and Borden 2005). These two examples suggest that the olfactive information isn't necessarily usable at all scales during host-selection, just as our results show. Most studies supporting the random attack hypothesis sampled hosts and non-hosts within the same patch, and were thus able to detect any erroneous landings by beetles that were initially attracted by good hosts present at proximity (Goeden and Norris 1965, Berryman and Ashraf 1970, Hynum and Berryman 1980, Witanachchi and Morgan 1981). Field experiments relying only on baited traps are unable to detect such random landings and may have erroneously concluded unequivocal primary attraction (Tunset *et al*. 1993, Brattli *et al.* 1998), while laboratory studies give no information whatsoever on the scale at which volatiles might be used. The question is thus not if there is primary attraction or not, but rather at which scale the insect can make good use of host-released volatiles.

The differential efficiency of insects in using volatile information at different scales that we observed could be explained by an increased difficulty of extracting directional information from the host-volatiles present in the air in some ranges. Unfortunately, little information has been published thus far on the shape of the relationship between volatile concentration in air and distance from the host. Some authors suggest that such gradients are unlikely to exist over a few centimetres because of air turbulence (Bernays and Chapman 1994). Instead, the insects flying upwind will intermittently come in contact with air pockets containing volatiles in varying concentrations. In such a context, it would be even more difficult for the insect to figure the exact location of the host without frequent random landings. The currently available information on the processes of in-flight host-finding is thus consistent with our view of a multi-scaled differential strategy pre-landing host-selection, which is also supported by our results.

Some of the results presented in this paper are composite responses (family-level analyses which generally include a few species). However, within-family variations in host-selection behaviour are usually correlated with the physiological state of the preferred host (Wood, 1982). All the bark beetle species captured within this study being secondary in nature, fewer variations in behaviour among these species can be expected, and the situation is similar for Cerambycidae. Family-level analyses thus, according to us, still convey relevant information. Results shown for some individual species suggest that such differential strategy could be a common phenomenon, if not a generality. Our results indicate that our understanding of host-selection can be improved by including scale considerations in our empirical approach; it is clear that studies looking at the use of volatiles at a single scale provide fragmentary information. In this study we limited our

efforts at comparing between- vs. within-patch use of volatiles, but the main ideas presented in this paper could be expanded at larger scales to give a more comprehensive understanding of dispersal and host selection, from landscape scale to tree scale. Also, results from our study could be applied to mass-trapping experiments and to the use of non-host antagonistic volatiles, of which the efficiency should also be considered at multiple scales.

4.7 Aknowledgements

We would like to thank A. Webb and V. Evans for their participation in field work, and E. Bolduc for her contribution to cleaning the specimens. This project was funded by the UQAM-UQAT NSERC industrial chair in sustainable forest management, the Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT) – Programme Action Concertées – Fonds forestiers (P. Drapeau), a FQRNT new researcher grant (C. Buddle) and a Discovery grant (C. Buddle) from the Natural Science and Engineering Research Council of Canada (NSERC). All experiments reported within this paper comply with Canadian federal laws and Quebec provincial laws.

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Table 4.1 Dominant taxa captured with mean landing rates (± standard error) for each treatment, and results from one-way ANOVA and Tukey-Kramer post-hoc tests. For each treatment n=3.

Taxon	CB	MK	CTRL	
Wood-feeding groups				
Cerambycidae	4.51 ± 1.4 **a**	3.97 ± 1.32 **a**	0.8 ± 0.32 **b**	P=0.042
Asemum striatum (L.)	1.46 ± 1.2	0	0	ns
Clytus ruricola (Olivier)	0.65 ± 0.16	0.49 ± 0.28	0.16 ± 0.16	ns
Psenocerus supernotatus (Say)	0.65 ± 0.16	0.65 ± 0.33	0	ns
Xylotrechus undulatus (Say)	0.81 ± 0.33 **a**	0 **b**	0 **b**	P=0.034
Others	1.14 ± 0.71	1.3 ± 0.33	0.65 ± 0.16	ns
Curculionidae	6.76 ± 0.97	5.47 ± 2.44	2.9 ± 0.28	ns
Melandryidae	53.5 ± 13.0	28.8 ± 10.4	30.5 ± 3.88	ns
Melandrya connectens (Newman)	8.71 ± 2.57	5.33 ± 0.73	3.22 ± 1.06	ns
Serropalpus coxalis Mank	34.3 ± 12.7	14.3 ± 7.72	13.9 ± 5.23	ns
Scolytidae	9.69 ± 1.86 **a**	2.13 ± 0.59 **b**	1.93 ± 1.0 **b**	P=0.004
Dryocoetes affaber (Mannerheim)	0.49 ± 0.49	0	0	ns
Dryocoetes autographus (Ratzeburg)	2.11 ± 0.43	0	0	P=0.002
Hylurgops pinifex (Fitch)	3.86 ± 0.74 **a**	0.97 ± 0.28 **b**	0.32 ± 0.32 **b**	P=0.039
Others	2.44 ± 0.84	0.65 ± 0.43	1.3 ± 0.86	ns
Others				
Alleculidae	2.9 ± 1.7	5.94 ± 0.23	3.06 ± 0.58	ns
Cantharidae	43.9 ± 5.34	107.0 ± 22.2	70.8 ± 13.6	ns
Cucujidae	1.16 ± 0.46	2.45 ± 0.76	2.25 ± 0.64	ns
Elateridae	73.1 ± 11.9	74.0 ± 12.6	70.6 ± 6.66	ns
Endomychidae	11.3 ± 3.28	13.0 ± 5.16	18.7 ± 8.49	ns
Eucinetidae	9.84 ± 2.75	5.47 ± 0.58	6.99 ± 2.43	ns
Lampyridae	35.0 ± 10.9	33.4 ± 2.55	16.2 ± 4.61	ns
Lathridiidae	70.5 ± 9.63	78.7 ± 5.34	67.2 ± 4.35	ns
Lycidae	6.15 ± 1.4 **ab**	4.18 ± 0.43 **a**	8.75 ± 0.46 **b**	P=0.026
Melyridae	22.4 ± 4.71	61.1 ± 15.8	30.9 ± 16.9	ns
Mordellidae	10.2 ± 0.98	11.3 ± 1.51	7.64 ± 2.09	ns
Nitidulidae				
Epuraea spp.	9.05 ± 2.28 **a**	16.1 ± 1.26 **b**	4.83 ± 1.0 **a**	P=0.007
Melandryidae				
Scraptia sericea (Melsheimer)	10.4 ± 1.69 **a**	19.1 ± 1.78 **b**	8.53 ± 0.58 **a**	P=0.005
Staphylinidae	49.5 ± 10.9	38.1 ± 5.43	29.2 ± 7.75	ns
Throscidae	6.96 ± 1.89	11.7 ± 2.11	8.57 ± 3.05	ns

List of figures

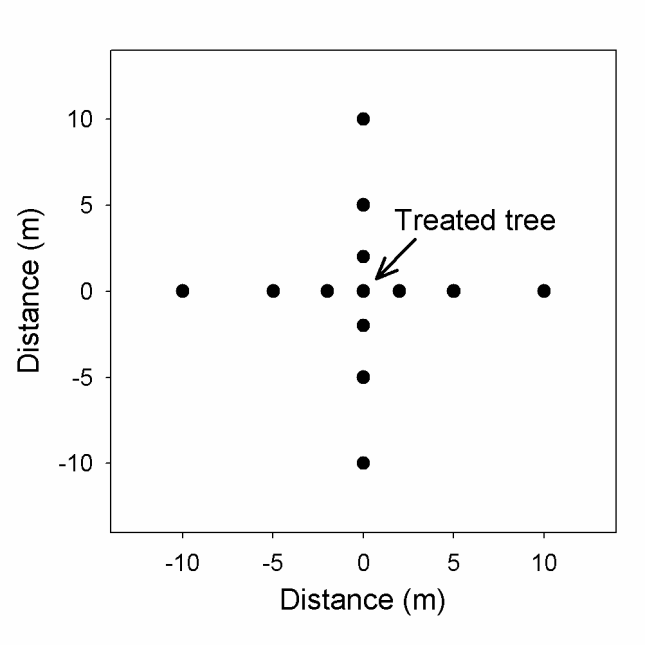

Figure 4.1

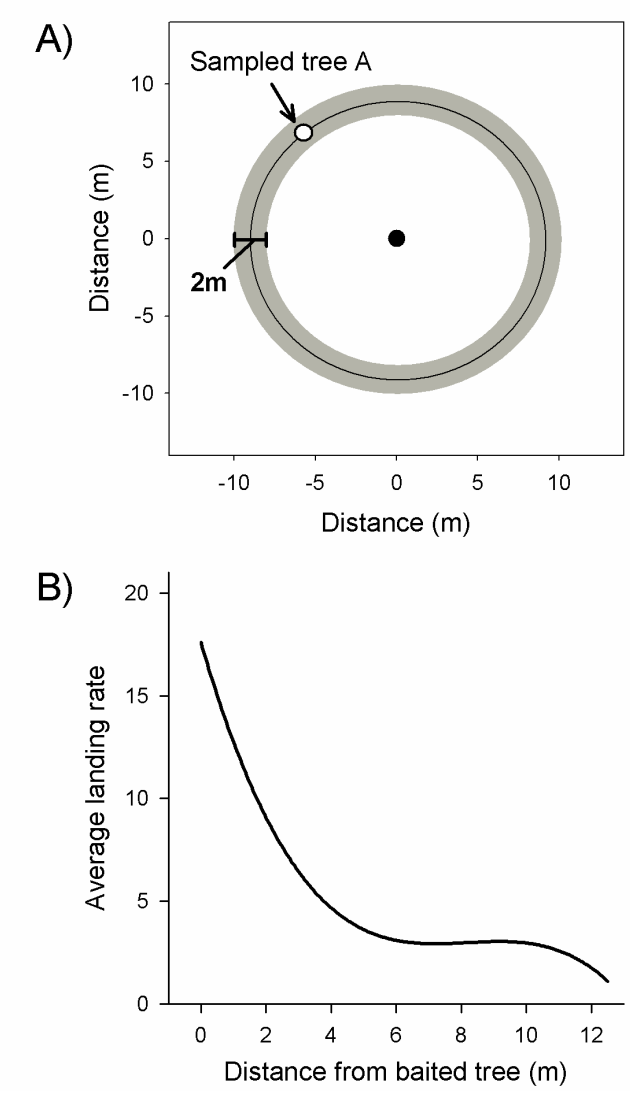
A)
Sampled tree A
2m
Distance (m)
10
5
0
-5
-10
-10
-5
0
5
10
Distance (m)
B)
Average landing rate
20
15
10
5
0
0
2
4
6
8
10
12
Distance from baited tree (m)

Figure 4.2

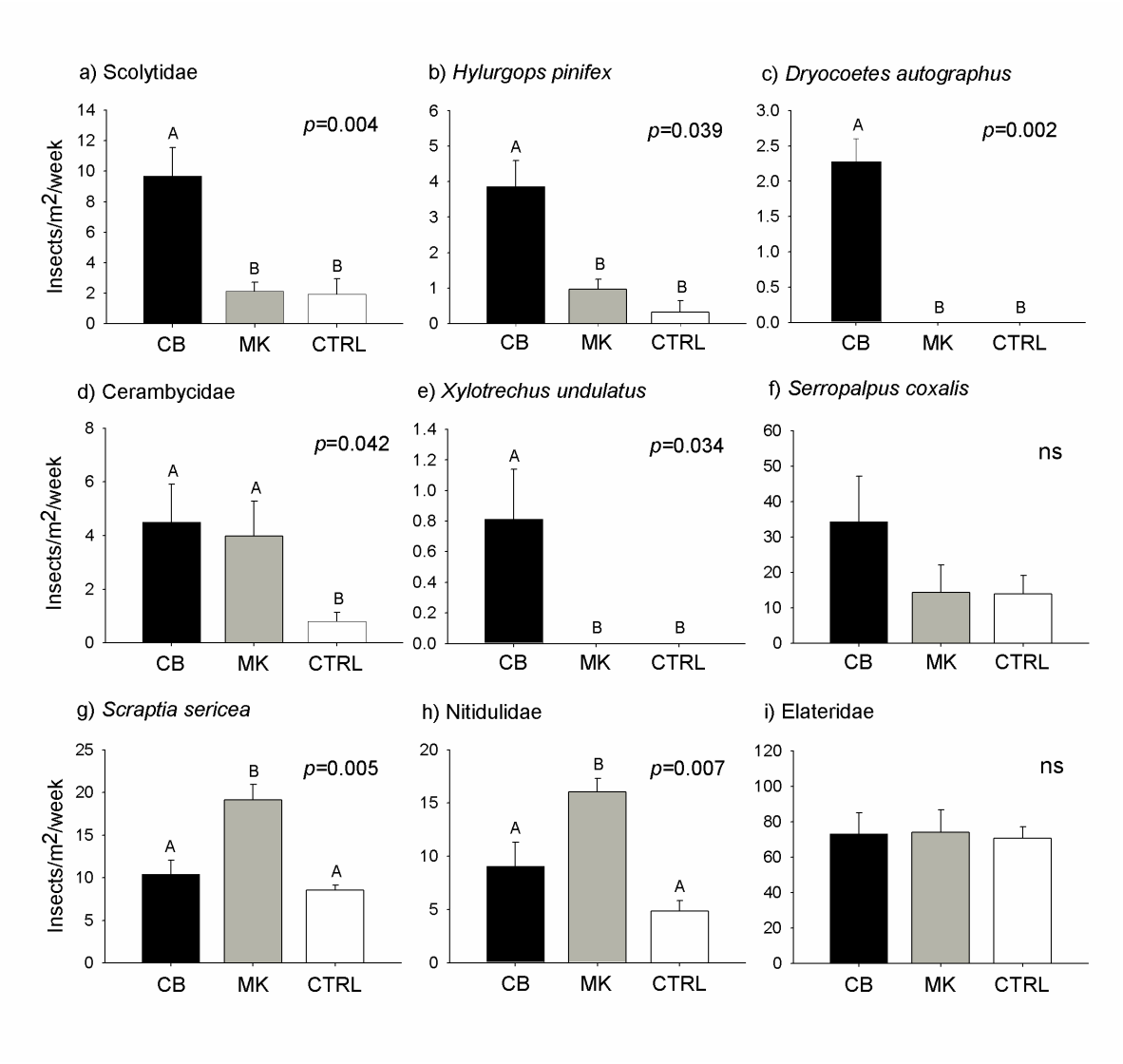
a) Scolytidae
b) Hylurgops pinifex
c) Dryocoetes autographus
d) Cerambycidae
e) Xylotrechus undulatus
f) Serropalpus coxalis
g) Scraptia sericea
h) Nitidulidae
i) Elateridae
Insects/m2/week
p=0.004
p=0.039
p=0.002
p=0.042
p=0.034
ns
p=0.005
p=0.007
ns
A
B
CB
MK
CTRL

Figure 4.3

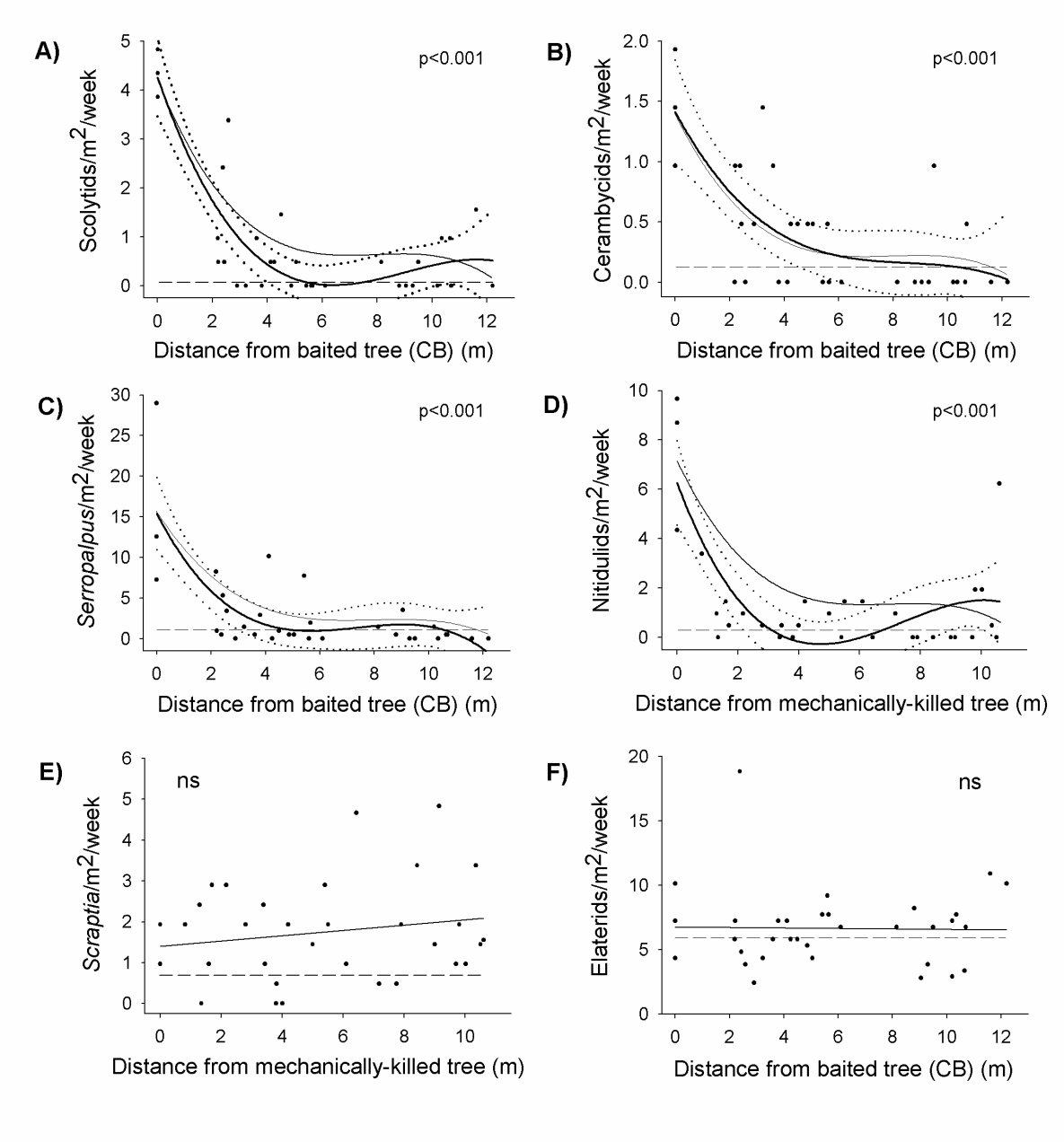
A)
p<0.001
Scolytids/m2/week
Distance from baited tree (CB) (m)
B)
p<0.001
Cerambycids/m2/week
Distance from baited tree (CB) (m)
C)
p<0.001
Serropalpus/m2/week
Distance from baited tree (CB) (m)
D)
p<0.001
Nitidulids/m2/week
Distance from mechanically-killed tree (m)
E)
ns
Scraptia/m2/week
Distance from mechanically-killed tree (m)
F)
ns
Elaterids/m2/week
Distance from baited tree (CB) (m)

Figure 4.4

5. Host-use patterns of adults and larvae of saproxylic wood-feeding Coleoptera in black spruce, *Picea mariana* (Mill.), and aspen, *Populus tremuloides* Michaux.

Michel Saint-Germain[1,2], Pierre Drapeau[1] and Christopher M. Buddle[2]

[1] Groupe de Recherche en Écologie Forestière interuniversitaire, Département des sciences biologiques, Université du Québec à Montréal, CP 8888, succ. Centre-ville, Montréal, Québec, Canada, H3C 3P8

[2] Department of Natural Resource Sciences, McGill University, 21111 Lakeshore Road, Saint-Anne-de-Bellevue, Québec, Canada, H9X 3V9

5.1 Preface

Chapters 3 and 4 provided insight into the contribution of pre-landing host-selection mechanisms to the overall host-selection process and on the extent to which they can affect subsequent host-use patterns. The following chapters focus on the host-use patterns *per se* following host selection, and on potential post-landing determinants of such patterns. Chapter 5 presents data on host-use patterns of wood-feeding saproxylic families using snags of aspen and black spruce through the decay gradient. Data were gathered though snag dissection, a method almost never used to sample saproxylic insects, probably because of the logistics involved, but also because most of the biological material collected is in larval stage, which creates potential taxonomical problems. During the course of this project I was able to identify over 95% of all cerambycid larvae found to species; this chapter thus present unprecedented information on wood-feeding larvae assemblages, especially in mid to late stages of decay in black spruce, and throughout the gradient in aspen. A good example of the quality of the information given through dissection is the presence in the presented data, in some cases in abundance, of the species *Meriellum proteus* (Kirby) and *Phymatodes dimidiatus* (Kirby) in black spruce, and *Anthophylax attenuatus* (Haldeman) and *Bellamira scalaris* (Say) in aspen, which are almost never present in biodiversity data obtained through other sampling methods, including rearing.

5.2 Abstract

Wood-feeding insects play important functional roles in forest ecosystems as they contribute significantly to wood decay processes. However, we know little about their precise host-use patterns because assemblages are difficult to characterize at the host scale. To cope with these difficulties, we used a novel approach, snag dissection, to investigate occurrence patterns of wood-feeding Coleoptera adults and larvae. We selected 80 snags of both black spruce and aspen along four classes of decay in five different stands distributed over the tree species' ranges within the province of Quebec, Canada, and dissected a one-meter section of each. All adults and larvae of Buprestidae, Cerambycidae and Scolytidae were collected and identified to the lowest taxonomical level possible. Wood density and snag age were also calculated for each sampled snag. In black spruce, host-use was mostly concentrated at the beginning of the decay gradient. Patterns observed in aspen were opposite, as few insects were found in fresh snags, while most snags in middle to late stages of decay contained insects, often in large numbers, in some reaching densities of over 1000 cerambycid larvae/m^3. For both tree species, patterns observed were similar across regions sampled. Differences in diversity patterns between the coniferous and deciduous host species may be due to differences in secondary chemistry, mechanical defense mechanisms, stand dynamics typically associated with each tree species or the decay process itself which differs between the two host species.

Keywords: Biodiversity, boreal forest, Buprestidae, Cerambycidae, dead wood, host-use patterns, Scolytidae.

5.3 **Introduction**

Dead wood is a key habitat element in forest ecosystems. Among the numerous functions attributed to dead wood, it is an important pathway in geochemical cycles (Harmon *et al*. 1986, Krankina *et al*. 1999) and supports a considerable proportion of forest biodiversity. Dead wood, in its different stages of decay, harbors hundreds of species of plants, animals and fungi (Harmon *et al*. 1986, Berg *et al*. 1994, Grove 2001). Among major groups, insects are probably one of the most diverse (reviewed by Grove 2001). For example, Siitonen (2001) estimated that saproxylic insects (i.e., species that are dependant on dead wood at least at some stage of their life cycle) represent over 25% of all known species living in boreal forests of Finland.

Several nutritional guilds are recognized within saproxylic insects (Vanderwel *et al*. 2006). Among them, wood-feeders, which directly consume plant tissue, play especially important functional roles. Dispersing adults act as vectors for spores of wood-decay fungi (Paine *et al*. 1997, Haberkern *et al*. 2002), and the galleries excavated by larvae structurally weaken dead wood and help fungi penetrate radially into the sapwood (Rayner and Boddy 1988). The activity of wood-boring beetles can greatly increases the rate of decay of dead wood, and hence speed up the release rate of immobilized nutrients (Edmonds and Eglitis 1989, Dajoz 2000). Species of this guild are difficult to study because they live most of their lives as larvae deep in the wood, and adults, which are generally targeted in biodiversity studies (Martikainen 2001, Hammond *et al*. 2004, Lindhe and Lindelöw 2004, Vanderwel *et al.* 2006), live only for a few weeks and are difficult to sample with most commonly-used techniques (Saint-Germain *et al.* 2006). As

a result, wood-boring species are generally poorly-represented in saproxylic insect datasets (Martikainen 2001, Sverdrup-Thygeson and Ims 2002, Hammond *et al*. 2004, Saint-Germain *et al*. 2006).

Host-use patterns of wood-feeding insects have seldom been studied on extended portions of the decay gradient. Fragmentary information suggests that the occurrence of coniferophagous wood-feeding species varies along the decay gradient. Some studies looking at the whole saproxylic community, all trophic guilds included, report shifts in dominance of the different saproxylic trophic guilds along the decay gradient (Graham 1925, Savely 1939, Howden and Vogt 1951, Vanderwel *et al*. 2006). In these studies very diverse and abundant wood-feeding guilds usually dominate in the first stages of decay, to be eventually replaced by fungivores, saprophages and predators as most diverse groups. Other studies exclusively focusing on fresh coniferous snags also report abundant and species-rich wood-feeding assemblages (Zhong and Schowalter 1989, Schroeder and Eidmann 1993, Schroeder *et al*. 1999). We found few or no comprehensive studies focusing on wood-feeding assemblages in coniferous snags or logs of more advanced decay. Information from deciduous host species is even scarcer. Lindhe and Lindelöw (2004) report wood-feeding species found in four species of deciduous trees sampled using eclector traps, but do not present the data according to sampling year following tree death.

Hanks (1999) classified cerambycid wood-feeders according to the physiological status of their hosts. Among these behavioural guilds, two can be found in succession in dead wood. Stressed-host species will attack hosts that are stressed to the point that death is

imminent, or are recently dead. Host-selection in this guild is strongly driven by host volatiles (Brattli *et al.* 1998, Allison *et al*. 2004), and most species feed in the nutrient-rich but ephemeral phloem and cambium, at least in their first larval stages. Only one generation of these species will usually develop on a specific host (Hanks 1999), and thus are expected to be found only in the very first stages of decay. Dead-host species are insects which will oviposit on hosts that are no longer green, and will feed mostly in the sapwood or heartwood. In such species several successive generations will usually develop in the same host (Hanks 1999). There is little documented evidence of succession among dead-host species along the decay gradient.

Because of the importance of dead wood as a support for biodiversity, modern forestry practices are moving towards leaving legacies (e.g., high stumps, partial cutting, green tree retention) in the managed landscape in an effort to insure spatial and temporal connectivity between habitat elements (Larsson and Danell 2001, Jonsson *et al*. 2005). However, we know relatively little about diversity patterns of saproxylic organisms among dead wood of different tree species and along the decay gradient, or about the mechanisms driving these patterns. This lack of knowledge limits our conservation efforts to coarse filter approaches when dealing with organisms dependent on dead wood, i.e., a context-dependent maximization of dead wood volume regardless of specialization patterns between host species or along the wood decay gradient.

The main objective of this study was to characterize species occurrence of wood-feeding Coleoptera along the decay gradient, snag stages only, on two tree species of the boreal mixed-wood forest of eastern North America, aspen (*Populus tremuloides* Michaux) and

black spruce [*Picea mariana* (Miller)]. These species were chosen for their ecological and economical prevalence in North American boreal forests. To characterize insect species assemblages and to determine whether observed patterns were dependant on landscape context (i.e., relative forest cover tree species composition), we sampled snags in five different sites distributed across the range of each tree species within the province of Quebec, Canada. Within each site, we dissected snags of all available stages of decay and collected both larvae and adults. Wood dissection is extremely useful to maximize the number of individuals collected and gives an instant portrait of the community using the sampled snag, with absolute estimates of density. It does not suffer from time constraints and excessive mortality seen in *in-situ* or *ex-situ* rearing or from severe biases inherent to trunk-window trapping when used to sample at tree level (Saint-Germain *et al*. 2006).

