Diss ETH No. 13236

Limiting factors of saproxylic insects: habitat relationships of an endangered ecological group

A dissertation submitted to the
SWISS FEDERAL INSTITUTE OF TECHNOLOGY
for the degree of
Doctor of natural sciences

presented by
Karin Gertrud Schiegg Pasinelli
Diploma in Zoology
University of Zurich
born March 27 1968
from
Olten, Solothurn, Steckborn, Thurgau, Zürich, Zürich

accepted on the recommendation of

Prof. Dr. Klaus C. Ewald, examiner
Prof. Dr. Peter Duelli, coexaminer

1999

'Preserving biodiversity requires us to see a forest as a community of species rather than a wood factory'

(Simberloff 1999)

Acknowledgements

I express my gratitude to K.C. Ewald for the opportunity to carry out this dissertation in his research group and to P. Duelli for many fruitful discussions and inputs. B. Merz patiently introduced me into the world of Diptera and gave selfless aid whenever needed. Many discussions with W. Suter enlarged my horizon in all directions of conservation biology. M. Obrist managed the species data, P. Wirz provided sophisticated technical support and from T. Walter I learnt a lot about insect ecology. Many thanks are also due to all the experts who identified the species for me and to the colleagues that helped me with dead wood recording. I also would like to thank my parents which made it possible for me to study. My deepest thank goes to my beloved Gilberto for being with me during all phases of the study and especially for carefully reading my manuscripts. The Swiss National Science Foundation supported this study with the grant No 31-45’911.95.

Contents

Zusammenfassung

Die jahrhundertelange intensive Waldbewirtschaftung, insbesondere die radikale Entfernung von totem und absterbendem Holz wirkte sich sehr negativ auf die Artenvielfalt aus. Nebst dem Verlust von Lebensraum wird auch die Isolation von Populationen für die schwindenden Artenzahlen von Totholzinsekten verantwortlich gemacht. Es fehlen jedoch quantitative Daten über den Einfluss der Menge und räumlichen Verteilung von Totholz auf die Artenzahl und Diversität von Totholzinsekten. Solche Angaben sind unerlässlich, um wirkungsvolle Schutzmassnahmen für diese Gruppe zu erarbeiten.

In den Jahren 1996 und 1997 fing ich in 14 Probeflächen ($r = 200m$) im Naturwaldreservat Sihlwald (Kt. Zürich, Schweiz) Insekten mit Eklektoren und modifizierten Fensterfallen. Zudem kartierte ich in allen Probeflächen das vorhandene Totholz mit einem Durchmesser von mindestens 20 cm. Aufgrund der erhobenen Daten untersuchte ich den Einfluss der Menge, räumlichen Anordnung und der Dimension von Totholz auf die Artenzahl und Diversität von totholzlebenden Zweiflüglern (Diptera) und Käfern (Coleoptera).

Das erste Kapitel der vorliegenden Arbeit zeigt, dass sich in toten Buchenästen *Fagus sylvatica* mit einem Durchmesser zwischen 5 - 10 cm mehr Arten und eine höhere Diversität von totholzlebenden Dipteren und Käfern entwickeln als in toten Buchenstämmen mit einem Durchmesser von mindestens 20 cm. Die Art-Abundanzverteilungen von Dipteren und Käfern unterscheiden sich nicht voneinander, was zeigt, dass der Lebensraum die relativen Häufigkeiten der Arten eher beeinflusst als taxonomische Beziehungen. In eine ähnliche Richtung deutet der Befund, dass die Artengemeinschaften, die sich in den Stämmen entwickelt haben, einer log-normalen Abundanzverteilung folgen, die der Äste jedoch nicht. Es scheint daher, dass die Artengemeinschaften der Äste und Stämme sowohl bei den Dipteren als auch bei den Käfern als zwei eigenständige Gruppen zu betrachten sind.

Im zweiten Kapitel untersuche ich den Einfluss der Menge und räumlichen Verteilung von Totholz auf die Diversität von totholzlebenden Dipteren und Käfer. Dabei betrachte ich einzelne Totholzstücke als 'Habitatinseln'. Entsprechend werden die Begriffe 'Inselgrösse' als 'Volumen eines Totholzstückes' und 'Vernetzung von Inseln' als 'Vernetzung von Totholzstücken' definiert. Das durchschnittliche Volumen von Totholz mit einem Durchmesser von mindestens 20 cm betrug 6.3 $m^3 ha^{-1}$, was rund 2 % des Holzvorrates entspricht. Die Analysen ergeben, dass die Diversität dieser Insektengruppen weniger vom vorhandenen Totholzvolumen in einer Fläche, als vielmehr von der räumlichen Anordnung der einzelnen Totholzstücke bestimmt wird: Je gleichmässiger die Stücke im Raum verteilt

sind, desto höher ist die Artenzahl und Diversität der Dipteren und Käfer. Enthalten also zwei Flächen die gleiche Menge Totholz, so ist diejenige Fläche artenreicher, in welcher die mittleren Abstände zwischen einzelnen Totholzstücken kleiner sind. Dies deutet darauf hin, dass Isolationseffekte bei Totholzinsekten bereits auf lokaler Ebene auftreten können, was wiederum auf eine geringe Mobilität vieler Arten schliessen lässt.