5.4 Methods

5.4.1 Snag selection and sampling

Early during the summer of 2004, one site was selected for each tree species in western Quebec: Lake Duparquet research and teaching forest (LDRTF) for aspen and Selbaie 1 for black spruce (Table 5.1, Figure 5.1). Both sites were mature forests and had high volumes of dead standing trees in diverse stages of decay. In each of these sites, transects distanced 40 m apart were set up perpendicular to the road, along which 24 snags over 15 cm in diameter were selected arbitrarily, equally distributed in numbers among 4 decay classes based on visual appearance. Decay classes were based on the criteria described in

Table 5.2, according to Maser *et al*. (1979), in addition to wood texture, presence of insect entry holes and presence of polypore fungi.

At the end of July 2004, the selected snags were cut down and a 1-m section, taken in average between 0.5 and 1.5 m in height, was sealed and taken to the laboratory for insect sampling (dissection). Wood samples were also taken to determine the time of death of the tree and to measure wood density (see below). Bark was removed and examined, and every larva and adult beetle was collected. Then, the bole segments were cut into ~20-cm long sections, and these were dissected with axes and hatchets, following galleries or other signs of use, and all insects were collected. Large cerambycid larvae were boiled in water before being put in 70% ethanol for preservation. Most Cerambycidae larvae were identified to species, Buprestidae larvae to genus, and adult Scolytidae (representing the vast majority of scolytid specimens) to species.

We replicated our characterization of host-use patterns by sampling additional sites in 2005 to test whether patterns were similar between stands and across regions. For each species, we selected 4 additional sites, 2 within the same region near the location of the main sites, in which we sampled 12 snags each, and 2 others distributed throughout the tree species' distribution within the province, in which we sampled 16 snags each (Table 5.1, Figure 5.1). Snags were felled between the end of July and early September 2005 depending on the sites. The same snag selection and sampling procedures as in 2004 were used. For each tree species we sampled a total of 80 snags (24 in main sites, 56 in supplementary sites) over two years. The average diameters (±1 SD) were of 20.6±4.0 cm

(range 15.1-30.4 cm) for black spruce snags and 23.3±5.8 cm (range 14.9-40.1 cm) for aspen snags.

5.4.2 Assessing degree of decay

Assessment of decay classes based on visual appearance sometimes gives inaccurate results as most of the criteria used are subjective in their appraisal and some, like a broken top, can occur in different contexts. Also, decay does not necessarily proceed in the same manner in different tree species (e.g., some species might retain their bark longer than others). Therefore, we also measured wood density for all 160 snags, and we estimated the time of death of the 48 snags from the main sites using dendrochronology. Wood density was measured by averaging density (dry weight/volume) of three ~50 ml wood samples taken systematically at 120° around the bole from a wood disk taken at ~1.5 m from the ground. Volume was measured by water displacement. To age tree death, we measured growth rings for the 48 snags from LDRTF and Selbaie 1 on 4 radii from two wood disks taken at 1.5 and 5 m above ground, respectively. Measurements were crossdated using the software COFECHA (Grissino-Mayer 2001) with master chronologies previously produced for the same sites (Bergeron *et al*. 2002, Lecomte *et al*. 2005). Most class 6 and some class 5 spruce snags could not be dated because growth rings were no longer discernable. In the light of the results given by each technique, we opted to use wood density to represent the decay gradient in the presentation of our results and in our analyses, mainly because we could not measure the age of all 160 snags sampled and also because of some problems we had at precisely aging spruce (see below).

5.4.3 Statistical analyses

To determine to what extent results from the different methods we used to quantify decay were similar, we first compared the wood density of the different decay classes using a one-way analysis of variance, followed with a Tukey's honestly significant difference (HSD) post-hoc test. An analysis of covariance was conducted to compare the slopes of aspen and black spruce with regards to the relationship between wood density and snag age. Wood density was used in following analyses to represent the decay gradient as an independent variable. The wood density of all snags in which a given insect species was found was used to characterize preferences of that species over the decay gradient. Differences in preference among insect species in terms of degree of decay were tested both in aspen and in black spruce with one-way analyses of variance and Tukey's HSD. Results from these ANOVA and observations from the literature were used to discriminate between stressed-host and dead-host species. Probability plots from logistic regressions were used to illustrate host-use patterns of Cerambycidae along the decay gradient, with wood density as the independent variable and presence-absence of larvae as the dependant variable. For the two tree species, this was done with all species combined, and then with behavioural guilds separated. Analyses of variance and covariance were performed on SPSS 10.0.5 for Windows (SPSS Inc., Chicago, IL, USA), while logistic regressions were performed on SYSTAT 11.00 (Systat Software Inc., Point Richmond, CA, USA).

5.5 Results

5.5.1 Assessment of wood decay

There were significant differences in wood density between early and late visually-assessed decay classes for both tree species, but not between all four classes. For spruce, wood density of class 3 snags was significantly higher than that of class 5 and 6 snags, but class 4 snags were not different from either class 3 or 5 ($F_{3,75}$=21.13; P<0.001; Figure 5.2a). For aspen, class 3 and 4 snags were significantly different from class 5 and 6 snags ($F_{3,75}$=20.22; P<0.001; Figure 5.2b). As for the effect of time since tree death, wood density decreased significantly with snag age (F=25.50; P<0.001; R^2_{spruce}=0.198; R^2_{aspen}=0.556). This decrease was significantly faster in aspen when compared to spruce (significant interaction, F=15.37; P<0.001) (Figure 5.3), indicating different wood decomposition patterns for these two tree species. However, spruce of late-decay stages could not be included in the analysis, and for the trees that were included there are some clear indications that aging was less accurate for spruce than for aspen. Cherubini *et al.* (2002) showed that it is commonplace in coniferous species that the tree stops producing discernable growth rings well before it actually dies. In our study, stressed-host insect species were found in snags which were aged as having been dead for more than 10 years; the presence of such species suggests that these age estimates were inaccurate. No such problem was suspected for aspen.

5.5.2 Host-use patterns

A total of 1433 wood-feeding coleoptera was collected (709 in spruce, 724 in aspen), including 22 taxa identified to species level (16 in spruce, 6 in aspen), four identified to genus (two in spruce, three in aspen) and 13 individuals identified only to family (details in Tables 5.3 and 5.4). Assemblages were dominated by Cerambycidae in aspen, while Scolytidae were more frequently dissected from spruce snags.

In spruce, assemblages of wood-feeders were most diverse and numerous in the early stages of decay (Figure 5.4a). In Cerambycidae, stressed-host species dominated the assemblages. *Acmaeops proteus* was the most commonly collected, occurring at every site. Other early species were locally common but absent at some sites (i.e., *Acanthocinus pusillus, Meriellum proteus, Phymatodes dimidiatus, Tetropium cinnamopterum*). Only two of the 10 species of Cerambycidae collected, *Cosmosalia chrysocoma* and *Stictoleptura canadensis,* can be considered as dead-host species. *C. chrysocoma* was infrequently collected, and while *S. canadensis* was rather common in some Abitibi sites, it was absent from the more eastern sites (Table 5.3). Differences between cerambycid species in host condition, when compared with an ANOVA, were detected between *S. canadensis* and all other common early cerambycid species (*Acmaeops proteus, Meriellum proteus, Phymatodes dimidiatus*), ($F_{6,63}$=4.02; P=0.002; Figure 5.4a). For Scolytidae, again all species were found at the beginning of the decay gradient, where both ambrosia beetles (*Trypodendron lineatum*) and species feeding on subcortical tissue (all others) were found. No differences were detected within Scolytidae in terms of preference for specific part of the gradient (Figure 5.4a). Some species were only found in

eastern sites (*Dryocoetes affaber* and *Trypodendron lineatum*), while *Ips latidens* was only found in Abitibi. The species-rich buprestid genus *Dicerca*, which likely included several species in our samples, was found throughout early and middle stages of decay (Figure 5.4a).

When analysed with logistic regression, probability of presence of cerambycid larvae (all sites and species pooled) was significantly higher in early stages of decay of black spruce (χ^2_1=8,651; P=0.003) (Figure 5.5a). Although the species composition of assemblages at the five sites was somewhat different, the relationship between wood density and probability of occurrence was similar for all 5 sites when analysed separately (Figure 5.5b). This pattern is largely driven by the occurrence of the stressed-host guild (χ^2_1=21.611; P<0.001; Figure 5.5c), which numerically dominated the dead-host guild, absent from most sites. However, probability of presence of *S. canadensis* and *C. chrysocoma* do increase from near 0 in early stages of decay to over 80% in later stages in Selbaie 2 and Selbaie 3 sites (χ^2_1=7.263; P=0.007; Figure 5.5d), in which these species are more numerically important. In the data we collected the two dead-host species found in spruce co-occurred in the same stages of decay, so there is no evidence of succession among this guild in this tree species.

Patterns observed in aspen were different (Figure 5.4b). Scolytidae were marginal in numbers (Table 5.4) and mostly restricted to early decay stages (Figure 5.4b). Cerambycids were less diverse but more numerous, with *Anthophylax attenuatus* being the dominant species (Table 5.4). All cerambycid species were concentrated in middle to late stages of decay; aspen cerambycid assemblages were thus exclusively composed of

dead-host species. We saw no significant difference in preference (P>0.05) between the two numerically important species (*A. attenuatus* and *Bellamira scalaris*) (Figure 5.4b). These two species were found in all five sites sampled. Again the species-rich buprestid genus *Dicerca* was widespread and covered most stages of decay.

Probability of presence of cerambycid larvae (all sites and species pooled) was significantly higher in late stages of decay (Figure 5.6a; χ^2_1=13.067; P=0.001). Again, the observed patterns were similar in all sites, but with two sites in which probability of presence appeared lower in middle stages (LDTRF, Magusi 1) (Figure 5.6b). No similar analysis was made for stressed-host species, as they were totally absent from our samples in aspen.

5.6 Discussion

The use of dissection as a sampling method allowed in this study for an unprecedented characterization of wood-feeding saproxylic Coleoptera assemblages, as most published studies focusing on coniferous hosts generally considered only the first few years following tree death (e.g., Gardiner 1957, Zhong and Schowalter 1989, Lindhe and Lindelöw 2004, Saint-Germain *et al*. 2004a), frequently by using suboptimal sampling methods, while such characterization of assemblages is almost absent from the extant literature for deciduous host species. Our results showed communities dominated by stressed-host species in spruce, in which most species of Cerambycidae and Scolytidae were found only in the early stages of decay. Few species were found in later stages of

decay, and those species were totally absent from several of the sites we sampled. Patterns observed in aspen were opposite from those seen in black spruce. Communities were dominated by a few dead-host cerambycid species, and only a few scolytids and buprestids were found in early stages. This divergence in patterns between coniferous and deciduous host is of particular interest, as it as rarely been demonstrated to this level in the literature before, and because it is likely to affect management strategies that would be appropriate to preserve associated assemblages.

5.6.1 Host-use patterns in black spruce

Fifteen of the seventeen taxa found in spruce in our study, representing over 95% of collected specimens, were restricted to early-decay classes. Such importance of the stressed-host guild has been reported in the literature in spruce, as seen in our study, and in other coniferous genera in different contexts. Early studies (Graham 1925, Savely 1939) and Vanderwel *et al*. (2006), which investigated changes in species composition of whole saproxylic communities along several decay classes but in logs, noted the general predominance of wood-feeding guilds in recently-dead trees and a shift in dominance towards fungivore and saprophage species in later stages of decay. Several other studies investigating more precisely insect assemblages in snags recently killed by fire (Parmalee 1941, Gardiner 1957, Saint-Germain *et al*. 2004a) or insect defoliators (Belyea 1952) reported abundant and species-rich assemblages. However, we found no reports of species occurrence of wood-feeding beetles in later stages of decay, probably because later decay stages were rarely investigated with appropriate methods, not because of the paucity of the dead-host guild itself.

Not only do the abovementioned studies report similar occurrence patterns in fire-killed trees and in other types of disturbance, they also observed similar species composition. *Monochamus scutellatus* has been found in early stages of decay in all four of the above-mentioned studies, whether it be in spruce (Saint-Germain et al. 2004a), in pine (*Pinus* spp., in Gardiner 1957) or in balsam fir (*Abies balsamea* (Miller), in Belyea 1952). *Acmaeops proteus*, the most abundant species in our samples, has been reported in fire-killed spruce and pine one year after fire (Gardiner 1957, Saint-Germain 2004a). Other species found in unburned forests in our study, such as *Acanthocinus pusillus, Tetropium cinnamopterum* and *Xylotrechus undulatus*, are also reported in one or more of those studies. The two species classified in the dead-host guild in our study, *Cosmosalia chrysocoma* and *Stictoleptura canadensis*, were occasionally found in recent disturbances in pine (Gardiner 1957), albeit in very small numbers. This may indicate that these species may not be deterred by very fresh snags, and their preferences may thus cover the entire decay gradient we covered in our study.

Although probability of occurrence varied along the wood density gradient in similar ways among the five sites sampled, several species were locally common in one site and absent from others. We do not have sufficient data to link these variations with the different landscape contexts within which those stands were located. However, some of these species were found in only one or two trees (*Tetropium cinnamopterum* in Grands-Jardins, *Acanthocinus pusillus* in Selbaie 3). This may indicate a very agregated distribution in some species; in such cases, the absence of some species in our samples may not indicate absence from site altogether, but rather insufficient sampling effort to

detect species with such distribution. This difference in distribution between common, widespread species and aggregated species could reflect differences in host-selection and mating behaviour. Some other species which were reported in earlier literature but were not found in our study (*Pogonocherus* sp., *Rhagium inquisitor* L.) were found in spruce in undisturbed forests in another sampling effort involving snag dissection (Nappi *et al.* in prep.). A considerable sampling effort would be needed to establish whether these variations in species composition are due to landscape context or to differences in distribution within a system (i.e., absence due to aggregation and insufficient sampling).

5.6.2 Host-use patterns in aspen

We found no previous studies reporting wood-feeder assemblages for aspen from eastern North America. Some studies produced in western Canada (Hammond *et al*. 2001, Hammond *et al*. 2004) reported the presence of *Trypodendron retusum*, *Xyloterinus politus* and *Agrilus* sp. in early stages of decay of aspen, but not the presence of abundant *Anthophylax attenuatus* or *Bellamira scalaris*. In this case, the choice of sampling techniques may explain their absence from these studies.

It was notable that stressed-host species were absent from aspen snags. Some notorious species are known to be of widespread occurrence on dying aspen, such as the poplar borer *Saperda calcarata* Say, which was not dissected from any of our snags in this study. There is some indication that such species occur earlier during the decline of aspen, as Hanks (1999) classifies *S. calcarata* as a weakened-host species, i.e., hosts which are alive and growing but whose defences are compromised in some way, instead of a

stressed-host species. An observation we made may indicate this pattern to be common in aspen; galleries from buprestid *Agrilus* sp. were seen on a high proportion of the snags sampled, but live larvae were found in only one tree which died a few weeks prior to sampling, as it still had foliage.

Contrary to what was seen in black spruce, there were no major differences in species composition between the different stands of aspen. *Anthophylax*, *Bellamira* and *Dicerca* were dissected from snags in every site, and other species were either marginal or found at extremities of the sampled decay gradient. However, there were important differences in terms of abundance, as very few individuals were collected at Oka and Magusi 1 sites. This was expected in Oka, as aspen is marginal at that site, but that was not the case at Magusi 1. Snags at Magusi 1 were smaller in diameter than other sites, but the landscape context alone as considered in our sampling design cannot explain differences in abundance of species or species composition.

5.6.3 Differences between black spruce and aspen as hosts

There are many factors that could explain the opposite host-use patterns seen in black spruce compared to aspen. The different plant defense mechanisms and secondary compound profiles of aspen and spruce could provide an explanation on why stressed-host species are dominant in spruce, while this niche seems to be occupied by weakened-host species in aspen. Besides some species of Scolytidae which have evolved complex behavioural systems enabling them to overcome healthy trees' defenses (Wood 1982), there are very few healthy-host or weakened-host wood-feeding species thriving on

coniferous trees in North America, especially when compared to deciduous trees (Hanks 1999). This may be due in part to the production of oleoresin, composed mainly of monoterpenes and resin acids. It circulates in resin ducts, and flows freely from physical wounds affecting the tree (Lombardero *et al*. 2006). The flow of resin will increase following physical damage or introduction of a pathogen; resin flow is thus to some degree an induced defense mechanism (Klepzig *et al*. 2005, Lombardero *et al*. 2006). This resin flow prevents the establishment of insect larvae in healthy trees, and reduction of the resin flow in heavily-stressed trees gives a window of opportunity to secondary insects to successfully colonize the tree (Lombardero *et al*. 2006). Oleoresin is not produced by deciduous trees and this may be one explanation why healthy-host and weakened-host species are common in deciduous trees and rare in coniferous trees.

For specialization to evolve for a host in a very specific physiological state, some cues allowing the insect to locate appropriate hosts must exist. In coniferous trees, a dying or recently dead individual releases both monoterpenes (α-pinene being the most important in terms of quantity) and ethanol, produced by fermentation occurring in dead plant cells (Chararas 1980). This mixture of compounds occurs in a definite proportion only at this very moment, because ethanol is not produced in significant quantities in a healthy tree, and the release of monoterpenes decreases and eventually ceases following the death of the tree, as they are oxidized or polymerized by bacteria (Chararas 1981). Ethanol and monoterpenes act synergistically to elicit a behavioural response in stressed-host species, but may not do so singly, or much less strongly (Chenier and Philogène 1989, Byers 1992). Coniferophagous stressed-host species thus benefit from a clear chemical signal contributing significantly to their host selection. Unfortunately little is known about the

secondary chemistry of deciduous trees along different physiological state and decay gradient. It is thus unknown at this stage if such a clear chemical signal is present in stressed or recently dead aspen.

Typical stand dynamics of the two tree species, which differ significantly, could also provide an explanation for the observed differences in host-use patterns. In the northern boreal forest mostly dominated by coniferous species, stand dynamics are mostly driven by stand-replacing disturbances, mostly fire but also occasional insect epidemics (Bergeron *et al*. 2001, Bouchard *et al*. 2005). These disturbances produce, more or less periodically, large numbers of freshly-killed trees. Aspen is less prone to fire, and it rather exhibits gap-type dynamics (Hill *et al*. 2005). Because stressed-host species are receptive to a recently-dead tree for only a few weeks (Alya and Hain 1985), host availability is more restrictive to stressed-host species than to any other behavioural guild. There are important differences in the snag recruitment regimes between these two species, and the disturbance-driven dynamic might be more favourable to the evolution of stressed-host insect species. Most of the stressed-host species collected during our sampling are also believed to respond to stimuli produced during forest fires, especially smoke (Gardiner *et al*. 1957, Saint-Germain *et al*. 2004b, Saint-Germain *et al*. 2004c); this emphasizes the possibility of a link between the stand dynamics typical of such species and the evolution of communities of wood feeders dominated by stressed-host species.

Another of the main differences in host-use patterns between these two tree species was the paucity of dead-host species in spruce. More extensive sampling may have yielded different results, but observations that were made during dissection could explain why

middle and late stages of decay harbored so few species in spruce. There were sharp differences between the way aspen and black spruce decayed at the macroscopic level. Black spruce wood tended to become more porous, or 'honeycombed' in middle and late stages of decay, while aspen remained solid, even with a lower relative wood density (Figure 5.7). This difference in the decay process is possibly linked to the structure of the sapwood, which is constituted of tracheids in spruce and vessels in aspen. The very porous structure of decayed spruce wood may hinder larval movement, force the larva to consume higher quantities of wood for equivalent nutrient intake, retain water less efficiently and thus constitute a less stable environment, etc. Any of these factors could explain why the evolution of dead-host species in coniferous hosts was not favored, contrary to aspen and possibly other deciduous trees.

5.6.4 Conservation and management implications

Our results show that for wood-feeding Coleoptera, fresh snags have higher conservation value in spruce, and previous literature suggests that this pattern may be true for other coniferous species (Howden and Vogt 1951; Gardiner 1957). At first glance, it may appear that there is no need to alter management practices to conserve stressed-host species, as they are often abundant in recently harvested landscapes (Kaila *et al*. 1997). The disturbance by itself usually induces some tree mortality, and the new conditions created by the opening often increase tree mortality in the forest remnants. However, increased mortality seems to be restricted to the first few years following harvest (Harper and Macdonald 2002). It is questionable if these favorable conditions persist for longer than a few years, especially if the forest remnants are young or of insufficient area.

Creating high stumps will provide substrate for stressed-host species for one or two years, but has little long-term conservation value for this behavioural guild. Green tree retention, which has been recently introduced in Scandinavian forest practices (Jonsson *et al*. 2005), may alleviate this problem to some degree, as these trees will die on a longer time frame.

The situation is very different for aspen, in which snags having the highest conservation value were over 10 years old. Snags retain their conservation value much longer for dead-host than for stressed-host species, but must persist in the ecosystem longer to become valuable. In this case, efforts must be made to preserve snags already on site, and the creation of high stumps can contribute at maintaining spatial and temporal connectivity between suitable hosts.

In this study, snag dissection proved to be a very productive method to characterize wood-feeding assemblages, despite the logistic implications of the method and the time and labor required to complete the sampling. It provided unprecedented information that cannot be collected using traditional sampling methods. Further efforts should be made to study wood-feeding insects in different tree species and landscape contexts, and the information provided by this method should be seen as an additional tool of great interest to study the impact of management on such insects.

5.7 **Acknowledgements**

We would like to thank E. Bolduc, A. Dechene, D. Lesieur, Z. Sylvain and T. Work for field or laboratory work, and Oka National Park and the Lake Duparquet research and teaching forest for facilitating our work within their boundaries. This project was funded by *Action Concertées - Fonds forestiers* grant (P. Drapeau, C. Buddle and coll.) and a new researcher grant (C. Buddle) from the *Fonds Québécois de la Recherche sur la Nature et les Technologies* (FQRNT), by a Discovery grant to C. Buddle from the Natural Science and Engineering Research Council of Canada (NSERC), and by the partners of the NSERC industrial chair in sustainable forest management of Université du Québec en Abitibi-Témiscamingue (UQAT) and Université du Québec à Montréal (UQAM).

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Table 5.1 Characteristics of all sites sampled for both tree species, including number of snags sampled, geographic coordinates and information on the landscape context around each site (forest cover).

Sites	# Snags	Coordinates		Landscape context
Black spruce				
Selbaie 1	24	49° 25' N	79° 00' W	Black spruce-dominated
Selbaie 2	12	49° 33' N	78° 59' W	Black spruce-dominated
Selbaie 3	12	49° 48' N	78° 55' W	Black spruce-dominated
Chauvin	16	48° 26' N	70° 05' W	White spruce/balsam fir-dominated; black spruce <10%
Grands-Jardins	16	47° 41' N	70° 51' W	Balsam fir/black spruce co-dominants
Aspen				
LDRTF	24	48° 28' N	79° 16' W	Aspen-dominated, some spruce and birch
Magusi 1	12	48° 24' N	79° 27' W	Aspen-dominated, some jack pine
Magusi 2	12	48° 26' N	79° 24' W	Aspen-dominated, some jack pine
Chauvin	16	48° 26' N	70° 05' W	White spruce/balsam fir-dominated, aspen <10%
Oka	16	45° 29' N	74° 01' W	Beech/maple-dominated, aspen marginal <2%

Table 5.2 Criteria used to classify snags in decay classes according to their visual appearance, based on classification by Maser et al. (1979).

Stage	Twigs	Branches	Bark	Top
3	Present	Present	Tight	Present
4	Absent	Present	Loose	Usually present
5	Absent	Stubs	Mostly peeling	Usually absent
6	Absent	Absent	Usually absent	Absent

Table 5.3 Number of individuals found for each species (number of snags in parenthesis) at all sites sampled in black spruce snags, according to behavioural guild.

	Selbaie 1 n=24	**Selbaie 2** n=12	**Selbaie 3** n=12	**Chauvin** n=16	**G-J** n=16	**Total**
Cerambycidae						
Stressed-host species						
Acanthocinus pusillus Kirby	1 (1)	0	22 (2)	0	5 (1)	28
Acmaeops proteus (Kirby)	28 (9)	30 (5)	13 (3)	16 (4)	20 (6)	107
Meriellum proteus (Kirby)	7 (3)	3 (2)	6 (3)	0	2 (2)	18
Monochamus scutellatus (Say)	2 (1)	0	1 (1)	0	2 (1)	5
Phymatodes dimidiatus (Kirby)	0	0	3 (1)	21 (3)	0	24
Tetropium cinnamopterum Kirby	0	1 (1)	0	0	13 (1)	14
n. *Trachysida aspera* (LeConte)	0	2 (1)	2 (1)	0	0	4
Xylotrechus undulatus (Say)	0	0	5 (3)	3 (1)	9 (3)	17
Dead-host species						
Cosmosalia chrysocoma (Kirby)	1 (1)	0	3 (1)	0	0	4
Stictoleptura canadensis (Olivier)	1 (1)	11 (4)	12 (4)	0	0	22
Not identified	2 (2)	1 (1)	0	0	1 (1)	4
Buprestidae						
Chrysobothris sp.	0	0	1 (1)	0	0	1
Dicerca sp.	13 (6)	18 (6)	14 (3)	0	0	45
Scolytidae						
Crypturgus borealis Swaine	4 (2)	2 (1)	118 (1)	0	11 (2)	135
Dendroctonus rufipennis (Kirby)	0	0	0	1 (1)	0	1
Dryocoetes affaber (Mannerheim)	0	0	0	16 (2)	6 (2)	22
Ips latidens (LeConte)	17 (4)	12 (3)	47 (1)	0	0	76
Polygraphus rufipennis (Kirby)	25 (1)	12 (2)	48 (1)	3 (1)	68 (4)	156
Trypodendron lineatum (Olivier)	0	0	0	0	26 (1)	26

Table 5.4 Number of individuals found for each species at all sites sampled in aspen snags, according to behavioural guild.

	LDRTF n=24	**Magusi 1** n=12	**Magusi 2** n=12	**Chauvin** n=16	**Oka** n=16	**Total**
Cerambycidae						
Dead-host species						
Anthophylax attenuatus (Haldeman)	162 (15)	6 (1)	280 (8)	46 (6)	8 (3)	502
Bellamira scalaris (Say)	8 (4)	2 (1)	1 (1)	11 (5)	10 (5)	32
Clytus ruricola (Olivier)	0	0	0	0	1 (1)	1
n. *Trachysida mutabilis* (Newman)	0	0	0	4 (2)	0	4
n. *Trigonarthris* sp.	1 (1)	0	0	0	0	1
Not identified	2 (2)	1 (1)	0	2 (2)	2 (2)	7
Buprestidae						
Agrilus sp.	0	0	0	20 (2)	0	20
Dicerca sp.	9 (5)	5 (3)	3 (2)	26 (4)	11 (3)	54
Scolytidae						
Trypodendron retusum (LeConte)	5 (1)	0	0	46 (2)	0	51
Xyloterinus politus Say	10 (2)	0	0	36 (1)	0	46
Larvae	0	0	6 (1)	0	0	6

List of figures

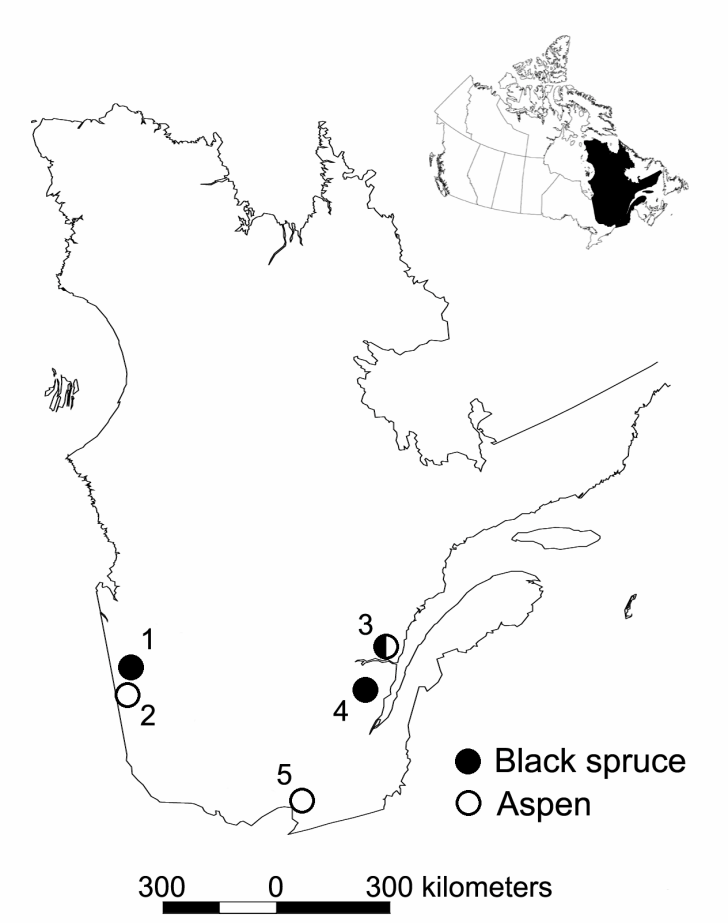

Figure 5.1

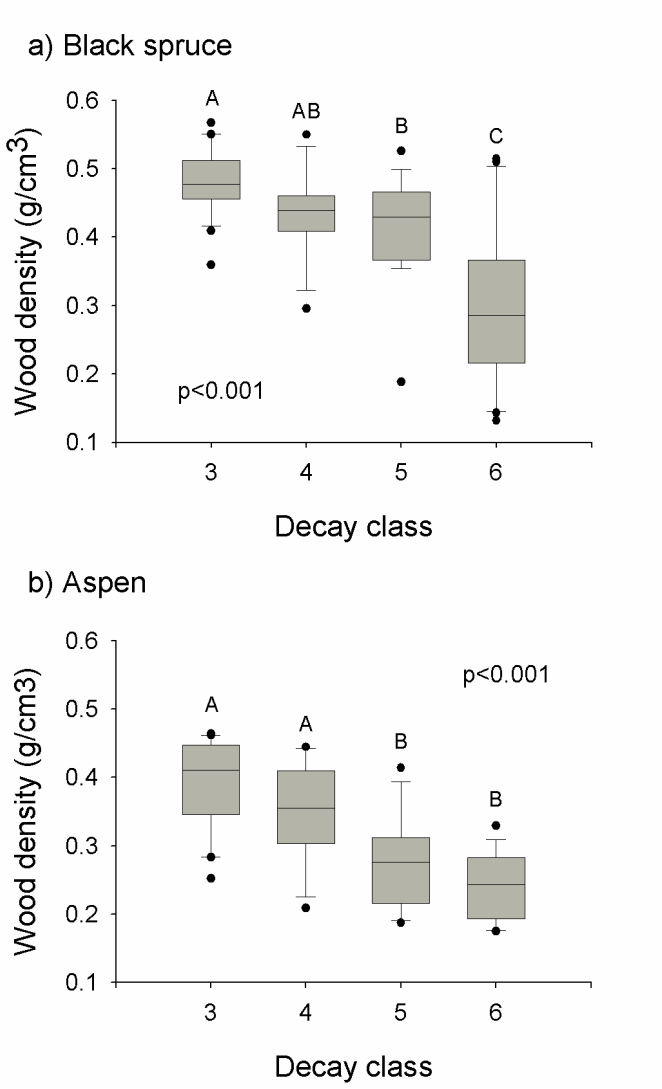
a) Black spruce
Wood density (g/cm3)
0.6
0.5
0.4
0.3
0.2
0.1
A
AB
B
C
p<0.001
3
4
5
6
Decay class
b) Aspen
Wood density (g/cm3)
0.6
0.5
0.4
0.3
0.2
0.1
A
A
B
B
p<0.001
3
4
5
6
Decay class

Figure 5.2


Age × T sp *
Age ***
T sp ***
S
A
Wood density (g/cm3)
Years since tree death
0.6
0.5
0.4
0.3
0.2
0.1
0
5
10
15
20
25
30
35
40

Figure 5.3

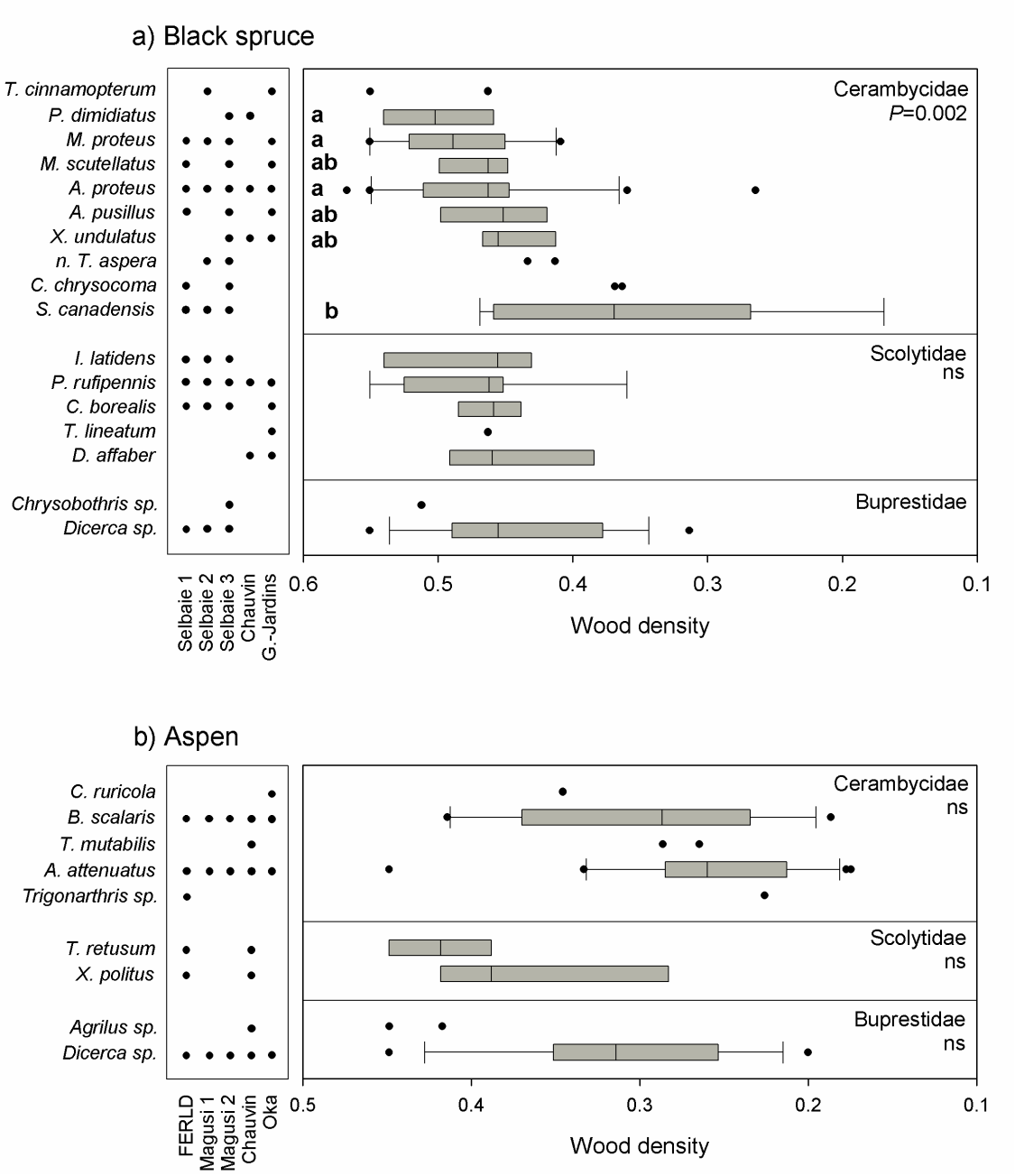
a) Black spruce
T. cinnamopterum
P. dimidiatus
M. proteus
M. scutellatus
A. proteus
A. pusillus
X. undulatus
n. T. aspera
C. chrysocoma
S. canadensis
I. latidens
P. rufipennis
C. borealis
T. lineatum
D. affaber
Chrysobothris sp.
Dicerca sp.
a
a
ab
a
ab
ab
b
Cerambycidae
P=0.002
Scolytidae
ns
Buprestidae
Selbaie 1
Selbaie 2
Selbaie 3
Chauvin
G.-Jardins
0.6
0.5
0.4
0.3
0.2
0.1
Wood density
b) Aspen
C. ruricola
B. scalaris
T. mutabilis
A. attenuatus
Trigonarthris sp.
T. retusum
X. politus
Agrilus sp.
Dicerca sp.
Cerambycidae
ns
Scolytidae
ns
Buprestidae
ns
FERLD
Magusi 1
Magusi 2
Chauvin
Oka
0.5
0.4
0.3
0.2
0.1
Wood density

Figure 5.4

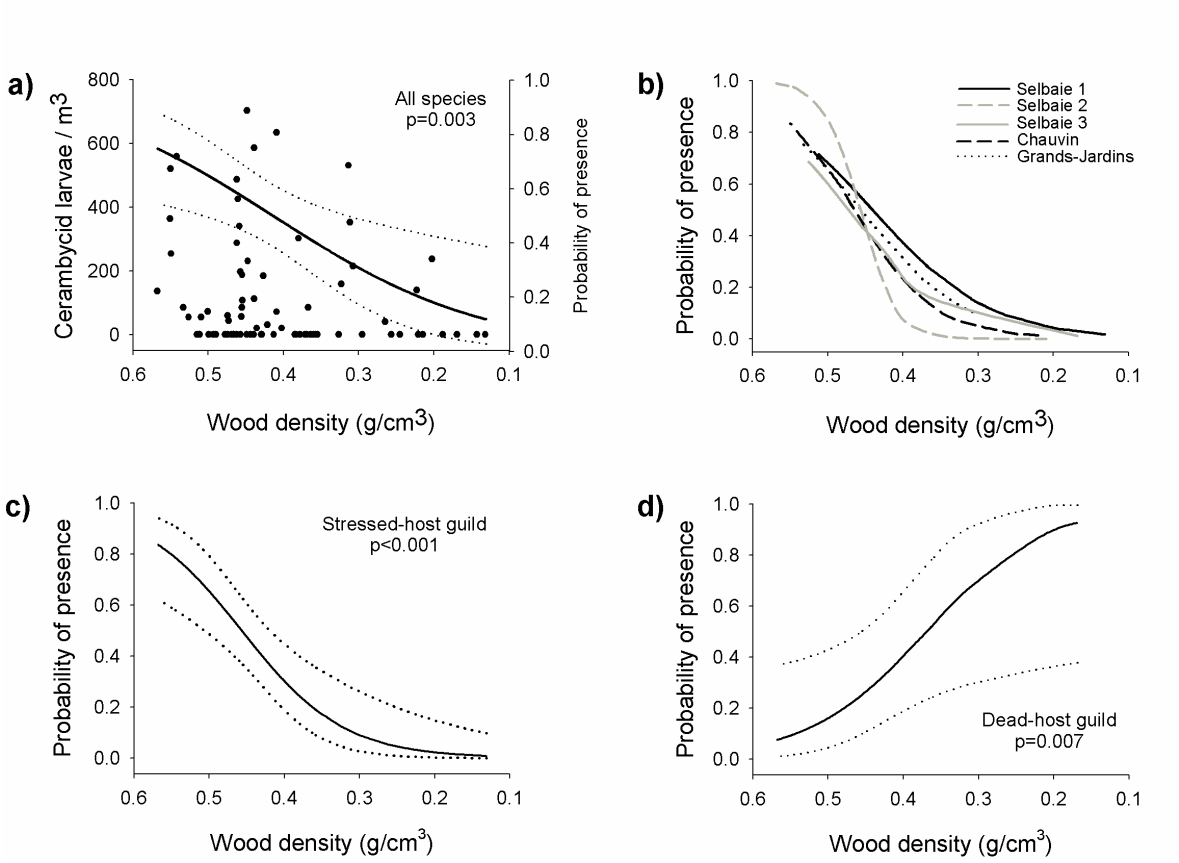
a)
Cerambycid larvae / m3
All species
p=0.003
Probability of presence
Wood density (g/cm3)
b)
Probability of presence
Selbaie 1
Selbaie 2
Selbaie 3
Chauvin
Grands-Jardins
Wood density (g/cm3)
c)
Probability of presence
Stressed-host guild
p<0.001
Wood density (g/cm3)
d)
Probability of presence
Dead-host guild
p=0.007
Wood density (g/cm3)

Figure 5.5

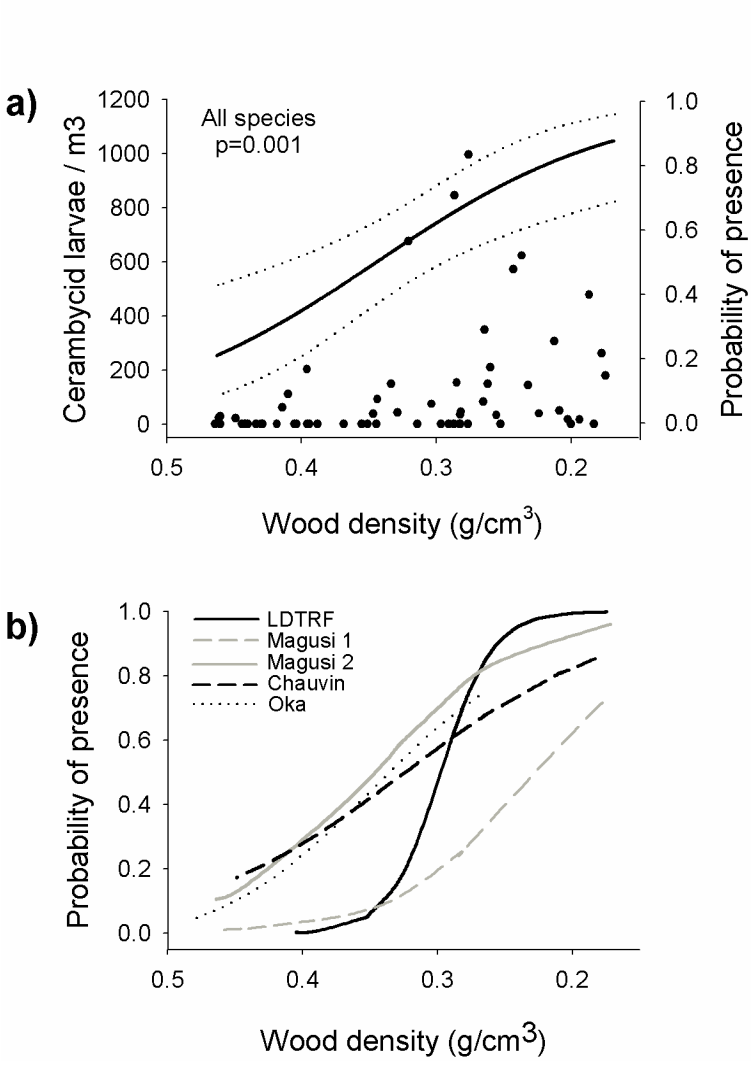
a)
All species
p=0.001
Cerambycid larvae / m3
Probability of presence
1200
1000
800
600
400
200
0
1.0
0.8
0.6
0.4
0.2
0.0
0.5
0.4
0.3
0.2
Wood density (g/cm3)
b)
LDTRF
Magusi 1
Magusi 2
Chauvin
Oka
Probability of presence
1.0
0.8
0.6
0.4
0.2
0.0
0.5
0.4
0.3
0.2
Wood density (g/cm3)

Figure 5.6

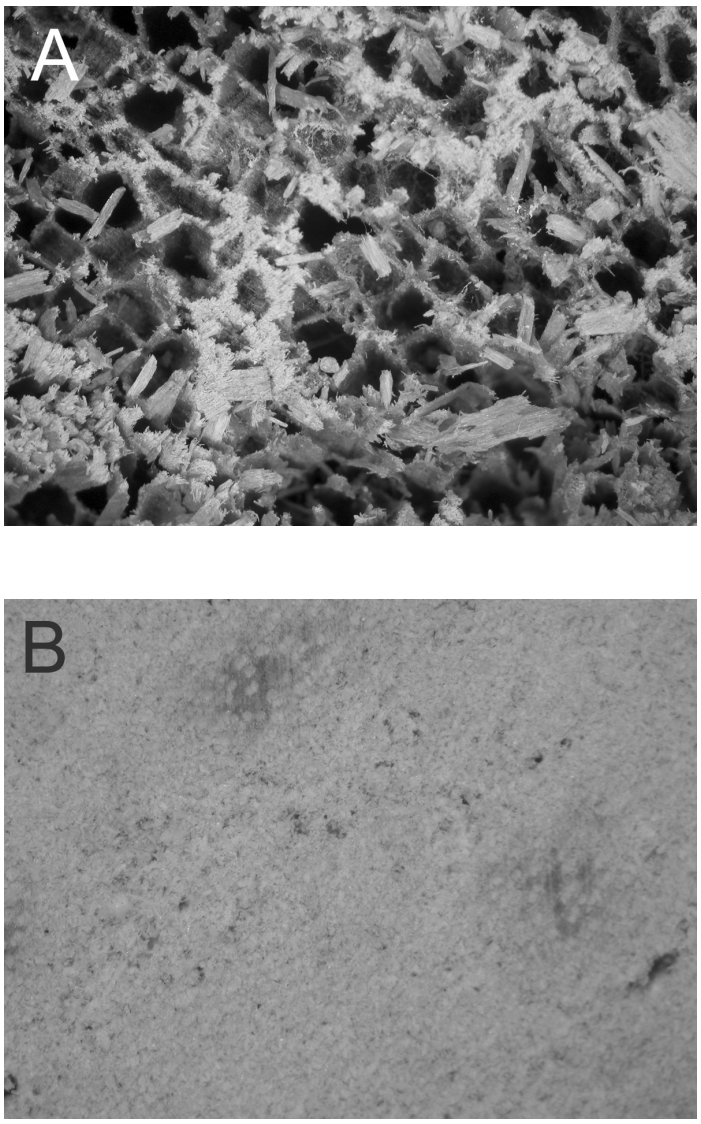

Figure 5.7

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

Michel Saint-Germain[1,2], Pierre Drapeau[1] and Christopher M. Buddle[2]

[1] Groupe de Recherche en Écologie Forestière interuniversitaire, Département des sciences biologiques, Université du Québec à Montréal, CP 8888, succ. Centre-ville, Montréal, Québec, Canada, H3C 3P8

[2] Department of Natural Resource Sciences, McGill University, 21111 Lakeshore Road, Saint-Anne-de-Bellevue, Québec, Canada, H9X 3V9

6.1 Preface

Chapter 5 reported opposite host-use patterns in aspen and black spruce along the decay gradient. Assemblages were dominated by stressed-host (early decay) species in spruce, and by dead-host species in aspen. The colonization dynamics of stressed-host species are rather well-known, as their host-use patterns are mainly driven by the necessity on the part of the first larval instars to develop in fresh snags, possibly because of a dependence on simple sugars still present in subcortical tissues at that stage. Dynamics of dead-host species are less well understood. Questions whether there is a succession of dead-host species along the decay gradient, and whether they actively select for specific host types along the gradient or not remain. In chapter 6, I investigate relationships between occurrence patterns of dead-host species in aspen and potential mechanisms on which active selection would be based. Biodiversity studies of snag-level occurrence patterns usually do not go beyond the descriptive stage. The characterization of substrate quality as decay proceeds constitutes by itself an original contribution to the field, as well the investigation of its relationship with insect occurrence. The consideration of neutral mechanisms to explain observed host-use patterns (i.e., random mechanisms to explain apparently non-random patterns) is also unprecedented for dead-host cerambycid species.

6.2 **Abstract**

Determinants of host-use patterns have been extensively studied in plant-feeding insects, usually within the framework of optimality theory. Comparatively, factors driving host selection in saprophagous insects have received little attention. In this study, we investigated mechanisms creating occurrence peaks of saprophagous wood-borers (Cerambycidae: Coleoptera) in standing dead aspen of middle and late stages of decay by correlating insect occurrence to variations in substrate-related nutritional and physical parameters. We dissected 24 snags of 4 decay stages 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. 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, and the one including snag age only performed the best, with a w_i of 0.873. 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 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.

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

6.3 **Introduction**

Host-use patterns and host-selection behaviour have been extensively studied in plant-feeding insects. Most insects show some degree of specialization in their host choice, whether as feeding or oviposition material (Jaenike 1990, Bernays and Chapman 1994). Host selection and specialization have typically been approached within the framework of optimality theory (e.g., Pianka 1976, Thompson 1988, Mayhew 2001, Scheirs and De Bruyn 2002), which requires that behaviours be interpreted in terms of the contribution 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 maximize their fitness (Jaenike 1978), is a direct application of optimality theory. Specialization may arise from tradeoffs between abilities at dealing with different physical and/or nutritional contexts. Specialization thus produces smaller-breadth niches that can result in successional-type patterns when different groups of organisms evolve tradeoffs leading to specialization in 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 and Boddy 1988, Haberkern *et al*. 2002). Because of this, dead trees colonized by wood-feeding insects usually exhibit a high rate of decay (Edmonds and Eglitis 1989, Dajoz 2000). Insects are also particularly diversified in dead wood, as

assemblages often comprise several trophic levels that 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 (chapter 5). However, the mechanisms creating these host-use patterns are not currently understood.Although insects feeding on dead plant material do not face the same constraints as 'green' phytophagous insects do (e.g., no induced defence mechanisms), the optimality theoretical framework could still be relevant but has received little attention in studies describing host-use by insects feeding on dead wood. Several environmental factors known to vary along the wood decay gradient may create opportunities for active selection and specialization by wood-boring insects. Links with species occurrence and/or larval performance have been suggested in the literature for both nutritional and physical factors. Some studies showed a positive impact of higher nitrogen content on larval growth rates of some Cerambycidae (Coleoptera) (Becker 1977, Hosking and Hutcheson 1979, Forcella 1982, Shibata 1998), and nitrogen content of dead wood has been shown to vary significantly along the decay gradient (Lambert *et al*. 1980, Fahey 1983, Alban and Pastor 1993, Holub *et al*. 2001). The importance of non-structural carbohydrates has also been suggested for some wood-feeding species that lack the ability to digest structural polysaccharides (Parkin 1940); however, variation of non-structural carbohydrates along the decay gradient is still poorly known. Some physical characteristics like wood density and water content obviously vary along the decay gradient (Lambert *et al*. 1980), and could also have an influence on host selection and larval performance (Graham 1925, Becker 1977).

We know little, 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. Understanding mechanisms leading to these patterns should be pursued. In this study, we approach this issue by considering two conceptual models of host selection (see Figure 1), and discussing relative support obtained by each in correlative analyses relating physical and nutritional qualities of dead wood to insect occurrence over the decay gradient. Following is a brief description of these models.

1. *Active selection model*. – Two conditions are prerequisites for active selection of 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 specialization to take place. If different species specialize for different parts of the gradient, a succession-type pattern occurs as shown in Figure 1a.

2. *Temporal autocorrelative neutral model*. – In this model, dispersal constraints and temporal autocorrelation in probability of occurrence are the only factors at play in creating occurrence patterns. Because of some elements of behaviour seen in wood-borers feeding on dead hosts, the fact that a snag is used one year increases the probability that it will still be used by the same species the following year. This temporal autocorrelation effect can be explained by larval development spanning over 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 Figure 1b, each snag has a given probability of being colonized each year, but once colonized, it remains so for the following years until it is no longer suitable (i.e., snags fall). Hence, older snags have higher probabilities of being used by larvae, without any active selection for substrate quality beyond choosing a dead deciduous tree.

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

6.4 Methods

In May 2004, we selected a mature closed-canopy aspen stand 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 harbored a high density of snags of all

decay stages of average diameter >25 cm, and is located in a landscape mainly composed of similar ~85-years 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 six snags of each of the 4 decay classes covering all snag stages of decay (Table 6.1) as described in Maser *et al.* (1979).

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

At the end of July, the 24 snags were cut down, and a 1-m long section (between 0.5 and 1.5 m above groundg) was taken to the laboratory for insect sampling. Three 4-cm-thick wood disks, two over the 1-m section and one at 5 m, were also taken to determine the time of tree death and to measure physical parameters. Presence of fruiting bodies of wood-decaying fungi was also noted for all snags. Insect sampling was done by first peeling 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, and all insects found were collected. Large cerambycid larvae were boiled in water before being put in 70% ethanol for better preservation.

6.4.1 Determination of the age of the snags

The time of death of the 24 snags was estimated using dendrochronology. For each snag growth rings were measured on 4 radii on two of the wood disks taken at 1.5 and 5 m above ground, respectively. Measurements were crossdated using the software COFECHA (Grissino-Mayer 2001) with master chronologies previously produced for the same sites (Bergeron *et al*. 2002, Lecomte *et al*. 2005).

6.4.2 Measurement of physical parameters

Three parameters related to the physical characteristics of the substrate were measured: wood density, the capacity of the wood to absorb water and the capacity of wood to hold water. Wood density was measured by averaging density (dry weight/volume) of three ~50 ml wood samples taken systematically at 120° around the bole from one of the wood disks taken at ~1.5 m above ground. Volume was measured by water displacement. Wood density was used for subsequent analyses as an index of decay. Direct measurement of water content could not be taken at the moment of sample collection. Instead, we measured the capacity of the wood to absorb water by saturating the wood samples (same as the ones used to measure wood density) by immerging them in water for 72 hours. We then weighted them and oven-dried them at 60° C to weight constancy. Their capacity to

absorb water was calculated as ml of water held by 1 cm^3 of wood when saturated. To complement this information, we also measured the water loss rate of saturated wood put to dry in an oven at 60° C (capacity to hold water). Samples were weighed every hour for eight hours, and the loss rate was measured as the slope of a regression made on the % of total water lost every hour.

6.4.3 Measurement of nutritional parameters

Three parameters related to the nutritional quality of the substrate were measured: total nitrogen, non-structural carbohydrates and phenols. Nitrogen and carbohydrates are among the most important and limiting nutrients for insects in general and phenols constitute an important class of secondary compounds often having negative effects on insect performance (Haack and Slansky 1987). Wood samples were oven-dried at 60° C, milled to a fine powder, and then stored at -80° C until analyzed. For nitrogen, 50 mg of wood powder were digested in 10 ml of acid mix as described in Parkinson and Allen (1975). Samples were then diluted to 100 ml with deionized water and nitrogen levels were measured with a Lachat QuickChem 8000 flow injection auto-analyzer (Hach Company Inc., Loveland, CO, USA). For non-structural carbohydrates, which include here glucose, fructose, sucrose and starch, 50 mg of wood powder were 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 16h on an orbital shaker. One hundred µl aliquots were then assayed with the Folin-Ciocalteu method, as described in Waterman and Mole (1994).

6.4.4 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 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, nitrogen, phenols and NSCs) were also related to occurrence (presence/absence) of behavioural guilds using simple logistic regressions, and to log-transformed abundance of cerambycid larvae with linear regressions. Linear regressions were also 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, we used both model selection and standard hypothesis testing. Model selection is an analytical approach in which several competing hypotheses are simultaneously confronted with data (Johnson and Omland 2004). Models are then ranked according to their relative weighted support. We used second order Aikake's information criteria (AIC_c), which corrects for low sample sizes, to compare competing models. Each model was also tested using simple or multiple logistic regressions. Tested models are described in Table 6.2. Analyses of variance and linear

regressions were performed on SPSS 10.0.5 for Windows (SPSS Inc., Chicago, IL, USA), while logistic regressions were performed on SYSTAT 11.00 (Systat Software Inc., Point Richmond, CA, USA).