Im dritten Kapitel werden diejenigen Dipteren- und Käferarten betrachtet, die auf eine hohe Vernetzung von Totholzstücken angewiesen sind. Diese Arten werden mit drei verschiedenen Methoden zur Festlegung von biologischen Charakterarten bestimmt. Die biologischen Merkmale dieser Arten werden mit den Merkmalen der übrigen Arten verglichen. Arten, die charakteristisch für Flächen mit einer hohen Vernetzung von Totholz sind, sind in einem höheren Grad spezialisiert und häufiger mit seltenen Totholzstrukturen assoziiert als andere Arten. Zudem weisen sie einen höheren Anteil an Rote-Liste Arten auf. Diese Eigenschaften sind typisch für Arten, die auf eine hohe Kontinuität ihres Lebensraumes angewiesen sind.

Der letzte Teil der Arbeit gibt eine Übersicht über die gefangenen Artenzahlen und beschreibt einen von mir entwickelten Eklektortyp. Insgesamt wurden 699 Käferarten (29'690 Individuen) und 953 Dipterenarten (61'866 Individuen) nachgewiesen. Von den letzteren sind 186 Arten neu für die Schweiz. Zusätzlich wurden noch etwa 20 Dipterenarten gefunden, die der Wissenschaft bisher unbekannt waren. Der Einfluss der räumlichen Heterogenität auf die gefangenen Arten ist gering, mit nur 50 % der Fallen können rund 75 % der Arten nachgewiesen werden, unabhängig davon, ob die Anzahl Fallen pro Standort oder die Anzahl Standorte reduziert worden ist. Drei verschiedene Methoden zur Schätzung der Artenzahl lassen vermuten, dass sich im Sihlwald rund ¼ der gesamten in der Schweiz bekannten Dipterenarten befinden und knapp $^1/_6$ aller Käferarten der Schweiz.

Aufgrund dieser Arbeit können folgende Schlüsse für die Bewirtschaftung von Wäldern der collinen Stufe Mitteleuropas gezogen werden: Anstrengungen, um Totholz in den Wäldern zu fördern, dürfen sich nicht nur auf starkes Totholz beschränken, sondern müssen auch dicke Äste einschliessen. Somit kann ein wertvoller Beitrag zur Förderung der Biodiversität geleistet werden, wenn beispielsweise auf eine Schlagräumung verzichtet wird. Im weiteren sollte Totholz möglichst auf der gesamten Waldfläche gefördert werden, um ein gleichmässiges Angebot an Lebensraum für Totholzinsekten zu bieten und damit zu verhindern, dass Teile von Populationen voneinander isoliert werden. Alternativ könnten bereits ausgeschiedene Totholzinseln miteinander durch totholzreiche Korridore verbunden werden.

Summary

The intensive forest management during the last centuries has greatly reduced biodiversity in forests. Mainly the consequent removal of dead and dying wood resulted in a considerable loss of species. Beside the destruction of their habitat, saproxylic insects are suspected to suffer from fragmentation effects. However, there are no quantitative data about the influence of the amount and spatial arrangement of dead wood on species richness and diversity of saproxylic insects. Furthermore, the ultimate causes why this group should be particularly vulnerable to fragmentation are purely speculative. Such data are indispensable, however, to develop effective conservation strategies for these species.

In the forest reserve Sihlwald (Kt. Zurich, Switzerland), I collected in 14 sites ($r = 200m$) in 1996 and 1997 insects by eclectors and trunk-window traps. In each site, all pieces of dead wood larger than 20 cm in diameter were measured and their location recorded on a map. Based on these data, I explored the influence of dead wood dimension, volume and spatial arrangement on species richness and diversity of saproxylic Diptera and Coleoptera.

The first chapter demonstrates that limbs of beech, *Fagus sylvatica*, with a diameter of 5-10 cm host more species and a higher diversity of saproxylic Diptera and Coleoptera than logs of beech with a diameter of at least 20 cm. The species abundance distributions of Diptera and Coleoptera do not differ, indicating that the habitat rather than taxonomic relations determine relative species abundances. This view is supported by the fact that the species having emerged from logs, display a lognormal species abundance distribution but not those having emerged from limbs. This may indicate that limbs and logs may harbour different communities of saproxylic insects.