6.5 Results

6.5.1 Host-use patterns along the decay gradient

A total of 173 dead-host cerambycid larvae were found in the 24 snags, ranging in density from 0 to 964.1 larvae/m^3 of dead wood. The assemblages were species-poor, as *Anthophylax attenuatus* and *Bellamira scalaris* represented 93.6% and 4.6% of larvae found (Table 6.1). Assemblages of wood-feeding Coleoptera living in aspen are further described in chapter 5. Occurrence of these species was concentrated at the end of the decay gradient. Most snags of early decay stages contained no or few larvae, while all snags with a wood density below 0.282 g/cm^3 contained larvae (covered density range: 0.405-0.175). Because of the dominance of *A. attenuatus*, and because *B. scalaris* had similar occurrence patterns, further analyses were done with pooled species data. Figure 6.2a illustrates the probability of occurrence along a wood density gradient as calculated using a binary logistic regression (χ^2_1=17.375; P<0.001). In this figure probability of occurrence (presence of at least 1 larva) is near zero at the beginning of the gradient, and goes up in a sigmoid fashion to near 1 in middle to late stages of decay. The increase is steeper when the probability of occurrence is calculated with snag age, and it reaches 1 around 10 years of age (Figure 6.2b). Log-transformed abundance increases in the second half of the covered decay gradient ($F_{1,23}$=8.505; P=0.008) (Figure 6.2c). However, there

is no apparent trend in abundance within the part of the gradient in which all trees are colonized. This relationship is not significant when snag age is used as the independent variable (Figure 6.2d).

6.5.2 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 at tree death to ~0.2 g/cm^3 in older snags ($F_{1,23}$=27.52; P<0.001) (Figure 6.3a). 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 extant of decay more precisely than snag age. The capacity of the wood to absorb water increased in more decayed wood ($F_{1,23}$=35.19; P<0.001; Figure 6.3b), while the water loss rate decreased ($F_{1,23}$=11.88; P=0.002; Figure 6.3c); more decayed aspen wood thus absorbs more water and looses it more slowly in dry conditions. Nitrogen levels were low, but increased significantly as wood decayed ($F_{1,23}$=18.51; P<0.001; Figure 6.3d). Non-structural carbohydrates were also in low concentrations, and decreased significantly along the gradient ($F_{1,23}$=5.57; P=0.028; Figure 6.3e). Phenols were rather stable throughout the gradient at around 10 mg/g, except for a few trees which had much higher concentrations (P>0.05; Figure 6.3f).

6.5.3 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. Insect occurrence (probability of presence) was significantly associated with snag age, wood density, water content, water loss rate and nitrogen (Table 6.3). Probability of occurrence of larvae decreased with wood density (χ^2_1=17.38; P<0.001) and water loss rate (χ^2_1=12.68; P<0.001), and increased with snag age (χ^2_1=22.67; P<0.001), water content at saturation (χ^2_1=15.33; P<0.001) and nitrogen (χ^2_1=9.83; P=0.002). Relationships with insect abundance were weaker. Log-transformed abundance increased with water content ($F_{1,23}$=5.33; P=0.031), and decreased with wood density ($F_{1,23}$=8.51; P=0.008). Interpretation of these results is difficult because most of these variables were autocorrelated (Table 6.3).

We tested different multivariate models with suspected biological significance to explain species occurrence with both multivariate logistic regressions and model selection (Aikake's information criteria). Models are listed with results in Table 6.4. Several logistic regression models had a P≤0.001, including different combinations of physical and nutritional parameters, and snag age. Best models included snag age, wood density, nitrogen and water-related parameters. The model including only snag age showed the strongest relationship (Table 6.4). Snag age was also the most highly rated model in model selection, with a w_i of 0.873. The model including only wood density was second with a w_i of 0.062. All other models had a w_i<0.050 (Table 6.3). Snag age thus appears to be the most significant parameter among all these highly correlated variables.

6.6 Discussion

We obtained low occurrence of cerambycid larvae in the first stages of decay but high occurrence, rapidly reaching a probability of presence of 1, in mid to late stages, as described in chapter 5. The few species found showed similar preferences. In the introduction we presented two conceptual models predicting different distributions based on different underlying mechanisms. The observed concentration of larvae in mid to late stages could either be the result of active selection of a single group of species for the later stages of decay (Figure 1a, but with only one group of species and thus no succession), or produced by neutral autocorrelative mechanisms as modelled in Figure 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 nitrogen and NSC varied significantly along the decay gradient. We observed a positive relationship between nitrogen 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 having higher levels of nitrogen. Hosking and Hutcheson (1979) also observed an increase in larval growth in nitrogen-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 for their first instars.

Whereas these studies have documented the positive impact of higher nitrogen levels on cerambycid larval growth, they did not assess the importance of nitrogen content in host selection *per se*, and thus the real impact of nitrogen on insect occurrence patterns remains unknown. Furthermore, some studies suggest that dead-host cerambycid larvae have the ability to acquire nitrogen through other sources than the wood they ingest. Some dead-host cerambycid species can grow and reach adulthood in wood containing as little as 0.03% nitrogen (Becker 1963), and it is likely that in such a context they acquire atmospheric nitrogen through symbiotic microorganisms living in their gut (Mishra *et al*. 1985). Variations of nitrogen seen in dead sapwood in our study are at very low levels compared with what is seen in other plant materials in which these compounds are known driving factors. Nitrogen concentrations represent generally between 1-5% of dry weight in subcortical tissues (Haack and Slansky 1987) and around 3% in aspen foliage (Hemming and Lindroth 1999), in comparison to an average of 0.15% seen in our study. Hence, variations of nitrogen we observed may not be of substantial biological significance.

Non-structural carbohydrates also showed significant variations along the decay gradient. However, NSCs were negatively correlated with insect occurrence, and thus cannot be considered as a driving factor for dead-host species host-use patterns. Although the importance of NSCs in larval survival has been shown for some stressed-host cerambycid species (*Arhopalus syriacus* Reitter, in Chararas 1981), a prevalence of enzymes degrading structural polysaccharides is suspected in dead-host species (Parkin 1940, Chararas *et al*. 1983, Haack and Slansky 1987, Kukor *et al*. 1988, Zverlov *et al*. 2003); NSCs may thus not be a key factor in host-selection for this behavioural guild, since these

insects can obtain glucose from cellulose and hemicellulose constituting the cell walls. Since phenolic compounds concentrations were not significantly related to insect occurrence and that observed nitrogen and NSC variations do not seem to cover biologically-significant levels, measured nutritional parameters apparently do not offer basis for nutrition-based active selection among aspen-feeding dead-host species, despite the significant relationship observed between nitrogen and insect occurrence in hypothesis testing.

All physical parameters varied significantly with snag age and wood density. More decayed snags had the capacity to hold more water, and lost their water at slower rates; older snags are thus more stable environments for wood-feeders. Some species have been shown to respond to moisture gradients. The cerambycid genus *Asemum* were 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 dependant, especially near the surface of the wood, on recent meteorological conditions. Like nitrogen, moisture content probably influences larval performance but not host-selection *per se*, and thus may create non-random patterns rather through differential mortality.

Interpretation of our results is complicated by the high number of correlated 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 relativize actual support for each of these models. Only two models had w_i>0.05, and the model consisting of only snag age received 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 have a major influence, or by the existence of another parameter correlated with age that we did not measure.

Few parameters known to be biologically significant for wood-borers were not measured in our study. Among those are host-produced volatiles, which are a dominant factor in host selection for other behavioural guilds, especially stressed-host 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 host selection in saproxylic species, at least before landing on a potential host, as similar assemblages were captured using sticky traps on old snags of five different tree species, including coniferous species and inert stovepipe controls, showing no form of selection while in flight, although assemblages captured contained few wood-boring species. Also, we have to keep in mind that host volatiles should be

seen as a proxy for another biologically-significant factor related to performance, and thus cannot be considered as a basis for host selection in themselves.

During our sampling we noted the presence of fungal fruiting bodies on the snags that were sampled. 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 could 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 seven years following the death of the tree in snags of different tree species including aspen, a timeframe that coincide with a sharp increase in occurrence we observed 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. The importance of a potential relationship between wood-decay fungi and wood-borer occurrence should thus be the focus of future investigation involving mechanistic experimental studies, and not just correlative ones.

Most nutritional and physical parameters measured in our study received marginal relative support when compared to snag age in model selection as predictors of insect occurrence. These results suggest that the measured parameters may not offer 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 we assume that the pattern we observed is

not linked to some unmeasured parameter, then we have to consider the involvement of neutral (i.e., random) mechanisms related to the time elapsed since the death of the tree. Host-use patterns observed in this study and in other sites (chapter 5) can be reproduced by a simple model in which no active selection takes place (Figure 1b). Because the developmental time of most dead-host species larvae usually lasts for more than one 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 one 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 as the one observed in our study. Further studies on the behaviour of these species will be needed to test this neutral autocorrelative hypothesis.

Because of its correlative nature, our study does not bring decisive evidence towards neutral mechanisms as drivers of the host-use patterns observed for aspen-feeding dead-host wood-feeding beetle species. However, we can question, based on the information provided by this study, the involvement of several nutritional and physical parameters in the host-selection behaviour of these species. Nitrogen and NSCs, so often involved in host selection in 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 still lower than the model including snag age only. Although we measured most parameters generally seen as being important for wood-feeding species, we did not found any basis for active selection along the decay gradient. Further study of occurrence patterns and behaviour of these species will be

needed to confirm if neutral mechanisms are effectively driving the preference of those species for middle and late stages of decay.

6.7 **Acknowledgements**

We would like to thank E. Bolduc, A. Dechene, D. Lesieur, Z. Sylvain and T. Work for field or laboratory work, H. Lalande and T. Motchula on their assistance in the analysis of nutritional parameters, and Oka National Park and the Lake Duparquet research and teaching forest for facilitating our work within their boundaries. This project was funded by *Action Concertées - Fonds forestiers* grant (P. Drapeau, C. Buddle and coll.) and a new researcher grant (C. Buddle) from the *Fonds Québécois de la Recherche sur la Nature et les Technologies* (FQRNT), by a Discovery grant to C. Buddle from the Natural Science and Engineering Research Council of Canada (NSERC), and by the partners of the NSERC industrial chair in sustainable forest management of Université du Québec en Abitibi-Témiscamingue (UQAT) and Université du Québec à Montréal (UQAM).

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Table 6.1 Characterization of all 24 snags sampled, and species and number of insects collected through wood dissection. Decay classes correspond to classification by Maser *et al*. 1979. Age refers to years elapsed since tree death. Wood density=dry weigth/volume.

Snag	Decay class	Diameter	Age	Density	Presence of fruiting bodies	*Anthophylax attenuatus* (Haldeman)	*Bellamira scalaris* (Say)	Others
1	3	40.1	3	.283	no	0	0	0
2	3	21.0	9	.287	no	0	0	0
3	3	19.9	4	.291	yes	0	0	0
4	3	20.2	3	.351	no	0	0	0
5	3	33.5	3	.388	no	0	0	0
6	3	19.8	3	.404	no	0	0	0
7	4	24.2	8	.237	no	27	2	0
8	4	35.3	14	.262	no	11	0	0
9	4	31.5	4	.314	no	0	0	0
10	4	25.3	6	.333	yes	6	0	1
11	4	19.6	2	.355	no	0	0	0
12	4	21.4	2	.405	no	0	0	0
13	5	25.3	11	.187	no	18	1	0
14	5	31.0	19	.203	no	1	0	0
15	5	22.4	7	.255	yes	1	0	0
16	5	31.7	10	.276	yes	59	1	1
17	5	22.0	12	.282	yes	1	0	0
18	5	27.2	10	.285	yes	7	0	0
19	6	28.4	13	.175	yes	8	0	0
20	6	29.6	21	.194	yes	1	0	0
21	6	33.6	22	.224	no	3	0	1
22	6	23.6	19	.232	no	1	4	0
23	6	20.0	11	.248	no	14	0	0
24	6	29.2	21	.265	yes	4	0	0

Table 6.2 Presentation of all models included in Aikake's information criteria-based model selection, with underlying theoretical basis.

Model	Theoretical basis	References
Nutritional		
Nitrogen	Larval performance ↑ with higher N levels	Hosking and Hutcheson 1979; Shibata 1998
Non-structural carbohydrates (NSC)	Some species dependent on high NSC concentrations	Parkin 1940
Phenols	Defence compounds; may influence larval performance	Haack and Slansky 1987
Nitrogen + Phenols	Combined nutritional effects	See above
Nitrogen + NSC + 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

Table 6.3 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). In the second part of the table, correlation matrix between all measured parameters.

	Age	**Density**	**Water content**	**Water loss rate**	**Diameter**	**Nitrogen**	**Phenols**	**NSC**
Presence (logistic reg.)	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$	ns	$P=0.002$	ns	ns
Log(Abundance+1) (linear reg.)	$P=0.065$ $R^2=0.147$	$P=0.008$ $R^2=0.279$	$P=0.009$ $R^2=0.270$	ns	ns	ns	ns	ns
NSC	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	$P<0.001$ $R^2=0.556$	-	-	-	-	-	-	-

Table 6.4 Ranking of different models including measured nutritional and physical parameters using model selection (second order Akaike's information criteria, AIC_c). Akaike weights (w_i) indicate the probability a given model has to be the best among the considered set of models. All models were also tested using logistic regression (right).

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

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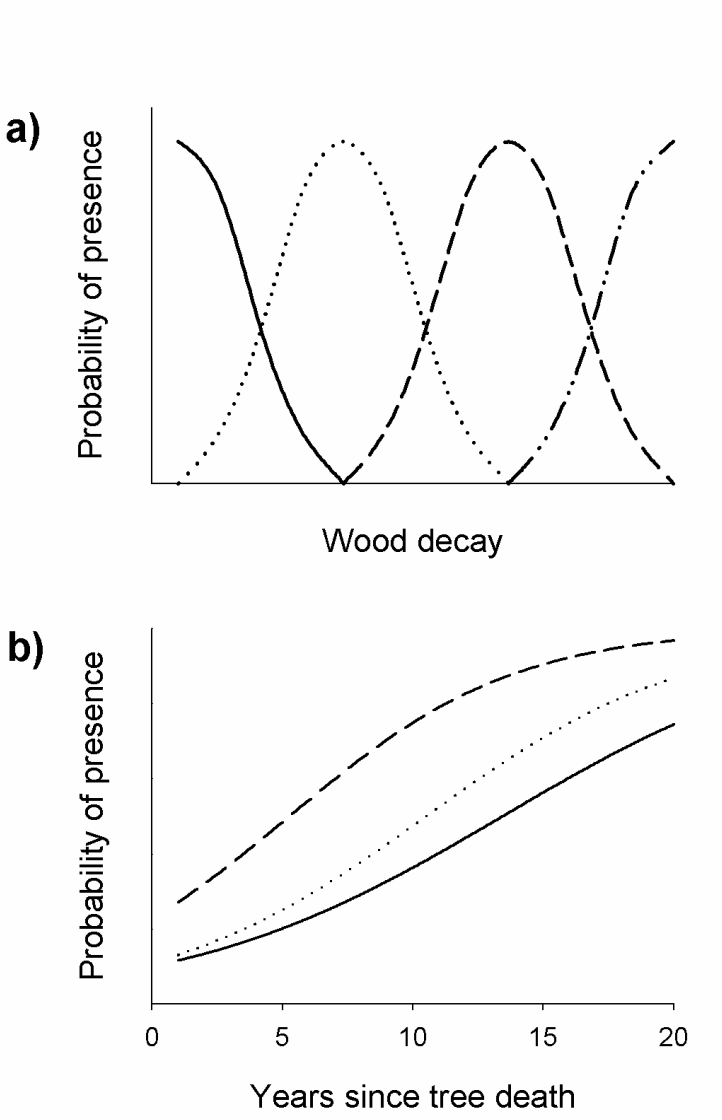
a)
Probability of presence
Wood decay
b)
Probability of presence
0
5
10
15
20
Years since tree death

Figure 6.1

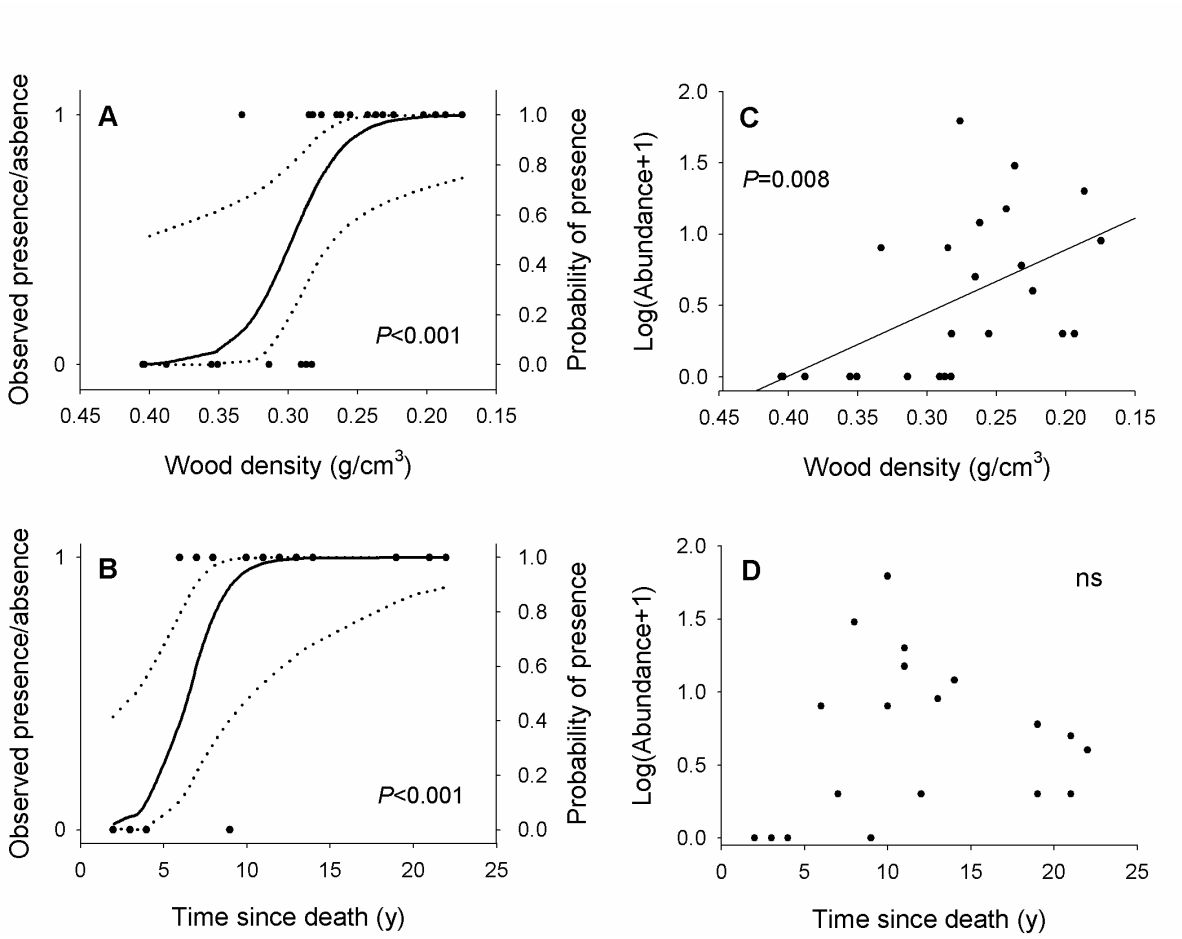
A
Observed presence/asbence
Probability of presence
P<0.001
Wood density (g/cm3)
B
Observed presence/absence
Probability of presence
P<0.001
Time since death (y)
C
P=0.008
Log(Abundance+1)
Wood density (g/cm3)
D
ns
Log(Abundance+1)
Time since death (y)

Figure 6.2

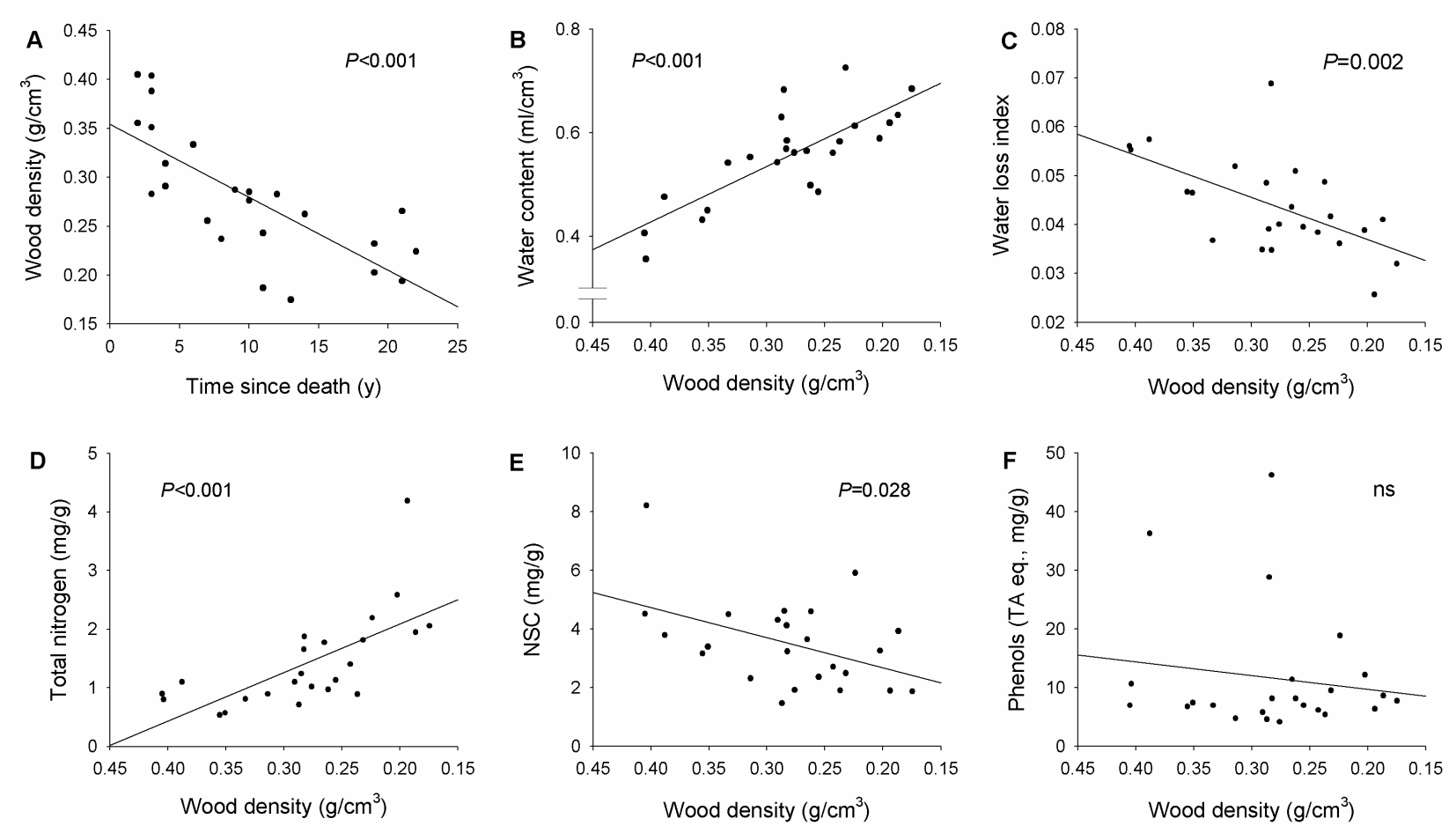
A
Wood density (g/cm3)
P<0.001
Time since death (y)
B
Water content (ml/cm3)
P<0.001
Wood density (g/cm3)
C
Water loss index
P=0.002
Wood density (g/cm3)
D
Total nitrogen (mg/g)
P<0.001
Wood density (g/cm3)
E
NSC (mg/g)
P=0.028
Wood density (g/cm3)
F
Phenols (TA eq., mg/g)
ns
Wood density (g/cm3)

Figure 6.3

7. High within-snag variability in decay and substrate selection by larvae restrict the importance of oviposition site in aspen-feeding saprophagous beetles (Coleoptera: Cerambycidae).

Michel Saint-Germain[1,2], Christopher M. Buddle[1] and Pierre Drapeau[2]

[1]Department of Natural Resource Sciences, McGill University, 21111 Lakeshore Road, Saint-Anne-de-Bellevue, Québec, Canada, H9X 3V9

[2]Groupe de Recherche en Écologie Forestière interuniversitaire, Département des sciences biologiques, Université du Québec à Montréal, CP 8888, succ. Centre-ville, Montréal, Québec, Canada, H3C 3P8

7.1 Preface

In chapter 6, dead-host cerambycid species occurrence was significantly related to several nutritional and physical parameters, but model selection indicated that snag age alone, which received much higher support, was the best predictor of insect occurrence. None of the measured factors were thus identified as being a basis for active selection between potential hosts. Whole snags are usually considered as the appropriate scale to study host-selection behaviour of these insects, which are parasitic, and thus restricted to a single host in immature stages. However, we observed during dissection significant within-snag variability in the extant of decay; this suggests that important mechanisms may take place at scales smaller than the one previously studied for this group of insects. In chapter 7, I first described the extant of within-snag variability in decay for snags of middle to late-decay classes and looked at larva distribution to determine if larvae were able to select specific substrate types. One important assumption of optimality models regarding host selection is that the oviposition site should be the **predominant** factor determining subsequent larval performance. However, if substrate quality varies significantly within the host, and if larvae do select specific substrate types in variable hosts, it violates the aforementioned assumption and may explain the lack of active selection suggested in chapter 6 for species that oviposit in dead hosts. Insect occurrence patterns have never been investigated before at that scale, and this whole paper, including the hypothesis presented, the methodology used and the results obtained, can be considered as original contributions to the field.

7.2 **Abstract**

Predicting host-selection of ovipositing insects has proven to be difficult, as hosts predicted as optimal for offspring performance are often rejected in experimental tests. In parasitic species, i.e., species completing their development within a single host, oviposition site is assumed to be the most determinant factor in offspring performance. However, we hypothesized that in highly variable host material movement by the larvae could decrease significantly the impact of the oviposition site, and selection of particular substrate types within single hosts by larvae could represent a shift of responsibility from the ovipositing mother onto the offspring. In this study, we first described within-host variability in substrate quality in standing dead aspen, and tested whether wood-boring larvae showed preference for specific decay types. For 24 snags, we assessed within-host variability by producing wood density profiles. We then collected larvae to which we attributed a density value by sampling wood around their galleries. Ratios of available and used substrate types were then compared using compositional analysis. Substantial witin-snag variation was observed in wood density. Larvae of Cerambycidae (Coleoptera) showed preference for the 0.274-0.375 g/cm^3 wood density class, and avoided highly decayed wood. High within-host variability and apparent selection of specific substrate types by larvae suggest that oviposition site may not be the predominant influence in offspring performance for aspen-feeding wood-borers. These observations could explain weak between-host selection seen in species ovipositing on seasoned dead wood.

Keywords: Cerambycidae, host selection, optimal oviposition, optimality theory, saproxylic insects.

7.3 Introduction

Under the assumption that evolution occurs by natural selection, observed behaviours should be interpreted in terms of the contribution they make to the individual's inclusive fitness (Pianka 1976, Maynard Smith 1978). Based on this conception of natural selection, optimization models are used to produce hypotheses about what should be optimal behaviours, whether it concerns food choice, mate choice, etc. (Maynard Smith 1978, Parker and Maynard Smith 1990). Such an approach has had tremendous success in some areas, for example in prey selection models, in which experimental tests usually confirm the predictions made (Stephen and Krebs 1986). However, in some other aspects of behaviour, results are generally not as convincing. In insects, one of such aspect is host-selection behaviour of ovipositing insects, in which females select the diet of their offspring rather than their own (Thompson 1988, Mayhew 2001). In such cases, the female is expected to maximize its fitness by preferentially selecting highly suitable hosts, on which its offspring will perform best (oviposition-preference-offspring-performance hypothesis, Jaenike 1978). However, in experimental tests, ovipositing females frequently reject hosts which were predicted to be the most appropriate for their offspring (Williams 1983, Courtney and Kibota 1989, Mayhew 1997, Dormont and Roques 2001, Digweed 2006).

Different mechanisms can cause such discrepancies between predicted and observed host choice. Mayhew (2001) summarized these mechanisms in three broad categories: theory inadequacy, data inadequacy, or situations in which behaviour truly makes little adaptive sense. The latter case usually consists of situations in which there are severe physical and

physiological constraints, or involving a novel host. Data inadequacy can be caused by laboratory experimental conditions which are not representative of those encountered under field conditions. Theory inadequacy arises frequently when underlying assumptions of optimality models are violated. An example of theory inadequacy was seen in the leafminer *Chromatomyia nigra* (Meigen) (Diptera: Agromyzidae), in which oviposition preference was correlated with the performance of the adult rather than that of the offspring (Scheirs *et al*. 2000). Data showed that poor host choice for offspring was the best strategy to maximize female realized fecundity by increasing the number of eggs laid, and thus led the authors to suggest that optimal foraging theory should be integrated to optimal oviposition theory when studying plant-insect relationships (Scheirs and De Bruyn 2002; Scheirs *et al*. 2004).

Although insects feeding on dead plant material, such as dead wood, do not necessarily face the same constraints as 'green' phytophagous insects do, some important nutritional and physical parameters do vary significantly along the decay gradient and host choice should thus affect offspring performance. Parameters such as nitrogen concentration and moisture content have been shown both to affect the performance and survival of larvae developing in dead wood (Hosking and Hutcheson 1979, Chararas 1981, Shibata 1998) and to vary significantly between decay classes (Lambert *et al*. 1980, Alban and Pastor 1993). However, we have shown in chapter 5 and 6 that saproxylic cerambycids *Anthophylax attenuatus* (Haldeman) and *Bellamira scalaris* (Say) (Coleoptera: Cerambycidae) are found mostly hthroughout snag stages of decay in aspen (*Populus tremuloides* Michaux) with little evidence for active selection beyond the choice of a

deciduous host over a coniferous one. Also, measured nutritional parameters did not emerge as potential determinants of insect occurrence in model selection.

Since adults of saproxylic wood-feeders, at least in Cerambycidae, do not feed on the same material as larvae do (Hanks 1999), optimal foraging theory cannot be invoked in this case. However, observations made during snag dissections suggested theory inadequacy may be responsible for the weak selection observed (see Figure 5.6a and chapter 6). Decay in aspen was highly variable within a single host and larvae were often found in wood of similar stages of decay. In most host selection models concerning parasitic species (i.e., species completing development in a single host, as opposed to grazing species, which move from host to host), oviposition site is expected to be the major influence on larval performance (Thompson 1988, Bernays and Chapman 1994). In cases in which the quality of a single host spatially varies significantly and the larvae is able to move within the host, then the orientation of this movement may have a bigger impact on performance than oviposition site *per se*. If larvae can discriminate between poor and good substrate and orient their movement accordingly, then this could be considered a significant shift in host-choice responsibility from the ovipositing mother onto its offspring, and the actual oviposition site would not be in such a context the major influence on offspring performance. In such situations, host selection by the ovipositing female according to the overall decay stage of a snag thus becomes less determinant.

In this study, we described within-snag variability in decay for standing dead aspen and tested whether larvae of two cerambycid species, *A. attenuatus* and *B. scalaris*, selected specific types of wood when feeding and excavating galleries within these snags. We

characterized the variability of decay in 24 snags by producing wood density profiles for each. We then collected larvae from the same snags through wood dissection, and associated a wood density value to each by taking a wood sample around each larva found. The two distributions were compared to see if these two cerambycid species showed preference for specific classes of decay. Substantial within-host variability in decay would by itself decrease the prevalence of oviposition site in determining offspring performance, and if indeed these two species are able to select specific decay types, then it would represent a significant shift in the responsibility of substrate selection from the mother to her offspring. Both of these factors could explain the unspecific host-selection behaviour seen in wood-boring insects ovipositing on seasoned dead wood of contrasting decay classes.

7.4 Methods

In the context of a larger study (see chapter 5), 3 mature aspen stands were selected across the province of Quebec, Canada (Figure 7.1). A total of 80 snags were selected arbitrarily according to visually-assessed decay classes. Among these snags, 24 were selected from middle to late decay classes for this study, 12 from the Abitibi site (48° 26' N, 79° 24' W), and 6 each from the Chauvin (48° 26' N, 70° 05' W) and Oka (45° 29' N, 74° 01' W) sites (see Table 1 for description of snags). Snags were felled in late summer 2005, and 1-m sections were taken between 0.5 and 1.5 m from the base. Each 1-m section was divided into three sub-sections. Four ~4-cm thick disks were taken, one from each sub-section plus one at the far end of the 1-m section, to be used in measuring wood

decay variability. Each of these disks was cut down to pieces (average volume of 8.29 cm^3), of which 40 were selected randomly, for a total of 160 samples per snag. We then measured the wood density of these samples (dry weight/volume) to quantify wood decay. Volume was measured using water displacement. These measurements were used to produce wood density profiles (Figures 7.2-7.4). The remains of the three sub-sections (about 0.85 m in length per snag) were dissected with axes and hatchets to collect cerambycid larvae. For every larva found, a wood sample was taken around its gallery (average volume of 8.66 cm^3), excluding frass. A wood density value was assigned to each larva using these samples. All larvae were identified to species.

7.4.1 Statistical analysis

We assessed the relationship between diameter at breast height and within-host variability, expressed as standard deviation of wood density, using an analysis of covariance to include any potential site effect. Compositional analysis (Aitchison 1986, Aebischer *et al*. 1993) was used to compare proportions of decay types available to decay types used by larvae. Compositional analysis uses MANOVA-type linear models to compare ratios of habitat types available to ratios of habitat types used. Data are log-ratio transformed to circumvent the non-independence of the ratios designating the different habitat types. Compositional analysis determines the statistical differences and the rank order of differences between habitat types. The wood density gradient was divided into 5 classes for analytical purposes (0.075-0.174; 0.175-0.274; 0.275-0.374; 0.375-0.474; 0.475-0.574 g/cm^3). For each snag the proportions of all wood samples falling in each decay class in terms of wood density were calculated. For the habitat-used proportions,

each larva was considered as 1 replicate with 1 localisation datapoint. Thus, each replicate had an occurrence of 100% in one of the classes and 0% in the four other classes. The limited information contained in data of this nature can be compensated for with a high number of replicates (Aebischer *et al.* 1993), and such a method is commonly used in habitat-use studies (Neu *et al*. 1974). Compositional analyses were performed first separately on each snag that contained at least 6 larvae, as the number of replicates must exceed the number of habitat types considered (Aebischer *et al*. 1993), and then for snags from all sites pooled. Snag-level analyses were performed using only larvae of *Anthophylax attenuatus*, which was dominant numerically, but pooled analyses were performed on both *A. attenuatus* (n=187) and *Bellamira scalaris* (n=37). Compositional analyses were conducted with the software Compos Analysis v5.1 (licence #CompAn-01-063A; Smith Ecology Ltd., Bettws, UK). ANCOVA was done with SPSS 10.0.5 for Windows (SPSS Inc., Chicago, IL, USA).

7.5 Results

Average wood density varied between snags, ranging from 0.205 (O1, Figure 7.3) to 0.430 g/cm^3 (A12, Figure 7.2). Some snags showed unimodal distributions with low variance in wood density (e.g., O5, $\bar{x}$=0.355, s_x=0.042, Figure 7.3), while others had broad distributions (e.g., A3, $\bar{x}$=0.278, s_x=0.111, Figure 7.2). Although diameter and average wood density were not correlated together (P>0.05, not shown), within-host variability of wood decay was significantly higher in snags with larger diameters (Figure

7.5) (whole model $F_{5,23}$=5.57; P=0.0029; effect test for diameter F=8.61; P=0.0089). Site effect and interaction between site and diameter were not significant (P>0.05).

Number of larvae found in each snag varied from 0 (6 snags) to 51 (A7, Table 7.1). When pooled together, *A. attenuatus* and *B. scalaris* represented 98.7% of cerambycid larvae found (224 of 228). The four remaining individuals were not included in the analyses, as all analyses were conducted separately by species. Compositional analysis of distribution of larvae of *A. attenuatus* found in snags from all sites pooled showed preference for the mid-decay class of 0.275-0.374 g/cm^3, which habitat-selected-to-habitat-available ratio was significantly higher then all other wood density classes (Wilk's λ=0.2841; χ^2_4=235.34; P<0.001). Significant differences were also seen between the two highest density classes (0.375-0.474; 0.475-0.574) and the lowest class (0.075-0.174). The latter was the most under-selected. Preferences of *A. attenuatus* are summarized in Table 7.2. Patterns were similar but weaker in *B. scalaris*. The habitat-used-to-habitat-available ratios for all snags and sites combined were significantly different between the 0.275-0.374 (highest) and the 0.075-0.174 and 0.375-0.474 g/cm^3 density classes (Wilk's λ=0.4722; χ^2_4=27.76; P<0.001). Ratios were also different between the 0.475-0.574 class and the 0.075-0.174 and 0.375-0.474 classes. Preferences of *B. scalaris* are summarized in Table 7.3. Differences between habitat availability and habitat used are illustrated on Figure 7.6 for both species.

Only nine snags contained enough larvae of *A. attenuatus* to be analysed separately with compositional analysis, eight in the Abitibi site and one in Chauvin. Eight Abitibi snags

showed significant differences between proportions of habitats used vs. habitats available. In seven out of nine snags, the 0.275-0.374 g/cm^3 wood density class was the most preferred, and was significantly more used than what could be predicted by chance. In most cases usage of the 0.275-0.374 g/cm^3 class was significantly different from the two classes representing lower wood densities (0.075-0.174; 0.175-0.274 g/cm^3). The ranking of the two higher density classes varied between snags (Table 7.1).

7.6 Discussion

The data we collected confirmed that, at least in high diameter aspen snags, the degree of decay as measured by wood density can vary significantly within a single host. In such cases, larvae of both *A. attenuatus* and *B. scalaris* showed significant preference for substrates of specific decay classes. These results confirm our observations and suggest that indeed the oviposition sites chosen by females of these species are not the only, or even predominant, determinant of larval performance.

The within-snag variability of wood density we documented in this study was in some cases higher than the between-snag variability in average density seen in chapter 5 which included aspen snags of all classes of decay as assessed using visual appearance. This variability in wood density should translate into variability in substrate quality, as several studies have showed significant relationships between wood density and nitrogen levels, moisture content and other nutrients which are essential to insect growth and survival (Lambert *et al*. 1980, Alban and Pastor 1993). Also, in chapter 6, wood-borer larvae

occurrence was better explained by wood density alone than by any other measured physical and nutritional explanatory variable. Thus there is in aspen, at least for high diameter snags, a basis for potential within-host selection of specific decay types by wood-boring larvae.

Results from the compositional analyses confirm that larvae of both *A. attenuatus* and *B. scalaris* were found more often in specific decay types than what would be expected by chance (Figure 7.6). The generality of this pattern was confirmed by the fact that similar results were obtained when using both pooled and snag-specific data. The methods used to collect our data give us information about trajectory of the galleries more than about actual wood consumption, i.e., larvae caught during the dissection may have been so while moving through sub-optimal substrate. However, the significantly higher ratios seen for some wood density classes indicate that the larvae spent more time within some decay types for purposes other than movement only, which would have resulted in ratios of habitat used equivalent to ratios of habitat available. Whether this extended period of time is spent feeding on a high-quality substrate or resting in a more favorable environment, this differential time allocation could have a direct influence on growth and/or survival. If this is the case, then the oviposition site is no longer the only determinant of larval performance for these species.

Within-host small-scale variability in quality renders specific host-selection behaviour on the part of the mother less determinant, as movement of the larva, as it excavates its gallery, will expose it to different decay types that probably will have differential effects on larval performance. If larvae can influence the type of substrate on which they will

feed, then there is an effective shift in responsibility from the ovipositing female to its offspring, which will determine by their subsequent behaviour the quality of the substrate they will feed on. If larvae are unable to detect differences in substrate quality, oviposition site still has little influence on larval performance because of the high substrate variability, and in such a context larval performance would rather be determined by random processes. Whether or not wood-boring larvae are able to evaluate substrate quality through gustatory or thigmotactic cues has not been, to our knowledge, investigated. However, such behaviours have been documented in other phytophagous insect groups, especially Lepidoptera (e.g., Panzuto and Albert 1998, Panzuto *et al*. 2002), of which some species can detect concentrations of specific amino acids and non-structural carbohydrates. This decreased impact of highly specific host-selection behaviour when dealing with high within-host variability in substrate quality could explain the patterns of insect occurrence seen in dead aspen, in which the same species occur throughout most snag stages of decay despite variations in host quality.

Mechanisms undelying the preference for the 0.274-0.375 g/cm^3 wood density class seen in *A. attenuatus* and *B. scalaris* are not known. Studies measuring nitrogen levels in dead wood usually show a constant increase through the decay gradient (Lambert *et al*. 1980, Alban and Pastor 1993; Saint-Germain *et al*., chapter 6). Moisture content also varies linearly with decay, and highly decayed wood may provide a more stable environment (see chapter 6). These studies thus suggest that the lower classes of wood density should offer the best substrate for the larvae. However, such studies characterizing changes in nutrient levels during wood decay always consider the entire snag as their sampling unit, and thus do not consider within-snag variability in the extent of decay. Such relationships

between wood density and nutritional and physical parameters have thus been established at a different scale than the one we investigated in the present study. Therefore, we cannot at this point reject any nutritional or physical basis for this apparent preference for the 0.274-0.375 g/cm^3 wood density class for both *A. attenuatus* and *B. scalaris*.

Our data suggest that, in cases in which there is high within-host variability in quality, the assumption of the predominance of the oviposition site in the determination of parasitic species offspring performance may be violated, resulting in an apparent poor host choice at the scale investigated. Dead wood is certainly one of these cases as was demonstrated in this study. In the case of *A. attenuatus* and *B. scalaris*, the within-snag variability observed in wood decay and this possible shift of the responsibility from the ovipositing female onto the offspring could explain the relative unspecificity seen in their host-use patterns in previous studies between different decay classes.

7.7 **Acknowledgements**

We would like to thank E. Bolduc, A. Dechene, D. Lesieur, Z. Sylvain and T. Work for field or laboratory work, and Oka National Park and the Lake Duparquet research and teaching forest for facilitating our work within their boundaries. This project was funded by *Action Concertées - Fonds forestiers* grant (P. Drapeau, C. Buddle and coll.) and a new researcher grant (C. Buddle) from the *Fonds Québécois de la Recherche sur la Nature et les Technologies* (FQRNT), by a Discovery grant to C. Buddle from the Natural Science and Engineering Research Council of Canada (NSERC), and by the partners of the NSERC industrial chair in sustainable forest management of Université du Québec en Abitibi-Témiscamingue (UQAT) and Université du Québec à Montréal (UQAM).

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Table 7.1 For snags sampled in the three sites, diameter at breast height, average density ±1 SD, number of larvae collected for cerambycid *Anthophylax attenuatus* and *Bellamira scalaris*, and rank of preference for the different wood density classes for *A. attenuatus*, as determined by compositional analysis. >>> denotes a significant difference between two consecutively ranked classes. Letters indicate significant differences between treatments.

Site	Snag	Diameter (cm)	Average density	*B. scalaris*	*A. attenuatus.*	Preferences of *A. attenuatus*
Abitibi	A1	18.3	0.219 ± 0.061	0	10	.175-.274**a**>.275-.374**a**>>>.075-.174**b**
	A2	18.7	0.275 ± 0.045	3	0	
	A3	40.8	0.278 ± 0.111	0	25	.275-.374**a**>.375-.474**a**>.175-.274**ab**>.075-.174**b**
	A4	18.7	0.282 ± 0.033	2	37	.275-.374**a**>>>.375-.474**b**>.075-.174**b**>>>.175-.274**c**
	A5	19.9	0.293 ± 0.085	1	6	.275-.374**ac**>.475-.574**a**>.175-.274**abc**>.075-.174**c**>>>.375-.474**bc**
	A6	16.9	0.296 ± 0.038	0	29	.275-.374**a**>>>.375-.474**b**>>>.175-.274**c**
	A7	22.6	0.324 ± 0.089	2	49	.275-.374**ab**>.475-.574**a**>.375-.474**abc**>.175-.274**bc**>.075-.174**c**
	A8	21.3	0.311 ± 0.077	0	10	.275-.374**a**>.375-.474**a**>>>.175-.274**b**
	A9	19.8	0.315 ± 0.058	0	6	.275-.374**ab**>.375-.474**a**>.075-.174**a**>>>.175-.274**b**
	A10	19.1	0.341 ± 0.065	0	0	
	A11	21.8	0.409 ± 0.051	0	0	
	A12	19.7	0.430 ± 0.068	0	0	
Oka	O1	23.4	0.205 ± 0.106	0	2	
	O2	21.7	0.211 ± 0.054	1	0	
	O3	17.6	0.269 ± 0.044	3	3	
	O4	19.0	0.315 ± 0.055	0	0	
	O5	15.9	0.355 ± 0.042	0	0	
	O6	19.9	0.364 ± 0.062	0	2	
Chauvin	C1	18.8	0.271 ± 0.084	5	0	
	C2	24.0	0.285 ± 0.094	11	0	
	C3	21.7	0.294 ± 0.089	4	0	
	C4	28.0	0.297 ± 0.092	2	6	.175-.274**a**>.275-.374**a**>.375-.474**a**
	C5	26.8	0.317 ± 0.078	0	0	
	C6	23.9	0.346 ± 0.057	3	0	

Table 7.2 Ranking matrix for preference of wood density classes in *Anthophylax attenuatus*, all snags combined, based on comparison of wood density values in which larvae were found to proportions of wood density characterization samples taken for each snag. +++ or --- denotes a $P<0.01$; ++ or – denotes a $P<0.05$.

	Wood density classes					
	.075-.174	**.175-.274**	**.275-.374**	**.375-.474**	**.475-.574**	**Rank**
.075-.174		-	---	---	---	0
.175-.274	+		---	-	-	1
.275-.374	+++	+++		+++	+++	4
.375-.474	+++	+	---		-	2
.475-.574	+++	+	---	+		3

Table 7.3 Ranking matrix for preference of wood density classes in *Bellamira scalaris*, all snags combined, based on comparison of wood density values in which larvae were found to proportions of wood density characterization samples taken for each snag. +++ or --- denotes a $P<0.01$; ++ or – denotes a $P<0.05$.

	Wood density classes					
	.075-.174	**.175-.274**	**.275-.374**	**.375-.474**	**.475-.574**	**Rank**
.075-.174		-	---	+	---	1
.175-.274	+		-	+	+	3
.275-.374	+++	+		+++	+	4
.375-.474	-	-	---		---	0
.475-.574	+++	-	-	+++		2

List of figures

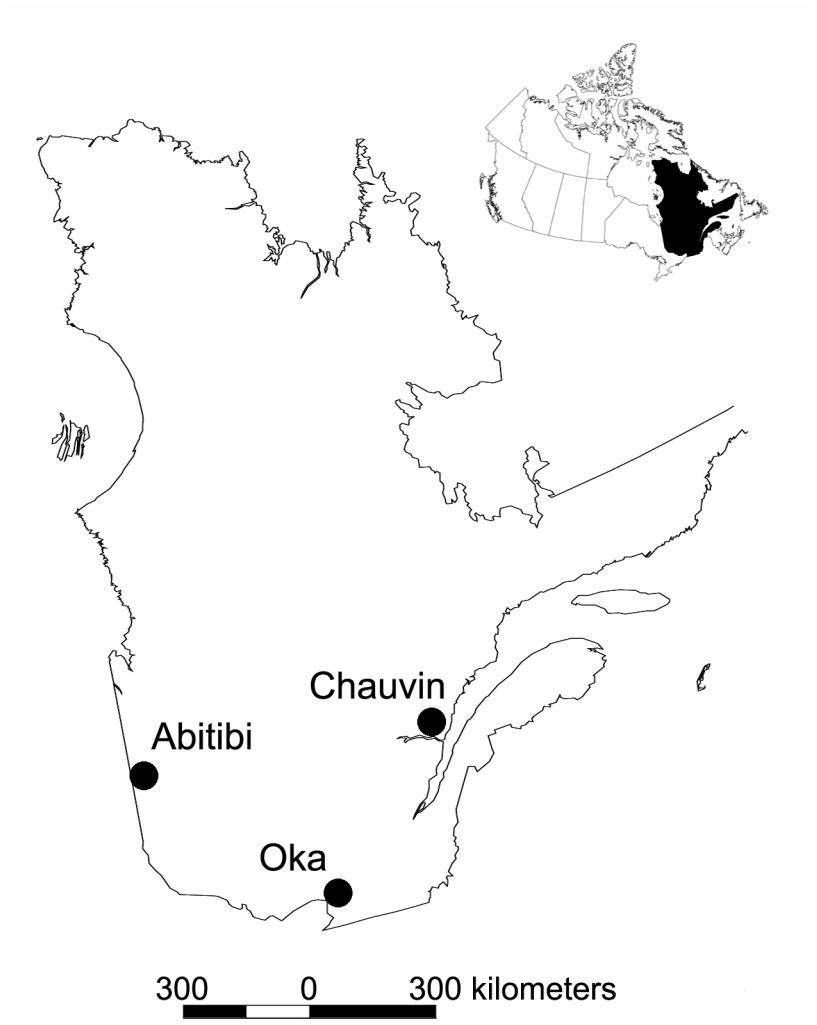

Figure 7.1

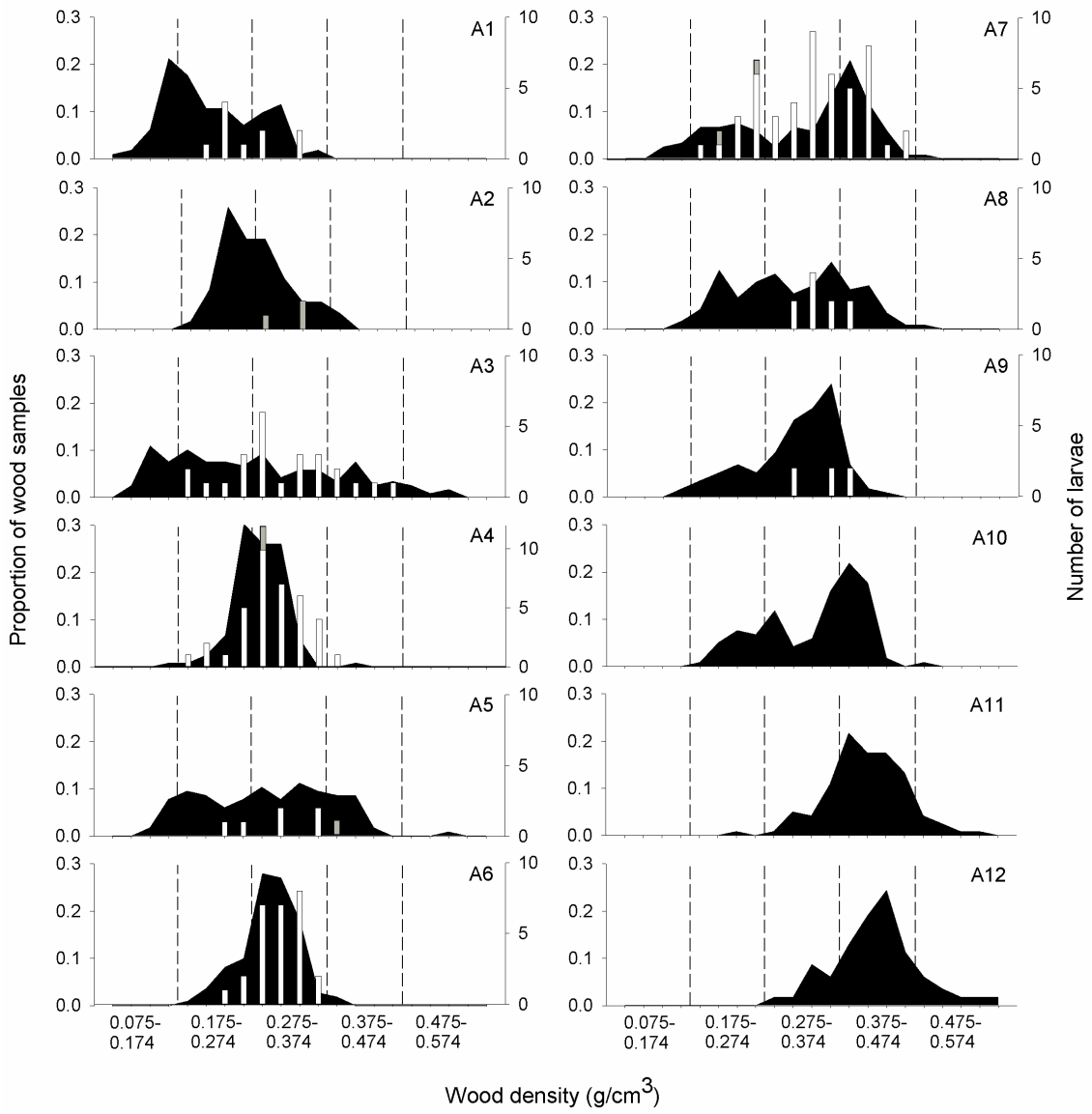
A1
A2
A3
A4
A5
A6
A7
A8
A9
A10
A11
A12
Proportion of wood samples
Number of larvae
0.0
0.1
0.2
0.3
0
5
10
0.075-
0.174
0.175-
0.274
0.275-
0.374
0.375-
0.474
0.475-
0.574
Wood density (g/cm3)

Figure 7.2

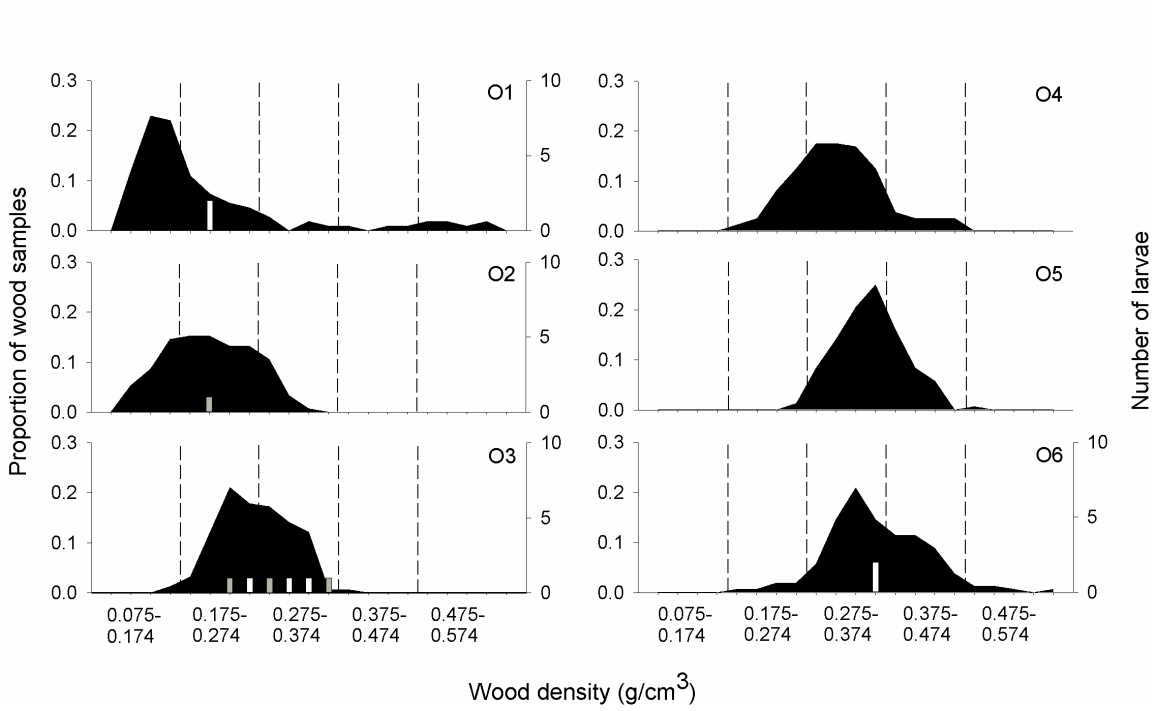
O1
O2
O3
O4
O5
O6
Proportion of wood samples
Number of larvae
0.0
0.1
0.2
0.3
0
5
10
0.075-
0.174
0.175-
0.274
0.275-
0.374
0.375-
0.474
0.475-
0.574
Wood density (g/cm3)