In the second chapter, I investigate the effects of the amount and spatial arrangement of dead wood on species richness and diversity of saproxylic Diptera and Coleoptera. Based on landscape ecological approaches, I consider single dead wood pieces as 'habitat islands'. Accordingly, the term 'patch size' is defined as 'volume of a piece of dead wood' and 'patch connectivity' as 'connectivity of single dead wood pieces'. Dead wood volume averages out at 6.3 m^3 ha^{-1} ,which is about 2 % of the wooden biomass in the Sihlwald. It is demonstrated that dead wood connectivity enhances species richness and diversity of saproxylic Diptera and Coleoptera, whereas the amount of dead wood present plays only a secondary role. Hence, when regarding two sites with the same amount of dead wood present, the site with the shorter mean distances between single dead wood pieces will contain more species than the other site.

The third chapter is dedicated to the species of saproxylic Diptera and Coleoptera that are characteristic for high dead wood connectivity. These species are identified using three different approaches. Species dependent on high dead wood connectivity share particular biological traits: They are closer habitat specialists and more often associated with rare dead wood types than other species. Further, they comprise a higher proportion of red list species. These are attributes that characterise species requiring high continuity of their habitat.

The fourth and last chapter gives an overview about the species numbers collected in the course of this study and describes the advantages of a new eclector type that I have developed. Totally, 699 species of Coleoptera (29'690 individuals) and 953 species of Diptera (61'866 individuals) have been identified. Among the latter are 186 species that have been recorded for the first time in Switzerland. Additionally, some 20 species of Diptera are new to science. Spatial heterogeneity did not greatly influence the species collected. Only 50 % of the traps yielded approximately 75 % of the species irrespective whether the number of traps per site or the number of sites has been reduced. Based on three methods for estimating total species richness about ¼ of the dipteran species recorded in Switzerland are supposed to be found in the Sihlwald and nearly $^1/_6$ of the Swiss beetle species.

The investigation presented here demonstrates that efforts made to preserve saproxylic insects should not only focus on dead wood of larger dimensions but must also include limbs. Furthermore, it is indispensable to leave dead wood distributed over the whole forest area to create a continuous supply of habitat for saproxylic insects and to prevent isolation effects. Alternatively, dead wood islands could be connected by corridors with large amounts of dead wood.

General introduction

The role of dead wood and of saproxylic insects in forest ecosystems

The intensive forest management in Central Europe during the last centuries has led to radical changes in forest area, structure and tree species composition (Heydemann 1982; Leibundgut 1993; Scherzinger 1996). In particular, old and dead trees have been continuously removed and consequently, the saproxylic fauna impoverished (Speight 1989; Hilt & Ammer 1994; Kaila et al. 1994). In natural forests, dead wood amounts can be as high as 200- 300 m^3 ha^{-1} (Korpel 1995), whereas in commercial forests, only 1-5 m^3 ha^{-1} are found (Albrecht 1991). Dead wood, however, is a key element in forest ecosystems, influencing their biological, physical and biochemical processes (e.g. Elton 1966; Maser & Trappe 1984) and providing habitat for a large variety of species. Approximately 20 % of the whole forest fauna is supposed to depend in some way or another on dead wood (Elton 1966; Harding & Rose 1986). Saproxylic insects form the largest and probably most vulnerable group among all dead wood species. 'Saproxylic' has been defined by Speight (1989) as 'to be dependent, during some part of the life cycle, upon dead or dying wood, or wood inhabiting fungi, or upon the presence of other saproxylic species'. Saproxylic insects not only contribute significantly to biodiversity in forests; as decomposers they also strongly influence nutrient supply and thus primary production (Didham et al. 1996). Hence, saproxylic insects must be regarded as ecological engineers, namely 'organisms that cause physical changes in their environment and modulate the availability of resources to other species' (Jones et al. 1994). Beside their central role in nutrient cycling, saproxylic insects are also an essential food resource for birds and mammals (Hutson 1978).

Saproxylic insects as an endangered ecological group

Today, some 90% of all saproxylic invertebrates are extinct or in need of protection (Speight 1989). Most saproxylic insects are closely associated with particular micro-habitats, mainly defined by stage of decay, moisture content, or moss cover of the dead wood (Warren and Key 1991). Particularly, some species depend on structures hardly found in commercial forests, such as hollow trees or burnt tree parts. In general, saproxylic species are adapted to the stable conditions in old-growth forests where dead wood of various qualities is abundant.