Figure 7.3

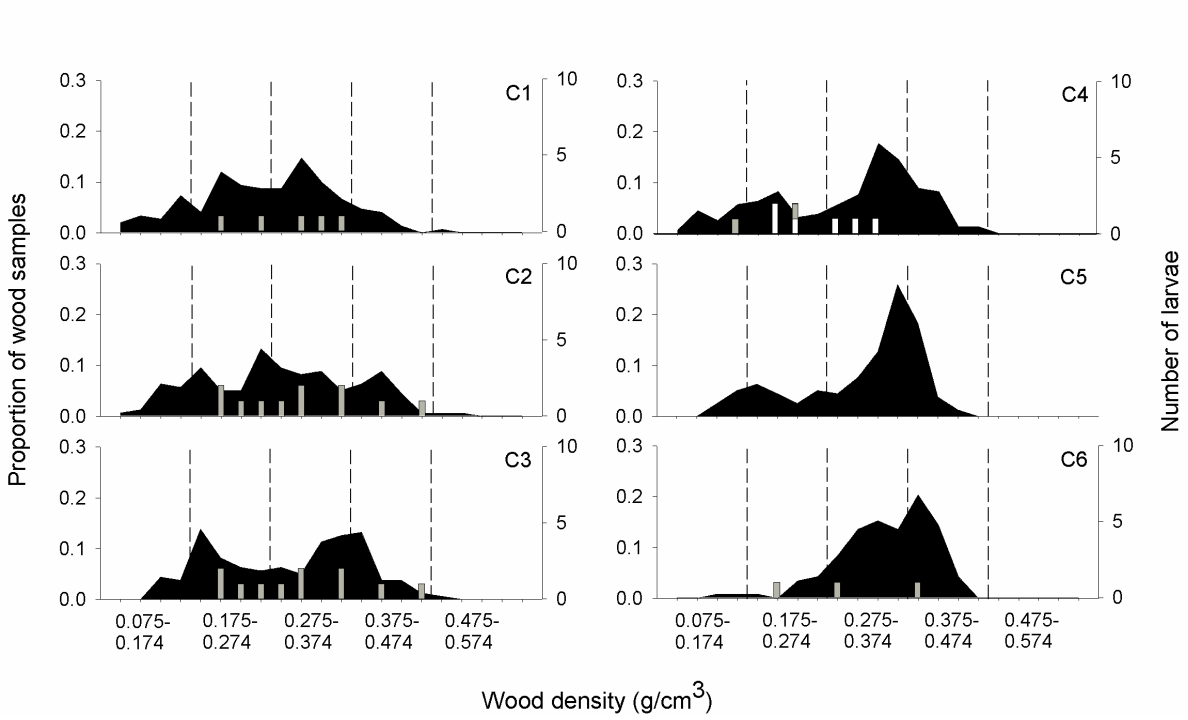
C1
C2
C3
C4
C5
C6
Proportion of wood samples
Number of larvae
0.0
0.1
0.2
0.3
0
5
10
0.075-
0.174
0.175-
0.274
0.275-
0.374
0.375-
0.474
0.475-
0.574
Wood density (g/cm3)

Figure 7.4

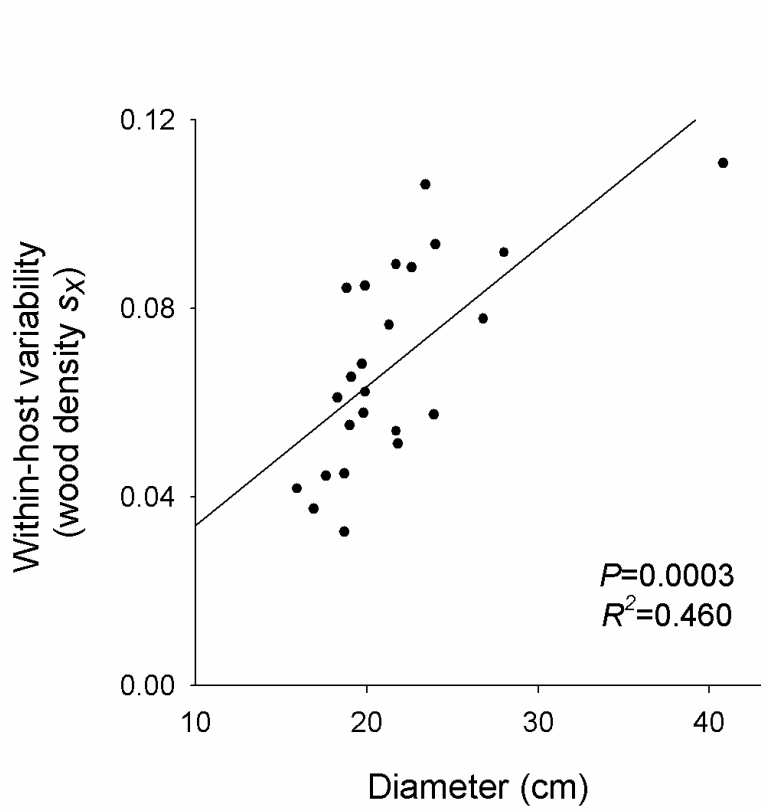
0.12
0.08
0.04
0.00
10
20
30
40
Within-host variability
(wood density s_X)
Diameter (cm)
P=0.0003
R^2=0.460

Figure 7.5

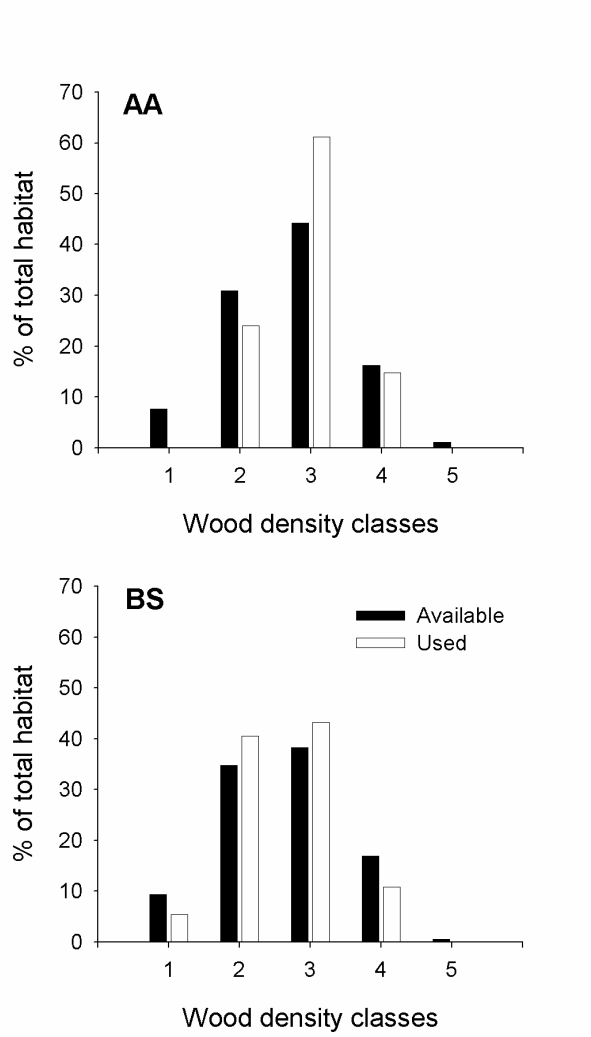
AA
% of total habitat
70
60
50
40
30
20
10
0
1
2
3
4
5
Wood density classes
BS
Available
Used
% of total habitat
70
60
50
40
30
20
10
0
1
2
3
4
5
Wood density classes

Figure 7.6

8. Summary and conclusions

Research presented in this thesis showed sharp differences in colonization and community dynamics between black spruce and aspen, and these results were consistent over moderately large geographic areas. The exact mechanisms driving host-use patterns were not formally identified, especially in aspen, but results from model selection suggest that temporal autocorrelative neutral mechanisms may be at play. Also, the use of novel sampling techniques, especially snag dissection, allowed for an unprecedented characterization of wood-feeding saproxylic assemblages with a degree of precision not possible with more common and traditional sampling techniques.

Chapter 3, comparing assemblages landing on different types of snags including old and fresh ones of five tree species and stovepipe controls, showed that pre-landing mechanisms were less important than expected from what is seen in the literature in the overall host-selection behaviour of saproxylic wood-feeding species. Similar assemblages were captured on fresh and old snags of both coniferous and deciduous host species, and even more significantly, on black stovepipe controls. The curculionid *Pissodes fiskei* Hopkins was the only taxon to show some degree of pre-landing selection, occurring more often on coniferous snags. These results indicate that, at the tree level, volatiles do not have a determining influence on potential hosts landed on by beetles for post-landing appraisal for a majority of species, regardless of their trophic guilds. Results from chapter 4 confirm these observations, as random landing seems to be the primary mechanism of host location at close range, especially in Cerambycidae. However, chapter 4 also shows that volatiles are useful at longer range (stand level) by dispersing beetles to orient

towards habitat patches potentially containing suitable host(s). The use of volatiles is thus scale-dependent in saproxylic wood-feeders. These chapters contribute to the understanding of primary attraction in secondary insects, because much of the literature concerning these behaviours has been limited to primary species of scolytids.

Dissection data showed in chapters 5 and 6 opposite occurrence patterns along the decay gradient in black spruce and aspen. Stressed-host species were more abundant and diverse in black spruce, dominated by bark beetles *Polygraphus rufipennis* (Kirby) and *Ips latidens* (LeConte) and cerambycid *Acmaeops proteus* (Kirby). Dead-host cerambycid species *Cosmosalia chrysocoma* (Kirby) and *Stictoleptura canadensis* (Olivier) were never abundant and were absent from most sites. In aspen, some ambrosia beetles were present in early decay stages, but widespread dead-host cerambycids *Anthophylax attenuatus* (Haldeman) and *Bellamira scalaris* (Say) dominated the assemblages. Several nutritional (nitrogen) and physical (density, water content) parameters were significantly correlated with insect occurrence in aspen (chapter 6), but all were strongly correlated together and with snag age, which was selected as the best explanatory model using Akaike's information criteria. Support can be found in our results for both active selection and neutral mechanisms as processes underlying the concentration of host-use in middle to late stages of decay in aspen. However, the prevalence of snag age in model selection suggests either that temporal autocorrelation in probability of occurrence within single snags is responsible for this pattern, or that another parameter not measured in our study is more strongly correlated with insect occurrence. The temporal autocorrelation in probability of occurrence could be explained by long larval development periods and a

tendency on the part of the adults to oviposit on the host from which they emerged, a behaviour that has been observed in dead-host species.

Chapter 7 examined patterns of occurrence of wood-boring insects at a scale rarely or never investigated, within individual trees. During dissection sampling, we observed a high degree of variability within single snags of aspen, and a tendency in larvae to be associated with specific types of decay. These observations led me to state the hypothesis that in highly-variable hosts, larvae could be able to select specific types of substrate more advantageous to them. My results showed significant levels of selection, as classes of density near the middle of the gradient were generally favored by larvae. These results have important implications in our understanding of the host-selection behaviour of the ovipositing female, as high within-host variability in quality and selection by the larvae necessarily decreases the impact of the original oviposition site on subsequent larval performance. It violates an assumption of optimal oviposition models in which the site of oviposition should be the predominant determinant of larval success (Mayhew 2001). This active selection on the part of the larvae could thus explain weaker selection patterns seen at a larger scale in chapter 6.

By directly sampling larvae, the predominant life stage of wood-feeding Coleoptera and the one most dependent on specific habitat characteristics, snag dissection allowed for an unprecedented characterization of assemblages of these insects. Until now, knowledge on host-use patterns of these insects mainly consisted of scattered anecdotal observations or unreliable data collected using suboptimal sampling methods. The data collected through this thesis represent a considerable advancement in our understanding of host-use patterns

and dynamics of saproxylic wood-feeding species, a group on which limited knowledge is available in peer-reviewed literature except for some specific contexts (e.g., recent burns; Parmalee 1941, Gardiner 1957, Liu *et al*. 1991, Saint-Germain *et al.* 2004c). Opposite host-use patterns seen in black spruce and aspen are interesting in themselves, but also hint the possibility of a larger coniferous/deciduous tree species dichotomy in host-use dymanics. Further research will be needed to establish whether it is the case or not. Such opposite patterns can also have important implications for mitigation efforts implemented in forest management practices, as the dynamics and availability through space and time of fresh vs. old snags may not vary similarly under different management strategies.

My work demonstrated that snag dissection is an effective sampling method in itself. This method can be used to describe assemblages in the context of biodiversity studies, but can also yield data on density and occurrence patterns which should be usable in other types of studies, e.g., regarding response of these insects to fragmentation, disturbances or different levels of host availability. However, limitations still exist regarding larval taxonomy for most beetle groups, especially for species feeding on deciduous trees. In past decades, extensive rearing efforts were necessary to establish definite links between adult and larval forms. Since then, the description of larval stages has been made easier by the emergence of tools based on the use of DNA (e.g., Miller *et al*. 2005), and future efforts should focus on resolving these taxonomical shortcomings.

Several chapters of this thesis emphasized the fact that natural phenomenons are often scale-dependent, and that the scale at which the behaviour of an organism is studied is likely to deeply affect our understanding of it. In both broader sections of this thesis,

dealing respectively with pre-landing host-selection mechanisms and post-selection host-use patterns, the inclusion of multiple scales in the sampling designs allowed for a more insightful interpretation of the observed patters. Chapter 3 by itself suggested that no pre-landing host-selection occurs in most saproxylic groups, but the inclusion of a larger scale in chapter 4 demonstrated that the usability of host-produced volatiles by these insects is highly scale-dependent. Chapter 5 and 6 showed similar assemblages of aspen-feeding dead-host cerambycid species almost throughout the entire studied decay gradient, suggesting only weak or inexistant associations between the insect and specific substrate types. However, the within-host characterization of larval occurrence patterns in aspen presented in chapter 7 demonstrated a significant preference for middle classes of decay; we can legitimately hypothesize that the presence of those insect species over the entire decay gradient at snag scale may be explained by the high within-snag variability in the degree of decay observed in aspen.

My thesis did not bring definite answers regarding the processes creating observed host-use patterns of saproxylic wood-feeders along the decay gradient. However, it showed that these processes can differ significantly between host tree species, and it also introduced specific neutral processes as potential driving mechanisms. The importance of neutral processes are demonstrated in chapter 3 and 4 for pre-landing host-selection behaviour (i.e., random landing), while analyses presented in chapters 6 and 7 give support to such processes in post-landing steps of host-selection. Community and behavioural ecology have been dominated in the last decades by a somewhat biased ultra-adaptationist conception of nature (Gould and Lewontin 1979). However, the emergence of neutral theories of biodiversity introduced by Stephen P. Hubbell and others (Hubbell

1997, Bell 2000, 2001, Hubbell 2001) should be seen as a reminder that in several cases simple neutral alternatives exist to hypotheses involving complex and highly specific adaptations, however fascinating they might seem. My thesis shows that concurrent support can be found for both types of mechanisms; further research will be needed to establish which one of these mechanisms, if not both, play the leading role in shaping saproxylic Coleoptera assemblages.

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10. **Appendices**

10.1 Landing rates (individuals/m^2/week) of beetles by family collected in chapter 4.

Site	Diameter (cm)	Distance from center (m)	Orientation (°)	Alleculidae	Anobiidae	Buprestidae	Cantharidae	Carabidaae	Cephaloidae	Cerambycidae	Chrysomelidae	Cleridae	Coccinelidae	Cryptophagidae	Cucujidae	Curculionidae	Elateridae
CB1-1	27.7	4.5	110				5.79			0.48					0.48	1.93	5.79
CB1-2	35	8.15	71				0.97	0.48					0.97			0.48	6.76
CB1-3	25.1	2.21	21	0.97			4.34			0.97			1.93			0.48	7.24
CB1-4	25.6	6.1	34				6.76										6.76
CB1-5	25.4	10.35	0				5.79									0.97	7.72
CB1-6	25.5	4.25	262				7.72			0.48			0.97			0.48	5.79
CB1-7	23.5	8.8	310				4.83					0.48	1.93				8.21
CB1-8	33.5	2.38	188				3.38	0.48		0.97						0.97	18.8
CB1-9	25.9	5.6	170				4.83			0.48						0.48	9.17
CB1-10	23.3	12.2	180		0.48		6.76						1.45			0.97	10.1
CB1-11	21	0	-	0.48			3.38			1.45		0.48	2.41			0.97	10.1
CB2-1	28.8	2.58	131	0.48			3.38									0.48	3.86
CB2-2	24.4	3.6	96		0.48		1.93			0.97			0.48		0.48		5.79
CB2-3	28.8	10.65	64		0.48		0.48										3.38
CB2-4	26.5	2.9	356				1.45			0.48		0.97	0.97			1.45	2.41
CB2-5	16	4.87	10	0.48			2.41			0.48			0.97			1.45	5.31
CB2-6	21	11.6	10				15.6					1.56	6.22		1.56		10.9
CB2-7	20.4	3.22	282				1.93			1.45			1.45			0.48	4.34
CB2-8	23.5	9.3	284		0.48		2.90				0.48		1.45			0.97	3.86
CB2-9	25.5	5.05	186				1.45		0.48	0.48		0.48	0.97				4.34
CB2-10	17.1	9.5	180			0.48	4.34			0.97			0.48				6.76
CB2-11	21.4	0	-				2.41	0.48		1.93	0.97	0.97				2.90	7.24
CB3-1	20.4	3.8	43				2.90	0.48								0.48	7.24
CB3-2	19.2	5.65	111	0.97			4.83	0.48	0.97				0.48			0.48	7.72

10.1 (Continued)

Site	Endomychidae	Erotylidae	Eucinetidae	Lampyridae	Lathridiidae	Leiodidae	Lycidae	Melandryidae	Melyridae	Mordellidae	Nitidulidae	Pyrochroidae	Scolytidae	Scraptidae	Staphylinidae	Throscidae	Others
CB1-1	1.45		0.48		1.93	0.97	0.48	2.41	0.48	1.93	0.48		1.45		1.45		1.93
CB1-2	1.45		1.45	8.69	3.86	0.97	1.45	2.41	0.97	0.97			0.48		4.83	0.48	2.41
CB1-3	0.97		0.48	0.97	7.24	1.93		2.9	0.97	0.97			0.48		0.97		3.86
CB1-4	3.38		1.45		0.97	0.97	0.48	1.45	2.41	0.48	0.48			0.48	3.86	1.45	5.79
CB1-5	1.93		1.93	1.45	4.83			0.48	0.97	0.48			0.97		3.86	0.48	3.86
CB1-6	1.45	0.48	0.48	0.97	5.31	1.45	0.97	2.41	0.48	0.97	0.97		0.48	1.45	4.83	0.97	1.45
CB1-7	2.41		0.97		4.83	0.48	0.97	1.45	2.9	0.97	1.45			0.48	3.38	0.97	6.28
CB1-8	0.97			3.38	0.97			1.93	0.48	0.48	0.48		2.41	0.97	1.93		4.34
CB1-9			0.48		2.9			1.93	1.45	0.97				1.45			0.48
CB1-10	1.93		0.48	0.48	11.6	0.48	0.48	0.97	1.45	0.48				2.41	1.45	0.97	4.34
CB1-11	1.93		0.48	1.93	10.6	3.86	0.48	9.17	0.48	0.97	5.79		3.86		12.1		3.38
CB2-1			0.97	4.34	7.24	1.45	0.48	3.86	6.76	1.93	1.45		3.38	0.48	2.41	0.48	0.97
CB2-2	0.48		0.48	0.97	9.17	0.97	1.45	1.93	1.45	0.48	1.45		0.97		3.86	0.48	1.45
CB2-3			0.48	5.79	5.31	0.97		1.93			0.97		0.97	0.48	0.97		3.86
CB2-4	0.48		0.48	4.34	3.86	0.48		1.45							3.38	0.48	0.48
CB2-5			2.9	3.38	7.72	0.48		2.9	0.97		0.48			1.93	3.38	0.97	2.41
CB2-6			1.56	1.56	18.7		1.56	10.9	7.78	1.56	1.56		1.56	3.11		1.56	
CB2-7	1.45		1.45	10.1	9.17	1.45	0.97	2.9	0.48		0.48			0.97	2.41	1.45	2.41
CB2-8	0.97		2.41	4.83	1.93	0.48		3.38	1.93	1.45					6.76		2.9
CB2-9	1.45		0.48	9.66	6.76			4.83	1.93				0.48		2.9	0.48	3.86
CB2-10	3.38		2.41	4.83	9.17	0.97	1.93	1.93	2.9	1.93	2.41		0.48	1.93	3.38	3.86	2.9
CB2-11	0.48		1.45	5.31	9.17	0.97	2.41	29.4	1.93	1.45	3.86		4.83	1.93	9.17	0.97	1.45
CB3-1		0.48	0.97	3.38	3.86		0.48	4.34	2.41	0.48				1.45	0.97	0.48	0.97
CB3-2	1.93	0.48	0.48	2.41	4.34		0.97	3.38	3.38	1.45				4.34	1.45	0.48	3.38

10.1 (Continued)

Site	Diameter (cm)	Distance from center (m)	Orientation (°)	Alleculidae	Anobiidae	Buprestidae	Cantharidae	Carabidaae	Cephaloidae	Cerambycidae	Chrysomelidae	Cleridae	Coccinelidae	Cryptophagidae	Cucujidae	Curculionidae	Elateridae
CB3-3	21.2	10.2	60		0.48		7.24						0.97		0.48		7.24
CB3-4	25.2	4.12	310				3.38				0.48		0.48				7.24
CB3-5	22.2	10.2	346				2.90					0.48	0.97				2.90
CB3-6	15.6	2.19	188	0.48			7.24					0.97	1.93		0.48	1.45	5.79
CB3-7	20.3	5.42	272	2.41			5.31		0.48				0.48			0.48	7.72
CB3-8	21.1	10.7	254	0.48			1.93			0.48	0.48					0.97	6.76
CB3-9	22	2.43	161	1.93			1.45	0.48		0.48			0.48			0.48	4.83
CB3-10	17.6	9.05	185				0.70					0.70	0.70				2.80
CB3-11	22.3	0	-				0.97			0.97	0.48	1.93	0.48			0.48	4.34
MK1-1	25.1	5.4	100	0.97	0.48		13.0			0.48		0.48	0.97				9.66
MK1-2	26.4	5.5	78				12.1			0.48		0.48	3.86			0.97	9.66
MK1-3	27.5	10.6	44	1.56			28.0	1.56		3.11		1.56					14.0
MK1-4	20.8	2.8	332	0.97	0.48		9.17	0.48			0.48	0.48	1.93			0.97	6.76
MK1-5	31.9	8.42	336	0.97	0.97		16.4						0.97			0.97	6.28
MK1-6	23.1	3.44	194				12.1					0.97	0.97			0.97	4.83
MK1-7	24.2	10.35	245		0.48		10.1			0.48			3.38				4.83
MK1-8	23.5	1.3	188				8.69	0.48		0.97		3.38	4.34			0.97	12.1
MK1-9	25.9	6.1	176	0.48		0.48	13.0						2.41		0.48	1.45	6.76
MK1-10	23.8	10.5	181	1.45	0.48		13.5	0.48				0.48	2.90			0.48	2.90
MK1-11	22.3	0	-				8.21	0.48		0.97		0.97	2.41		0.48	3.38	7.72
MK2-1	28.4	2.17	125	1.45			9.66					0.48	2.41			1.45	12.1
MK2-2	26.5	9.14	71	1.45			3.38						4.83		0.48		11.1
MK2-3	26.9	3.38	18				6.76						0.97			0.48	8.69
MK2-4	22.7	9.8	29	1.93			8.21	0.48		0.97	1.45		1.45		0.48	0.48	4.83
MK2-5	26	4	259	0.97			2.90				0.48				0.48	0.48	5.79
MK2-6	26.7	7.75	268				3.38										4.83
MK2-7	32.7	1.7	294		0.48		4.34			0.48		0.97	1.45		0.48	0.48	7.72

10.1 (Continued)

Site	Endomychidae	Erotylidae	Eucinetidae	Lampyridae	Lathridiidae	Leiodidae	Lycidae	Melandryidae	Melyridae	Mordellidae	Nitidulidae	Pyrochroidae	Scolytidae	Scraptidae	Staphylinidae	Throscidae	Others
CB3-3	0.97		1.45	3.86	4.83			1.93	2.9		0.97			0.48	3.86		2.9
CB3-4	0.48		0.48	2.41	5.31	0.48	0.97	11.6	2.9	0.97			0.48	2.41	1.93		1.45
CB3-5	0.97	0.48		3.38	8.69	0.48	0.48	1.45	7.72	1.45	3.38			0.48	0.97	1.45	1.93
CB3-6	1.45	0.97		2.41	10.1		0.48	11.1	0.97				0.97	0.48	3.38	0.97	4.83
CB3-7	0.48		0.97	3.86	4.34		0.97	8.69	3.86	1.45				2.41	3.86		0.97
CB3-8	0.48	0.48		4.34	1.93			0.97	2.41	0.48				0.97	2.41	1.45	0.97
CB3-9				2.9	2.41			5.79		1.45			0.48		0.48		3.86
CB3-10	0.7		1.4	0.7	7			4.2							5.6		2.1
CB3-11		0.48		2.41	15.4			14	1.45	4.34	0.48		4.34		46.3		2.9
MK1-1	1.93	1.45	0.48	4.34	8.69	1.45		16.4	7.72	1.45				2.9	4.83	0.48	4.34
MK1-2	1.93	3.38		0.97	8.21		0.48	5.31	4.83	1.45	1.45		0.48	1.93	3.86	1.93	0.48
MK1-3		1.56		9.33	7.78			3.11	14	1.56	6.22			1.56	1.56		4.67
MK1-4	2.41	2.41	0.97	1.45	5.79		1.45	2.9	11.6	0.48	0.48			1.93	1.45	2.41	2.9
MK1-5	1.93	1.93	0.97	1.45	4.83	1.45		0.48	9.17	2.9				3.38	2.9	0.97	5.31
MK1-6	1.93	1.45		3.38	7.24			0.97	3.86	0.97	0.48		0.48	0.97	2.9	0.97	3.38
MK1-7	1.93	1.45		0.48	6.76			1.93	10.6		0.48		0.48	3.38		0.97	3.38
MK1-8	1.93	0.48	0.48	0.97	4.83			0.48	4.34		0.97			2.41	1.93	1.93	1.93
MK1-9	1.45	1.45	0.48	4.34	6.76	0.97	1.93	10.1	10.1	0.48	1.45		0.48	0.97	5.31	0.97	5.79
MK1-10	3.38	0.48	0.97	2.41	13.5	0.97		4.34	12.6	2.41				1.45	4.83	1.45	3.86
MK1-11	2.9			0.48	4.34	0.48	0.97	1.93	2.9	0.97	4.34		0.97	0.97	19.3	1.93	1.93
MK2-1	0.97			3.86	13	0.48		1.45	5.31	1.93	0.97			2.9	3.86	0.48	5.31
MK2-2	0.97		1.93	0.97	12.6	0.97		2.41	1.45	2.9			0.48	4.83	5.31	2.9	1.45
MK2-3	1.45		0.97	3.86	7.24	0.97		1.93	1.93	0.48				2.41	3.38	1.45	2.9
MK2-4	1.93		0.97	4.34	9.17	0.97		2.41	3.38	1.93	1.93			1.93	2.9	1.93	6.76
MK2-5	0.48	0.48	0.97	2.9	3.86	1.45		1.45	2.9	0.97	0.48				1.45	1.93	1.93
MK2-6	1.45		0.48	3.38	4.83		0.48	1.45	2.41					0.48	3.38	0.48	2.41
MK2-7	0.48			3.38	11.1		0.97	1.45	5.79	0.48	0.48			2.9	2.9	0.97	

10.1 (Continued)

Site	Diameter (cm)	Distance from center (m)	Orientation (°)	Alleculidae	Anobiidae	Buprestidae	Cantharidae	Carabidaae	Cephaloidae	Cerambycidae	Chrysomelidae	Cleridae	Coccinelidae	Cryptophagidae	Cucujidae	Curculionidae	Elateridae
MK2-8	21.5	1.6	239				10.6				0.97		3.38		0.48	0.97	5.79
MK2-9	30	3.81	161				4.34	0.48		0.48			1.45				9.66
MK2-10	25.4	7.9	164				6.28			0.48	0.48		2.90				10.1
MK2-11	24	0	-		0.48		7.72			0.97	1.93		2.90		0.48		7.24
MK3-1	29.4	3.8	14				6.76						0.97				3.38
MK3-2	28.5	9	86				5.31				0.48		1.93			0.48	6.28
MK3-3	23.3	4.2	319				7.72				0.48		0.48		0.48		3.38
MK3-4	33.6	7.18	348				9.17				1.45		0.48				3.38
MK3-5	24	10.02	348				6.76			0.48			0.97			0.48	3.86
MK3-6	26	6.43	266	4.67			24.9			1.56	3.11		1.56		1.56		6.22
MK3-7	23.5	9.7	272		0.48		9.66					0.48	3.86				2.41
MK3-8	15.6	1.35	311				4.20						0.70				3.50
MK3-9	15.3	0.82	196				9.17		0.48			0.48	0.97		0.48	0.48	3.86
MK3-10	20.4	5	160	0.97			17.4						1.45		0.97	0.48	8.21
MK3-11	22.1	0	-				7.72						4.34				4.34
CT1-1	27.8	4.26	154				1.93						0.97				8.69
CT1-2	25.8	10.6	91		0.48	0.48	6.28					0.48				1.45	5.79
CT1-3	21.2	2.55	65				4.34	0.48					0.97		0.48	0.48	4.83
CT1-4	24	5.7	22				8.69	0.48					1.93			0.48	8.21
CT1-5	23.5	9.71	8	0.48			2.90	0.48					0.97		0.48	0.48	4.34
CT1-6	24	3.36	333				3.86						0.48				4.83
CT1-7	22	6.23	286		0.48		7.72	0.48		0.48		0.48	0.48		0.48	0.48	10.6
CT1-8	19.5	9.4	279				10.6						2.41		0.48		7.72
CT1-9	18.5	2.35	193		0.48		8.21						0.48				9.17
CT1-10	17	10.4	172	0.97			17.9					0.48	1.93		0.48		5.79
CT1-11	21.2	0	-	0.48			4.34		0.48				0.97		0.48		9.17
CT2-1	32	3.3	160	0.48			10.1	0.48					0.48				10.6

10.1 (Continued)

Site	Endomychidae	Erotylidae	Eucinetidae	Lampyridae	Lathridiidae	Leiodidae	Lycidae	Melandryidae	Melyridae	Mordellidae	Nitidulidae	Pyrochroidae	Scolytidae	Scraptidae	Staphylinidae	Throscidae	Others
MK2-8	0.97			1.93	14	0.48	0.97	3.86	13	0.97	1.45	0.97		0.97	2.41	1.45	2.9
MK2-9	1.45			3.38	3.38	0.48		3.86		0.48				0.48	1.45		1.93
MK2-10	1.45	0.97		3.86	4.83	0.97	1.45	1.45	0.97	0.97				1.93	3.38	0.97	2.9
MK2-11	1.93	0.48	0.97	0.48	3.86		0.48	4.34	1.93	1.93	8.69	0.48	0.48	0.97	3.38	0.97	3.38
MK3-1	0.48		0.97	1.93	3.86	1.93		0.48	1.45	1.45					2.41	0.97	2.41
MK3-2	0.97	0.48	0.48	3.38	3.38			0.48	18.3	0.97				1.45	3.86		2.9
MK3-3	0.48			2.41	5.79	0.48	0.97	0.97	4.83		1.45			1.93	0.97	0.97	1.45
MK3-4			0.48	8.21	6.28			0.97	5.31	0.48	0.97			0.48	1.93	0.97	2.9
MK3-5	0.48		0.97	6.76	4.34		0.97	1.93	10.6		1.93			0.97	3.38		0.97
MK3-6					18.7			1.56	3.11	1.56			1.56	4.67	4.67	3.11	1.56
MK3-7			0.48	2.9	1.45			1.45	1.45	0.48				0.97	0.97	0.48	0.97
MK3-8		0.7		3.5				0.7	0.7						2.8		2.1
MK3-9				5.31	8.21	0.48	0.97	0.97	3.38	1.45	3.38		0.48	1.93	1.45	0.97	2.41
MK3-10	0.97		1.45	2.41	11.1	0.48		1.93	2.9	0.48	0.97		0.48	1.45	1.93		2.41
MK3-11	0.48		0.97	1.45	6.28		0.48	0.97	0.48	1.45	9.66			1.93	7.24		1.45
CT1-1	0.48		1.45	0.48	4.83			0.48		0.48			0.48	1.93	1.93		5.31
CT1-2	0.48	1.93	0.48	2.9	8.21	1.45	0.48	3.86	5.79					1.93	1.93	0.97	3.38
CT1-3	0.48		0.97	0.97	8.21	0.48	0.97	2.41	1.93	0.48	0.97			1.45	7.72		3.38
CT1-4				0.97	9.66		1.93	3.38	3.86	0.48			0.48	0.48	2.9	0.48	4.83
CT1-5	0.48		1.45	0.97	3.86		0.48	3.86	0.48	0.48	0.48			1.45	3.86		2.9
CT1-6	0.97		0.48	0.48	6.76	1.45	1.45	2.41	5.31		0.48			0.97	1.93	0.48	4.83
CT1-7	0.97				7.72		0.48	0.97	0.97	1.93					2.41	0.97	3.86
CT1-8	2.9		0.97		6.28	0.48	1.45	1.93	0.48				0.48		2.41	0.97	4.83
CT1-9	1.45		0.48		6.28	0.48	0.48	1.93		0.48					0.48	0.48	2.9
CT1-10	1.45			0.97	4.83	0.97	1.93	2.41	6.76	0.97	0.97				3.86		5.79
CT1-11	0.48		0.48		7.72				3.86		0.48				2.41	0.48	2.41
CT2-1	0.48	0.48	1.45	0.97	6.28		0.97	2.9	0.97	2.9					0.97	2.41	4.34

10.1 (Continued)

Site	Diameter (cm)	Distance from center (m)	Orientation (°)	Alleculidae	Anobiidae	Buprestidae	Cantharidae	Carabidaae	Cephaloidae	Cerambycidae	Chrysomelidae	Cleridae	Coccinelidae	Cryptophagidae	Cucujidae	Curculionidae	Elateridae
CT2-2	21.3	5.85	86	0.48			9.17									0.48	10.6
CT2-3	27.5	10	78	0.97			6.76						0.97				2.90
CT2-4	28	2.2	14	0.48			10.6						0.48		0.48	0.48	6.76
CT2-5	17.9	7.25	0				9.66				0.48	0.48	0.97		0.48	0.97	5.31
CT2-6	31.8	9.4	351				9.17					1.93	0.48			0.48	4.34
CT2-7	20	3	262		0.48		8.69	0.48		0.48			0.97		1.45		8.69
CT2-8	17.5	8.2	274	0.48			8.21	0.48	0.48			0.48			0.48	0.48	4.34
CT2-9	21.4	2.48	228	0.48			7.24						0.48				8.69
CT2-10	25.1	7.77	177				1.40	2.80			1.40		0.70				7.00
CT2-11	27.8	0	-				9.66				0.48	0.97					5.79
CT3-1	29.3	3.7	109	0.97			2.90		0.48				0.97				6.28
CT3-2	25.6	10.6	102				2.41						2.90	0.48			7.72
CT3-3	24.7	3.05	68	0.48		0.48	4.34			0.48			0.48				4.83
CT3-4	27.5	5.1	324	0.48			2.41		0.48		0.48	0.97	0.48			0.97	3.38
CT3-5	27.7	9.3	354	0.48			5.79	0.48		0.48							3.86
CT3-6	28	2.4	203				2.90						0.48			0.48	2.41
CT3-7	28.5	6.15	260	1.45			6.76	0.48					0.97			0.48	5.79
CT3-8	26.1	11.25	272				4.83	0.48		0.48		0.48	0.48				4.34
CT3-9	28	2.8	162				6.28						0.48				6.76
CT3-10	26.5	8.8	183				3.86	0.48			0.48					0.48	6.76
CT3-11	26.5	0	-				2.41						1.93		0.97		5.31

10.1 (Continued)

Site	Endomychidae	Erotylidae	Eucinetidae	Lampyridae	Lathridiidae	Leiodidae	Lycidae	Melandryidae	Melyridae	Mordellidae	Nitidulidae	Pyrochroidae	Scolytidae	Scraptidae	Staphylinidae	Throscidae	Others
CT2-2		0.48	0.48	1.45	1.93		0.97	1.93			1.93		0.48	0.97		1.45	2.9
CT2-3	0.97	0.48	0.48	2.9	7.72	0.97	1.93	8.21		0.97	1.45			1.45	0.97		2.9
CT2-4	1.45		4.34	1.93	6.28	0.48	0.48	1.45	0.48	1.93	0.48			0.48	2.41	0.97	1.45
CT2-5	0.48	0.48		0.97	8.21	0.48	0.48	0.97		0.48	0.97		0.97	2.41	2.41	0.48	1.93
CT2-6	1.45			0.97	7.72		0.48	1.93		0.48	0.48			1.45		1.45	0.48
CT2-7	1.93	0.48	2.41	2.9	1.45	0.48	0.48	2.9	0.97		0.97			0.48	1.45	0.48	1.93
CT2-8	0.97			2.9	3.38	0.48		3.86		0.48	0.48		1.45		0.97		2.9
CT2-9	1.93		0.97	2.9	11.6	0.97		3.86		1.45			0.48	2.41	0.97	1.93	1.45
CT2-10	0.7		0.7	2.8	1.4	1.4	2.1	2.8		0.7					3.5	3.5	2.8
CT2-11			0.48	2.9	3.38	0.97	0.48	6.28		2.41			0.48		0.97	1.93	0.97
CT3-1	4.83		0.48	0.48	8.69		0.97	0.48	5.79	0.48	0.48			0.97	5.31		6.28
CT3-2	2.41		0.97	0.48	13			0.97	2.41	1.45				1.45	2.41	0.97	6.28
CT3-3	5.79			2.41	10.1	0.48		3.38	7.24		0.48				7.72		12.6
CT3-4	3.38		0.48	1.45	5.31	1.45		1.93	4.83	0.97	0.48			0.48	3.86		5.31
CT3-5	1.93	0.48		1.45	3.86	0.97	0.97	2.41	5.31	0.97				0.48	3.86	1.45	2.9
CT3-6	2.41	0.48	0.48	2.9	3.86	0.48		9.17	2.9	0.48	0.48			0.97	3.38	0.48	3.38
CT3-7	1.45			1.45	3.38			0.97	4.83					0.48	0.97		2.41
CT3-8	1.93			2.9	3.86	0.48	2.9	3.38	6.28	0.48	0.97			1.45	3.38	1.45	2.41
CT3-9	2.9		0.48	0.97	2.41	0.48	1.45	7.24	5.31		0.48		0.48	0.48	0.97	0.97	5.79
CT3-10	3.86			1.93	3.86	0.48	1.93	0.97	2.41	0.97	0.48			0.48	3.86		3.86
CT3-11	4.83			0.97	9.66	0.48			13.5		0.48			0.48	5.31	0.97	6.28

10.2 Landing rates of wood-feeding beetles (individuals/m^2/week) collected in each stand sampled in chapter 4 (cb – commercial bait; mk – mechanically-killed; ctrl – control).

Species	CB1	CB2	CB3	MK1	MK2	MK3	CTRL1	CTRL2	CTRL3
Cerambycidae									
Acmaeops proteus (Kirby)			0.49	0.49					
Asemum striatum (L.)	3.41	0.98							
Clytus ruricola (Olivier)	0.49	0.98	0.49	0.98	0.49				0.49
Evodinus monticola (Randall)							0.49		
Grammoptera subargentata (Kirby)		0.49				0.49			
Hyperplatys aspersa (Say)				0.49	0.49				
Judolia montivagans (Couper)		0.49							
Phymatodes dimidiatus (Kirby)						0.49		0.49	
Pidonia ruficollis (Say)					0.49				
Pogonocherus mixtus Haldeman					0.49				0.49
Psenocerus supernotatus (Say)	0.98	0.49	0.49	0.98	0.98				
Ropalopus sanguinicollis (Horn)		0.49							
Tetropium cinnamopterum Kirby			0.49						
Tetropium n.sp.		0.49							
Xylotrechus schaefferi Schott		0.49			0.49				0.49
Xylotrechus undulatus (Say)	1.46	0.49	0.49						
Scolytidae									
Dryocoetes affaber (Mannerheim)			1.46						
Dryocoetes autographus (Ratzeburg)	1.95	1.46	2.93						
Hylurgops pinifex (Smith)	5.37	5.85	1.46	1.46	0.98			0.98	0.49
Others	2.44	3.90	0.98	0.49		1.46	0.98	2.93	

10.3 Physical and nutritional characteristics of spruce snags sampled in chapter 5.

Snag	Decay class	Wood density (g/cm^3)	Snag age (years)	Diameter (cm)	Water content (ml/cm^3)	Water retention	Nitrogen (mg/g)	Phenols (mg/g TAeq)	NSCs (mg/g)
Selbaie 1									
1	3	0.5121	10	15.9	0.4174	0.2237	0.530	20.71	1.10
2	3	0.4894	5	24.6	0.3263	0.2351	0.564	27.71	2.15
3	3	0.4628	4	14.2	0.3976	0.3080	0.363	8.60	1.53
4	3	0.4543	8	17.3	0.3739	0.2394	0.534	7.71	3.23
5	3	0.4438	7	19.1	0.3433	0.2704	0.479	30.93	2.26
6	3	0.4093	13	17.9	0.3592	0.1996	0.368	5.43	1.93
7	4	0.4690	13	24.4	0.2264	0.2514	0.579	9.70	3.39
8	4	0.4487	16	17.6	0.3290	0.1398	0.684	50.86	3.42
9	4	0.4398	13	24.2	0.3795	0.1981	0.542	39.31	2.62
10	4	0.4266	13	18.9	0.4402	0.1452	0.446	9.72	2.28
11	4	0.4021	25	16.2	0.4614	0.1889	0.443	29.05	2.21
12	4	0.2952	20	22.2	0.5491	0.2730	0.778	7.03	2.53
13	5	0.4740	24	15.1	0.4675	0.2324	0.610	13.04	3.91
14	5	0.4288	28	16.9	0.5344	0.2478	0.947	43.65	3.99
15	5	0.3778	36	18.4	0.5095	0.0715	1.225	73.67	2.94
16	5	0.3669	24	17.2	0.6478	0.2025	0.446	14.35	2.78
17	5	0.3634	13	22.3	0.5380	0.1922	0.510	23.75	2.39
18	5	0.1886	n/a	18.0	0.6112	0.1506	1.348	9.44	1.75
19	6	0.5095	10	16.3	0.4285	0.1897	0.365	11.24	1.24
20	6	0.3117	15	16.7	0.6182	0.1973	0.997	73.22	6.28
21	6	0.2645	n/a	20.0	0.5142	0.1297	0.811	14.86	3.47
22	6	0.2026	n/a	19.0	0.5293	0.1444	1.701	13.82	2.44
23	6	0.1427	n/a	19.4	0.4120	0.0842	1.857	16.73	0.00
24	6	0.1317	n/a	18.8	0.5626	0.1508	1.636	11.74	1.11

10.3 (Continued)

Snag	Decay class	Wood density (g/cm^3)	Snag age (years)	Diameter (cm)	Water content (ml/cm^3)	Water retention	Nitrogen (mg/g)	Phenols (mg/g TAeq)	NSCs (mg/g)
Selbaie 2									
1	3	0.5677	-	15.2	-	-	-	-	-
2	3	0.5507	-	16.6	-	-	-	-	-
3	3	0.5494	-	19.6	-	-	-	-	-
4	3	0.5416	-	15.6	-	-	-	-	-
5	4	0.4354	-	17.3	-	-	-	-	-
6	4	0.4212	-	20.5	-	-	-	-	-
7	5	0.4621	-	17.6	-	-	-	-	-
8	5	0.3638	-	15.7	-	-	-	-	-
9	5	0.2865	-	16.3	-	-	-	-	-
10	6	0.3136	-	21.8	-	-	-	-	-
11	6	0.2228	-	16.2	-	-	-	-	-
12	6	0.2145	-	16.4	-	-	-	-	-
Selbaie 3									
1	3	0.5121	-	18.5	-	-	-	-	-
2	3	0.5110	-	22.3	-	-	-	-	-
3	3	0.4776	-	19.3	-	-	-	-	-
4	4	0.4584	-	26.7	-	-	-	-	-
5	4	0.4127	-	30.4	-	-	-	-	-
6	4	0.4552	-	28.9	-	-	-	-	-
7	5	0.4992	-	27.9	-	-	-	-	-
8	5	0.4548	-	26.6	-	-	-	-	-
9	5	0.5259	-	21.6	-	-	-	-	-
10	6	0.3693	-	20.8	-	-	-	-	-
11	6	0.1690	-	22.8	-	-	-	-	-
12	6	0.3577	-	22.2	-	-	-	-	-

10.3 (Continued)

Snag	Decay class	Wood density (g/cm^3)	Snag age (years)	Diameter (cm)	Water content (ml/cm^3)	Water retention	Nitrogen (mg/g)	Phenols (mg/g TAeq)	NSCs (mg/g)
Chauvin									
1	3	0.4931	-	24.7	-	-	-	-	-
2	3	0.4661	-	27.6	-	-	-	-	-
3	3	0.4572	-	24.9	-	-	-	-	-
4	3	0.3596	-	29.8	-	-	-	-	-
5	4	0.5500	-	19.0	-	-	-	-	-
6	4	0.4091	-	24.0	-	-	-	-	-
7	4	0.3849	-	22.7	-	-	-	-	-
8	4	0.3229	-	19.2	-	-	-	-	-
9	5	0.4725	-	26.1	-	-	-	-	-
10	5	0.4473	-	17.9	-	-	-	-	-
11	5	0.4293	-	18.7	-	-	-	-	-
12	5	0.3836	-	17.3	-	-	-	-	-
13	6	0.4557	-	18.4	-	-	-	-	-
14	6	0.2568	-	26.2	-	-	-	-	-
15	6	0.2450	-	24.1	-	-	-	-	-
16	6	0.2208	-	23.2	-	-	-	-	-

10.3 (Continued)

Snag	Decay class	Wood density (g/cm^3)	Snag age (years)	Diameter (cm)	Water content (ml/cm^3)	Water retention	Nitrogen (mg/g)	Phenols (mg/g TAeq)	NSCs (mg/g)
Grands-Jardins									
1	3	0.5008	-	17.0	-	-	-	-	-
2	3	0.4622	-	25.3	-	-	-	-	-
3	3	0.4575	-	18.7	-	-	-	-	-
4	3	0.4482	-	20.7	-	-	-	-	-
5	4	0.5328	-	22.8	-	-	-	-	-
6	4	0.4740	-	16.2	-	-	-	-	-
7	4	0.4607	-	28.4	-	-	-	-	-
8	4	0.4387	-	19.5	-	-	-	-	-
9	5	0.4668	-	18.8	-	-	-	-	-
12	5	0.3547	-	25.8	-	-	-	-	-
13	6	0.5147	-	21.2	-	-	-	-	-
14	6	0.3799	-	18.9	-	-	-	-	-
15	6	0.3266	-	19.5	-	-	-	-	-
16	6	0.3074	-	28.4	-	-	-	-	-

10.4 Physical and nutritional characteristics of aspen snags sampled in chapters 5-7. Codes in parenthesis are those used in chapter 7.

Snag	Decay class	Wood density (g/cm^3)	Snag age (years)	Diameter (cm)	Water content (ml/cm^3)	Water retention	Nitrogen (mg/g)	Phenols (mg/g TAeq)	NSCs (mg/g)
LDRTF									
1	3	0.4038	3	19.8	0.3558	0.2512	0.799	10.64	8.21
2	3	0.3880	3	33.5	0.4760	0.2175	1.101	36.28	3.80
3	3	0.3509	3	20.2	0.4499	0.2817	0.572	7.42	3.39
4	3	0.2907	4	19.9	0.5430	0.1932	1.097	5.81	4.31
5	3	0.2870	9	21.0	0.6300	0.2196	0.715	4.58	1.47
6	3	0.2829	3	40.1	0.5685	0.1522	1.656	46.26	4.12
7	4	0.4051	2	21.4	0.4059	0.1711	0.896	6.98	4.51
8	4	0.3554	2	19.6	0.4316	0.3018	0.534	6.77	3.16
9	4	0.3333	6	25.3	0.5419	0.3143	0.812	6.97	4.50
10	4	0.3140	4	31.5	0.5531	0.1115	0.894	4.75	2.32
11	4	0.2621	14	35.3	0.4984	0.1572	0.972	8.17	4.60
12	4	0.2368	8	24.4	0.5832	0.1311	0.888	5.40	1.91
13	5	0.2850	10	27.2	0.6829	0.1945	1.240	28.85	4.61
14	5	0.2824	12	22.0	0.5851	0.2131	1.870	8.15	3.23
15	5	0.2761	10	31.7	0.5615	0.1618	1.021	4.16	1.92
16	5	0.2554	7	22.4	0.4855	0.2116	1.131	6.99	2.36
17	5	0.2025	19	31.0	0.5889	0.1811	2.584	12.20	3.26
18	5	0.1867	11	25.3	0.6345	0.1630	1.943	8.63	3.93
19	6	0.2653	21	29.2	0.5646	0.1809	1.773	11.41	3.64
20	6	0.2428	11	20.0	0.5610	0.1357	1.402	6.17	2.71
21	6	0.2319	19	23.6	0.7258	0.2026	1.813	9.50	2.49
22	6	0.2240	22	33.6	0.6135	0.2592	2.193	18.86	5.91
23	6	0.1938	21	29.6	0.6190	0.3754	4.186	6.41	1.89
24	6	0.1747	13	28.4	0.6850	0.2427	2.054	7.75	1.87

10.4 (Continued)

Snag	Decay class	Wood density (g/cm^3)	Snag age (years)	Diameter (cm)	Water content (ml/cm^3)	Water retention	Nitrogen (mg/g)	Phenols (mg/g TAeq)	NSCs (mg/g)
Magusi 1									
1	3	0.4603	-	24.3	-	-	-	-	-
2	3	0.4019	-	22.2	-	-	-	-	-
3	3	0.3941	-	24.4	-	-	-	-	-
4	4	0.4443	-	21.3	-	-	-	-	-
5	4	0.4414	-	24.1	-	-	-	-	-
6 (A11)	4	0.4335	-	21.8	-	-	-	-	-
7 (A2)	5	0.2895	-	18.7	-	-	-	-	-
8 (A12)	5	0.2745	-	19.7	-	-	-	-	-
9	5	0.2003	-	17.7	-	-	-	-	-
10	6	0.2825	-	18.8	-	-	-	-	-
11 (A5)	6	0.1776	-	19.9	-	-	-	-	-
12	6	0.2927	-	21.5	-	-	-	-	-
Magusi 2									
1	3	0.4642	-	29.3	-	-	-	-	-
2	3	0.4397	-	26.4	-	-	-	-	-
3	3	0.2523	-	30.1	-	-	-	-	-
4 (A7)	4	0.3241	-	22.6	-	-	-	-	-
5 (A4)	4	0.2820	-	18.7	-	-	-	-	-
6 (A1)	4	0.1698	-	18.3	-	-	-	-	-
7 (A9)	5	0.3179	-	19.8	-	-	-	-	-
8 (A8)	5	0.3063	-	21.3	-	-	-	-	-
9 (A6)	5	0.2961	-	16.9	-	-	-	-	-
10 (A10)	6	0.3541	-	19.1	-	-	-	-	-
11	6	0.3290	-	37.7	-	-	-	-	-
12 (A3)	6	0.2779	-	40.0	-	-	-	-	-

10.4 (Continued)

Snag	Decay class	Wood density (g/cm^3)	Snag age (years)	Diameter (cm)	Water content (ml/cm^3)	Water retention	Nitrogen (mg/g)	Phenols (mg/g TAeq)	NSCs (mg/g)
Chauvin									
1	3	0.4489	-	27.8	-	-	-	-	-
2	3	0.4301	-	21.0	-	-	-	-	-
3	3	0.4183	-	26.0	-	-	-	-	-
4	3	0.3960	-	17.4	-	-	-	-	-
5	3	0.3437	-	17.2	-	-	-	-	-
6	4	0.4099	-	14.9	-	-	-	-	-
7	4	0.3686	-	32.4	-	-	-	-	-
8	4	0.2086	-	31.0	-	-	-	-	-
9 (C6)	5	0.3444	-	23.9	-	-	-	-	-
10	5	0.3209	-	17.2	-	-	-	-	-
11 (C5)	5	0.2768	-	26.8	-	-	-	-	-
12 (C4)	5	0.2600	-	28.0	-	-	-	-	-
13	6	0.2868	-	16.1	-	-	-	-	-
14 (C1)	6	0.2641	-	18.8	-	-	-	-	-
15 (C2)	6	0.2126	-	24.0	-	-	-	-	-
16 (C3)	6	0.1832	-	21.7	-	-	-	-	-

10.4 (Continued)

Snag	Decay class	Wood density (g/cm^3)	Snag age (years)	Diameter (cm)	Water content (ml/cm^3)	Water retention	Nitrogen (mg/g)	Phenols (mg/g TAeq)	NSCs (mg/g)
Oka									
1	3	0.4614	-	24.4	-	-	-	-	-
2	3	0.4604	-	17.4	-	-	-	-	-
3	3	0.4423	-	23.4	-	-	-	-	-
4	3	0.4289	-	20.0	-	-	-	-	-
5	4	0.3957	-	16.6	-	-	-	-	-
6	4	0.3471	-	18.8	-	-	-	-	-
7 (O4)	4	0.3154	-	19.0	-	-	-	-	-
8	4	0.3037	-	20.2	-	-	-	-	-
9	5	0.4143	-	21.7	-	-	-	-	-
10 (O6)	5	0.3730	-	19.9	-	-	-	-	-
11 (O5)	5	0.3550	-	15.9	-	-	-	-	-
12 (O2)	5	0.2110	-	21.7	-	-	-	-	-
13	6	0.2965	-	15.6	-	-	-	-	-
14	6	0.2817	-	15.5	-	-	-	-	-
15 (O3)	6	0.2685	-	17.6	-	-	-	-	-
16 (O1)	6	0.2053	-	23.4	-	-	-	-	-

10.5 Insects collected in spruce snags sampled in chapter 5.

Snag	*Acanthocinus pusillus* (Kirby)	*Acmaeops proteus* (Kirby)	*Cosmosalia chrysocoma* (Kirby)	*Meriellum proteus* (Kirby)	*Monochamus scutellatus* (Say)	*Phymatodes dimidiatus* (Kirby)	*Stictoleptura canadensis* (Olivier)	*Tetropium cinnamopterum* Kirby	n. *Trachysida aspera* LeConte	*Xylotrechus undulatus* (Say)	Cerambycinae	Lepturinae	*Chrysobotris* sp.	*Dicerca* sp.	*Cryptturgus borealis* (Swaine)	*Dendroctonus rufipennis* (Kirby)	*Dryocoetes affaber* (Mannerheim)	*Ips latidens* (LeConte)	*Polygraphus rufipennis* (Kirby)	*Trypodendron lineatum* (Olivier)
Selbaie 1																				
1		1		1										2						
2		3												2						
3		1			2										1			5	25	
4		6		3										2						
5		7																		
6	1	7		3											3			7		
7		1					1							4						
8												1						3		
9																				
10																				
11																				
12																				
13																				
14																		2		
15														1						
16		1																		
17			1									1		1						
18																				
19																				
20																				
21		1																		
22																				
23																				
24																				
Total	1	28	1	7	2	0	1	0	0	0	0	2	0	12	4	0	0	17	25	0

10.5 (Continued)

Snag	*Acanthocinus pusillus* (Kirby)	*Acmaeops proteus* (Kirby)	*Cosmosalia chrysocoma* (Kirby)	*Meriellum proteus* (Kirby)	*Monochamus scutellatus* (Say)	*Phymatodes dimidiatus* (Kirby)	*Stictoleptura canadensis* (Olivier)	*Tetropium cinnamopterum* Kirby	n. *Trachysida aspera* LeConte	*Xylotrechus undulatus* (Say)	Cerambycinae	Lepturinae	*Chrysobotris* sp.	*Dicerca* sp.	*Crypturgus borealis* (Swaine)	*Dendroctonus rufipennis* (Kirby)	*Dryocoetes affaber* (Mannerheim)	*Ips latidens* (LeConte)	*Polygraphus rufipennis* (Kirby)	*Trypodendron lineatum* (Olivier)
Selbaie 2																				
1		9																		
2		6		1										8	2			10	1	
3		8		2				1										1	11	
4		5																		
5		2							2					2				1		
6														3						
7							2							2						
8							1							2						
9																				
10							6							1						
11							2													
12																				
Total	0	30	0	3	0	0	11	1	2	0	0	0	0	18	2	0	0	12	12	0

10.5 (Continued)

Snag	*Acanthocinus pusillus* (Kirby)	*Acmaeops proteus* (Kirby)	*Cosmosalia chrysocoma* (Kirby)	*Meriellum proteus* (Kirby)	*Monochamus scutellatus* (Say)	*Phymatodes dimidiatus* (Kirby)	*Stictoleptura canadensis* (Olivier)	*Tetropium cinnamopterum* Kirby	n. *Trachysida aspera* LeConte	*Xylotrechus undulatus* (Say)	Cerambycinae	Lepturinae	*Chrysobotris* sp.	*Dicerca* sp.	*Crypturgus borealis* (Swaine)	*Dendroctonus rufipennis* (Kirby)	*Dryocoetes affaber* (Mannerheim)	*Ips latidens* (LeConte)	*Polygraphus rufipennis* (Kirby)	*Trypodendron lineatum* (Olivier)
Selbaie 3																				
1	3	11		3						1			1					47		
2		2		2		3														
3														1						
4																				
5							1		2	3										
6	19	1		1			8			1				12	118				48	
7					1															
8																				
9														1						
10			3				2													
11							1													
12																				
Total	22	14	3	6	1	3	12	0	2	5	0	0	1	14	118	0	0	47	48	0

10.5 (Continued)

Snag	*Acanthocinus pusillus* (Kirby)	*Acmaeops proteus* (Kirby)	*Cosmosalia chrysocoma* (Kirby)	*Meriellum proteus* (Kirby)	*Monochamus scutellatus* (Say)	*Phymatodes dimidiatus* (Kirby)	*Stictoleptura canadensis* (Olivier)	*Tetropium cinnamopterum* Kirby	n. *Trachysida aspera* LeConte	*Xylotrechus undulatus* (Say)	Cerambycinae	Lepturinae	*Chrysobotris* sp.	*Dicerca* sp.	*Crypturgus borealis* (Swaine)	*Dendroctonus rufipennis* (Kirby)	*Dryocoetes affaber* (Mannerheim)	*Ips latidens* (LeConte)	*Polygraphus rufipennis* (Kirby)	*Trypodendron lineatum* (Olivier)
Chauvin																				
1		12				13														
2		2																		
3																	1			
4		2		1						3						1	15		3	
5						8														
6																				
7																				
8																				
9																				
10		1				1														
11																				
12																				
13																				
14																				
15																				
16																				
Total	0	17	0	1	0	22	0	0	0	3	0	0	0	0	0	1	16	0	3	0

10.5 (Continued)

Snag	*Acanthocinus pusillus* (Kirby)	*Acmaeops proteus* (Kirby)	*Cosmosalia chrysocoma* (Kirby)	*Meriellum proteus* (Kirby)	*Monochamus scutellatus* (Say)	*Phymatodes dimidiatus* (Kirby)	*Stictoleptura canadensis* (Olivier)	*Tetropium cinnamopterum* Kirby	n. *Trachysida aspera* LeConte	*Xylotrechus undulatus* (Say)	Cerambycinae	Lepturinae	*Chrysobotris* sp.	*Dicerca* sp.	*Crypturgus borealis* (Swaine)	*Dendroctonus rufipennis* (Kirby)	*Dryocoetes affaber* (Mannerheim)	*Ips latidens* (LeConte)	*Polygraphus rufipennis* (Kirby)	*Trypodendron lineatum* (Olivier)
Grands-Jardins																				
1		2									1						2		12	
2		1						13		1					5		4		4	26
3		6																	2	
4	5	9			2										6				50	
5																				
6																				
7		2																		
8																				
9		1		1						5										
10				1						3										
11																				
12																				
13																				
14																				
15																				
16																				
Total	5	21	0	2	2	0	0	13	0	9	1	0	0	0	11	0	6	0	68	26

10.6 Insects collected in aspen snags sampled in chapters 5-7. Codes in parenthesis are those used in chapter 7.

Snag	*Anthophylax attenuatus* (Haldeman)	*Bellamira scalaris* (Say)	*Clytus ruricola* (Olivier)	n. *Trachysida mutabilis* (Newman)	n. *Trigonarthris* sp.	T. Clytini	Cerambycinae	Lamiinae	Lepturinae	*Agrilus* sp.	*Dicerca* sp.	*Trypodendron retusum* (LeConte)	*Xyloterinus politus* Say
LDTRF													
1													
2												5	8
3													
4													
5													
6													2
7													
8											4		
9	6								1		2		
10											1		
11	11												
12	27	2									1		
13	7												
14	1												
15	59	1					1						
16	1												
17	1												
18	18	1											
19	4												
20	14										1		
21	1	4											
22	3				1								
23	1												
24	8												
Total	162	8	0	0	1	0	1	0	1	0	9	5	10

10.6 (Continued)

Snag	*Anthophylax attenuatus* (Haldeman)	*Bellamira scalaris* (Say)	*Clytus ruricola* (Olivier)	n. *Trachysida mutabilis* (Newman)	n. *Trigonarthris* sp.	T. Clytini	Cerambycinae	Lamiinae	Lepturinae	*Agrilus* sp.	*Dicerca* sp.	*Trypodendron retusum* (LeConte)	*Xyloterinus politus* Say
Magusi 1													
1								1					
2													
3													
4													
5													
6 (A11)													
7 (A2)		2									3		
8 (A12)											1		
9											1		
10													
11 (A5)	6												
12													
Total	6	2	0	0	0	0	0	1	0	0	5	0	0

10.6 (Continued)

Snag	*Anthophylax attenuatus* (Haldeman)	*Bellamira scalaris* (Say)	*Clytus ruricola* (Olivier)	n. *Trachysida mutabilis* (Newman)	n. *Trigonarthris* sp.	T. Clytini	Cerambycinae	Lamiinae	Lepturinae	*Agrilus* sp.	*Dicerca* sp.	*Trypodendron retusum* (LeConte)	*Xyloterinus politus* Say
Magusi 2													
1													
2													
3													
4 (A7)	136												
5 (A4)	41										1		
6 (A1)	10										2		
7 (A9)	10												
8 (A8)	14												
9 (A6)	31												
10 (A10)													
11	2	1											
12 (A3)	36												
Total	280	1	0	0	0	0	0	0	0	0	3	0	0

10.6 (Continued)

Snag	*Anthophylax attenuatus* (Haldeman)	*Bellamira scalaris* (Say)	*Clytus ruricola* (Olivier)	n. *Trachysida mutabilis* (Newman)	n. *Trigonarthris* sp.	T. Clytini	Cerambycinae	Lamiinae	Lepturinae	*Agrilus* sp.	*Dicerca* sp.	*Trypodendron retusum* (LeConte)	*Xyloterinus politus* Say
Chauvin													
1												31	36
2													
3		1							1				
4		4						1			21		
5	1									19	2	15	
6													
7		3											
8		2											
9 (C6)													
10	15								1		1		
11 (C5)	7												
12 (C4)													
13													
14 (C1)	11	1		1									
15 (C2)	4			3							1		
16 (C3)	8												
Total	46	11	0	4	0	0	0	1	2	19	25	46	36

10.6 (Continued)

Snag	*Anthophylax attenuatus* (Haldeman)	*Bellamira scalaris* (Say)	*Clytus ruricola* (Olivier)	n. *Trachysida mutabilis* (Newman)	n. *Trigonarthris* sp.	T. Clytini	Cerambycinae	Lamiinae	Lepturinae	*Agrilus* sp.	*Dicerca* sp.	*Trypodendron retusum* (LeConte)	*Xyloterinus politus* Say
Oka													
1						1							
2													
3													
4													
5													
6			1								1		
7 (O4)													
8		2									9		
9													
10 (O6)	2												
11 (O5)		1											
12 (O2)		2											
13	4	4							1				
14		1									1		
15 (O3)													
16 (O1)	2												
Total	8	10	1	0	0	1	0	0	1	0	11	0	0

10.7 Wood density and size data of larvae collected in chapter 7.

Snag	Id	Wood density (g/cm^3)	Species	Body length (mm)	Head capsule width (mm)
A1	1	0.247	*Anthophylax attenuatus*	9.2	2.1
A1	2	0.231	*Anthophylax attenuatus*	16.4	3.7
A1	3	0.286	*Anthophylax attenuatus*	11.7	2.2
A1	4	0.271	*Anthophylax attenuatus*	n/a	1.6
A1	5	0.281	*Anthophylax attenuatus*	6.8	1.6
A1	6	0.337	*Anthophylax attenuatus*	5.4	1
A1	7	0.323	*Anthophylax attenuatus*	7	1.4
A1	8	0.245	*Anthophylax attenuatus*	10.6	2.8
A1	9	0.231	*Anthophylax attenuatus*	12.5	2.3
A1	10	0.220	*Anthophylax attenuatus*	n/a	n/a
A2	1	0.343	*Bellamira scalaris*	27.1	4.4
A2	2	0.327	*Bellamira scalaris*	12.9	2.6
A2	3	0.294	*Bellamira scalaris*	9.7	3.5
A3	1	0.373	*Anthophylax attenuatus*	22.7	3.8
A3	2	0.469	*Anthophylax attenuatus*	20.5	3.6
A3	3	0.211	*Anthophylax attenuatus*	14	2.5
A3	4	0.290	*Anthophylax attenuatus*	17.1	4.1
A3	5	0.326	*Anthophylax attenuatus*	10.8	2.7
A3	6	0.292	*Anthophylax attenuatus*	9	1.6
A3	7	0.284	*Anthophylax attenuatus*	16.3	3.3
A3	8	0.308	*Anthophylax attenuatus*	20.1	3.4
A3	9	0.342	*Anthophylax attenuatus*	14	2.6
A3	10	0.400	*Anthophylax attenuatus*	11.1	2.2
A3	11	0.237	*Anthophylax attenuatus*	10.8	1.8
A3	12	0.250	*Anthophylax attenuatus*	14	2.5
A3	13	0.287	*Anthophylax attenuatus*	15.4	2.9
A3	14	0.363	*Anthophylax attenuatus*	9.1	2
A3	15	0.274	*Anthophylax attenuatus*	10.8	2.4
A3	16	0.441	*Anthophylax attenuatus*	12.2	2.8
A3	17	0.279	*Anthophylax attenuatus*	17.2	3.6
A3	18	0.251	*Anthophylax attenuatus*	14.8	3
A3	19	0.185	*Anthophylax attenuatus*	16.2	3.2
A3	20	0.376	*Anthophylax attenuatus*	19.4	4
A3	21	0.388	*Anthophylax attenuatus*	19.8	3.6
A3	22	0.298	*Anthophylax attenuatus*	19.8	3.8
A3	23	0.364	*Anthophylax attenuatus*	14.3	3.3
A3	24	n/a	*Anthophylax attenuatus*	11.9	2.2
A3	25	0.339	*Anthophylax attenuatus*	9.9	2.2
A3	26	0.181	*Anthophylax attenuatus*	18.2	3.7
A4	1	0.339	*Anthophylax attenuatus*	12.7	2.5
A4	3	0.300	*Anthophylax attenuatus*	10.2	2
A4	4	0.316	*Anthophylax attenuatus*	6.3	1.3
A4	5	0.285	*Anthophylax attenuatus*	8.4	1.6
A4	6	0.378	*Anthophylax attenuatus*	14.7	3.4

10.7 (Continued)

Snag	Id	Wood density (g/cm^3)	Species	Body length (mm)	Head capsule width (mm)
A4	7	0.354	*Anthophylax attenuatus*	9.8	1.9
A4	8	0.359	*Anthophylax attenuatus*	8.1	1.8
A4	9	0.322	*Anthophylax attenuatus*	17.5	3.7
A4	10	0.315	*Anthophylax attenuatus*	12.9	3
A4	11	0.284	*Anthophylax attenuatus*	9.9	2.1
A4	12	0.260	*Anthophylax attenuatus*	9.4	2
A4	13	0.257	*Anthophylax attenuatus*	10.5	2.2
A4	14	0.319	*Anthophylax attenuatus*	17.7	3.7
A4	15	0.303	*Anthophylax attenuatus*	11.5	2.8
A4	16	0.271	*Anthophylax attenuatus*	8.5	1.8
A4	17	0.201	*Anthophylax attenuatus*	12.5	2.6
A4	18	0.296	*Anthophylax attenuatus*	10.6	2
A4	19	0.287	*Anthophylax attenuatus*	14.4	3.5
A4	20	0.295	*Anthophylax attenuatus*	16.3	3.4
A4	21	0.289	*Anthophylax attenuatus*	10.9	2.5
A4	22	0.218	*Anthophylax attenuatus*	14	3.1
A4	23	0.197	*Anthophylax attenuatus*	9.9	2.4
A4	24	0.292	*Anthophylax attenuatus*	12	2.7
A4	25	0.250	*Anthophylax attenuatus*	13.2	2.5
A4	26	0.258	*Anthophylax attenuatus*	11.5	2.8
A4	27	0.275	*Anthophylax attenuatus*	9.5	2.2
A4	28	0.299	*Anthophylax attenuatus*	14.2	2.2
A4	29	0.365	*Anthophylax attenuatus*	6.6	1.4
A4	30	0.340	*Anthophylax attenuatus*	7.6	1.5
A4	31	0.344	*Anthophylax attenuatus*	10.6	2.7
A4	32	0.342	*Anthophylax attenuatus*	11.9	2.7
A4	33	0.337	*Anthophylax attenuatus*	11.2	2.7
A4	34	0.338	*Anthophylax attenuatus*	12.9	3.5
A4	35	0.246	*Anthophylax attenuatus*	n/a	3.9
A4	36	0.365	*Anthophylax attenuatus*	10.5	2.3
A4	37	0.305	*Anthophylax attenuatus*	16.6	3.6
A4	39	0.289	*Anthophylax attenuatus*	12.3	2.8
A4	2	0.282	*Bellamira scalaris*	n/a	n/a
A4	6	0.134	*Bellamira scalaris*	n/a	n/a
A4	38	0.280	*Bellamira scalaris*	12.5	2.8
A5	1	0.242	*Anthophylax attenuatus*	17.2	3.8
A5	2	0.316	*Anthophylax attenuatus*	24.2	4.6
A5	3	0.363	*Anthophylax attenuatus*	n/a	3.7
A5	5	0.355	*Anthophylax attenuatus*	18.5	3.7
A5	6	0.303	*Anthophylax attenuatus*	25.5	4.6
A5	7	0.266	*Anthophylax attenuatus*	13.5	3.2
A5	4	0.394	*Bellamira scalaris*	n/a	2.8
A6	1	0.337	*Anthophylax attenuatus*	19.9	4
A6	2	0.315	*Anthophylax attenuatus*	9.2	2.2

10.7 (Continued)

Snag	Id	Wood density (g/cm^3)	Species	Body length (mm)	Head capsule width (mm)
A6	3	0.338	*Anthophylax attenuatus*	5.3	1.4
A6	4	0.353	*Anthophylax attenuatus*	8	2
A6	5	0.321	*Anthophylax attenuatus*	6.7	1.5
A6	6	0.271	*Anthophylax attenuatus*	7.8	1.8
A6	7	0.289	*Anthophylax attenuatus*	8.3	2
A6	8	0.336	*Anthophylax attenuatus*	7.5	1.5
A6	9	0.272	*Anthophylax attenuatus*	18.5	3.8
A6	10	0.344	*Anthophylax attenuatus*	n/a	2.3
A6	11	0.338	*Anthophylax attenuatus*	12.7	2.9
A6	12	0.326	*Anthophylax attenuatus*	7.4	1.5
A6	13	0.304	*Anthophylax attenuatus*	8.5	1.7
A6	14	0.285	*Anthophylax attenuatus*	9	1.9
A6	15	0.317	*Anthophylax attenuatus*	11.6	2.9
A6	16	0.311	*Anthophylax attenuatus*	17.7	3.8
A6	17	0.278	*Anthophylax attenuatus*	5.1	1.1
A6	18	0.350	*Anthophylax attenuatus*	12.2	2.7
A6	19	0.317	*Anthophylax attenuatus*	11.8	2.6
A6	20	0.280	*Anthophylax attenuatus*	10	1.8
A6	21	0.298	*Anthophylax attenuatus*	19.3	3.7
A6	22	0.238	*Anthophylax attenuatus*	14.1	3
A6	23	0.275	*Anthophylax attenuatus*	19.2	3.6
A6	24	0.258	*Anthophylax attenuatus*	10.6	2
A6	25	0.337	*Anthophylax attenuatus*	10.8	2.3
A6	26	0.300	*Anthophylax attenuatus*	n/a	2.1
A6	27	0.275	*Anthophylax attenuatus*	n/a	n/a
A6	28	0.256	*Anthophylax attenuatus*	11.2	2.6
A6	29	0.338	*Anthophylax attenuatus*	6	1.5
A7	1	0.287	*Anthophylax attenuatus*	20	4.1
A7	2	0.225	*Anthophylax attenuatus*	16.7	3.3
A7	3	0.384	*Anthophylax attenuatus*	17.1	3.8
A7	4	0.417	*Anthophylax attenuatus*	20.3	4.1
A7	5	0.402	*Anthophylax attenuatus*	11.8	2.5
A7	6	n/a	*Anthophylax attenuatus*	15.5	2.8
A7	7	0.220	*Anthophylax attenuatus*	16.4	3.2
A7	8	0.175	*Anthophylax attenuatus*	12.6	2.5
A7	9	0.311	*Anthophylax attenuatus*	15.2	3.6
A7	11	0.361	*Anthophylax attenuatus*	12.5	2.7
A7	12	0.399	*Anthophylax attenuatus*	15.1	2.7
A7	13	0.341	*Anthophylax attenuatus*	9.8	2
A7	14	0.317	*Anthophylax attenuatus*	17.5	3.6
A7	15	0.364	*Anthophylax attenuatus*	28.2	4.2
A7	16	0.273	*Anthophylax attenuatus*	14.9	2.9
A7	17	0.337	*Anthophylax attenuatus*	20.2	4.1
A7	18	0.332	*Anthophylax attenuatus*	23	4.4

10.7 (Continued)

Snag	Id	Wood density (g/cm^3)	Species	Body length (mm)	Head capsule width (mm)
A7	19	0.326	*Anthophylax attenuatus*	n/a	n/a
A7	20	0.263	*Anthophylax attenuatus*	17.8	3.4
A7	21	0.252	*Anthophylax attenuatus*	21.7	4.1
A7	22	0.267	*Anthophylax attenuatus*	19.3	4.6
A7	23	0.272	*Anthophylax attenuatus*	15.2	3.5
A7	24	0.233	*Anthophylax attenuatus*	21.1	4.2
A7	25	0.237	*Anthophylax attenuatus*	21.3	4.4
A7	30	0.295	*Anthophylax attenuatus*	14	3.4
A7	31	0.287	*Anthophylax attenuatus*	24.8	4.5
A7	32	0.271	*Anthophylax attenuatus*	15.3	2.9
A7	33	0.396	*Anthophylax attenuatus*	21.5	4.3
A7	34	0.330	*Anthophylax attenuatus*	19.7	3.9
A7	35	0.400	*Anthophylax attenuatus*	14.8	3
A7	36	0.347	*Anthophylax attenuatus*	20.3	4.3
A7	37	0.317	*Anthophylax attenuatus*	18.2	3.3
A7	38	0.354	*Anthophylax attenuatus*	24	4.4
A7	39	0.373	*Anthophylax attenuatus*	18.2	3.3
A7	40	0.400	*Anthophylax attenuatus*	23.8	4.5
A7	41	0.425	*Anthophylax attenuatus*	18	3.6
A7	42	0.334	*Anthophylax attenuatus*	11.1	2
A7	43	0.420	*Anthophylax attenuatus*	18.8	3.9
A7	44	0.413	*Anthophylax attenuatus*	12.4	2.4
A7	45	0.379	*Anthophylax attenuatus*	20.6	4.3
A7	46	0.404	*Anthophylax attenuatus*	15.2	2.8
A7	47	0.385	*Anthophylax attenuatus*	24.7	4.3
A7	48	0.468	*Anthophylax attenuatus*	15.6	3.5
A7	49	0.465	*Anthophylax attenuatus*	18.2	4
A7	50	0.351	*Anthophylax attenuatus*	25.2	4.5
A7	51	0.332	*Anthophylax attenuatus*	13.9	3
A7	52	0.415	*Anthophylax attenuatus*	19	3.9
A7	53	0.368	*Anthophylax attenuatus*	24	4.5
A7	54	0.331	*Anthophylax attenuatus*	23.4	4.2
A7	55	0.300	*Anthophylax attenuatus*	12.2	2.5
A7	10	0.255	*Bellamira scalaris*	16.6	3.5
A7	26	0.204	*Bellamira scalaris*	16.1	3.3
A8	1	0.366	*Anthophylax attenuatus*	23.4	4.4
A8	2	0.341	*Anthophylax attenuatus*	6.1	1.1
A8	3	0.314	*Anthophylax attenuatus*	9.6	2
A8	4	0.332	*Anthophylax attenuatus*	19.4	3.9
A8	5	0.321	*Anthophylax attenuatus*	13.1	3
A8	6	0.342	*Anthophylax attenuatus*	6.5	1.3
A8	7	0.398	*Anthophylax attenuatus*	9.6	2.3
A8	8	0.333	*Anthophylax attenuatus*	10.7	2.2
A8	9	0.369	*Anthophylax attenuatus*	12.5	2.7

10.7 (Continued)

Snag	Id	Wood density (g/cm^3)	Species	Body length (mm)	Head capsule width (mm)
A8	10	0.388	*Anthophylax attenuatus*	8.8	1.7
A9	1	0.393	*Anthophylax attenuatus*	20.1	3.8
A9	2	0.305	*Anthophylax attenuatus*	9.8	2.3
A9	3	0.351	*Anthophylax attenuatus*	14.2	2.9
A9	4	0.380	*Anthophylax attenuatus*	n/a	n/a
A9	5	0.302	*Anthophylax attenuatus*	18.6	3.7
A9	6	0.374	*Anthophylax attenuatus*	17.1	3.5
C1	1	0.350	*Bellamira scalaris*	n/a	n/a
C1	4	0.212	*Bellamira scalaris*	20	3.7
C1	5	0.262	*Bellamira scalaris*	20.9	3.1
C1	6	0.301	*Bellamira scalaris*	23.3	4.7
C1	7	0.329	*Bellamira scalaris*	14.1	2.4
C1	2	0.403	*Trachysida mutabilis*	n/a	n/a
C1	3	0.304	*Trachysida mutabilis*	n/a	n/a
C1	8	0.250	*Trachysida mutabilis*	n/a	n/a
C2	1	0.241	*Bellamira scalaris*	31.2	4.6
C2	2	0.322	*Bellamira scalaris*	32.6	4.6
C2	3	0.207	*Bellamira scalaris*	n/a	n/a
C2	4	0.262	*Bellamira scalaris*	13.7	2.7
C2	5	0.298	*Bellamira scalaris*	33	4.2
C2	6	0.422	*Bellamira scalaris*	31.7	4.5
C2	7	0.307	*Bellamira scalaris*	12	2.4
C2	8	0.468	*Bellamira scalaris*	n/a	n/a
C2	9	0.223	*Bellamira scalaris*	20.6	3.2
C2	10	0.368	*Bellamira scalaris*	29	5
C2	11	0.370	*Bellamira scalaris*	n/a	n/a
C3	1	0.271	*Bellamira scalaris*	n/a	n/a
C3	3	0.186	*Bellamira scalaris*	n/a	n/a
C3	4	0.226	*Bellamira scalaris*	n/a	n/a
C3	12	0.154	*Bellamira scalaris*	n/a	n/a
C4	1	0.295	*Anthophylax attenuatus*	10	1.8
C4	2	0.246	*Anthophylax attenuatus*	9.1	1.6
C4	3	0.206	*Anthophylax attenuatus*	11.2	1.9
C4	5	0.335	*Anthophylax attenuatus*	13	2.5
C4	7	0.218	*Anthophylax attenuatus*	5.3	1.6
C4	8	0.319	*Anthophylax attenuatus*	5.2	1.9
C4	4	0.244	*Bellamira scalaris*	n/a	n/a
C4	6	0.174	*Bellamira scalaris*	n/a	n/a
C6	1	0.204	*Bellamira scalaris*	n/a	n/a
C6	2	0.294	*Bellamira scalaris*	n/a	n/a
C6	3	0.396	*Bellamira scalaris*	n/a	n/a
O1	1	0.218	*Anthophylax attenuatus*	10.5	2.3
O1	2	0.212	*Anthophylax attenuatus*	11.2	2.2
O2	1	0.210	*Bellamira scalaris*	16	2.6

10.7 (Continued)

Snag	Id	Wood density (g/cm^3)	Species	Body length (mm)	Head capsule width (mm)
O3	1	n/a	*Anthophylax attenuatus*	28.9	4.3
O3	2	0.257	*Anthophylax attenuatus*	21.4	3.9
O3	4	0.327	*Anthophylax attenuatus*	21	4.1
O3	7	0.304	*Anthophylax attenuatus*	22	3.8
O3	3	0.303	Other	10.9	2.5
O3	5	0.360	*Bellamira scalaris*	37.2	4.9
O3	6	0.289	*Bellamira scalaris*	24.1	3.7
O3	8	0.237	*Bellamira scalaris*	11.8	2
O6	1	0.360	*Anthophylax attenuatus*	22.5	4.5
O6	2	0.375	*Anthophylax attenuatus*	20.5	4