On the one hand, a high degree of specialisation is the basis of a community with a large number of coexisting species. On the other hand, habitat specialists generally are more sensitive to environmental alterations than generalists (Lawton 1995). Furthermore, ecological theory predicts that species occurring in stable habitats have low dispersal abilities and are therefore more vulnerable to habitat fragmentation than species adapted to unstable environments (Johnson & Gaines 1990; Noss & Csuti 1997). Consequently, some authors believe that saproxylic insects are poorly mobile and are therefore particularly vulnerable to habitat loss and isolation (Speight 1989; Warren & Key 1991; Nilsson & Baranowski 1997). However, there is only indirect evidence for such relations in saproxylic insects: The studies of Økland (1996) and of Nilsson & Baranowski (1997) revealed long-lasting changes in saproxylic communities due to past human disturbances. They conclude that recolonisation of habitats occurs only at a low rate, if at all. There is an urgent need for quantitative data on the habitat relationships of saproxylic insects and especially on the effects of fragmentation. Only on this basis promising conservation strategies can be developed.

Insects are not vertebrates

A large variety of studies report on the deleterious effects of habitat fragmentation on birds or mammals (see Saunders et al. 1991; Andrén 1994 for reviews), but the influence of habitat fragmentation on insect diversity is only poorly understood. Often, knowledge gained from the study of vertebrates (mostly birds) is applied to insects without being questioned (see Thomas 1994 for a review). The key for understanding the consequences of habitat loss and insularisation is to choose the appropriate scale, which is defined by the movement patterns of the focal organisms. Vertebrates and insects differ fundamentally in their dispersal abilities and guidelines about habitat connectivity drawn from bird studies may not apply to insects. Another field where studies on vertebrates govern conservation decisions is the focus on dead wood of larger dimensions: Efforts to increase dead wood amounts in managed forests mostly include solely pieces of larger dimensions, which are thought to be ecologically more valuable than limbs, branches or twigs (Rauh 1993; McCarthy & Baily 1994). It is argued that only snags (i. e., standing dead trees) and logs (i.e., fallen dead trees) can be used as shelter or nesting site for birds and mammals. Furthermore, small pieces are considered to be inappropriate for the development of saproxylic insects due to their stronger microclimatic fluctuations (Boddy 1983). The relative significance of branches or limbs and logs or snags for saproxylic insect diversity, though, has not been investigated yet.

Ecological research based on insects

Insects are increasingly appreciated in ecological research as powerful indicators of habitat quality due to the close and precise relationships with the environment of some species (Hengeveld 1986). Hence, investigations into the invertebrate fauna may be more representative of overall biodiversity than conventional plant and vertebrate surveys (Oliver et al. 1998). Usually, large insect samples are compiled in the course of ecological studies. These samples, however, frequently are analysed and published only partly. Consequently, valuable information about faunistically interesting species or the efficiency of the sampling techniques gets lost. Especially the latter aspect is of fundamental importance for consecutive studies, which can profit from formerly gained experience. A major drawback in ecological research on insects is the cost and time intensive sampling. Several authors propose methods for standardised sampling (e. g. Albrecht 1990; Duelli 1997) providing a basis to compare the outcomings of different investigations as well as to reduce sampling effort without considerable loss of information. Exploring the effects of spatial and temporal variability on the species numbers and abundances collected, provides a basis for developing habitat-specific standard sampling techniques.

Objectives

The aim of this investigation is to quantify the effects of the amount, spatial arrangement and dimension of dead wood on species richness and diversity of saproxylic Diptera and Coleoptera. In the first part of this study, I test the hypothesis that logs host more saproxylic insect species than limbs by comparing species diversity of saproxylic Diptera and Coleoptera breeding in logs and limbs. Additionally, the differences in the species abundance distributions of the two assemblages are discussed and a lognormal model to estimate true species richness is applied. The second part focuses on whether increasing dead wood volume and connectivity leads to an increase of species diversity and to a change in species composition of saproxylic insects. In the third part, I identify species that are characteristic for sites with high dead wood connectivity using three different approaches. The biological attributes, such as degree of habitat specificity or diet, of these species and of the other species are compared. The last part is devoted to the species collected during this study. I explore the effects of spatial and temporal variability on the species collected and apply parametric and non-parametric models as well as rarefaction techniques to estimate species richness. Finally, I present a modified trap type developed in the course of this investigation and discuss its efficiency in comparison with other traps.

References

Albrecht, L. 1990. Naturwaldreservate in Bayern. Band 1. Schriftenreihe Naturwaldreservate in Bayern. IHW-Verlag.

Albrecht, L. 1991. Die Bedeutung des toten Holzes im Wald. Forstwissenschaftliches Centralblatt 110: 106-113.

Andrén, H. 1994. Effects of habitat fragmentation on birds an mammals in landscapes with different proportions of suitable habitat: A review. Oikos 71: 355-366.

Boddy, L. 1983. Microclimate and moisture dynamics of wood decomposing in terrestrial ecosystems. Soil Biology and Biochemistry 15: 149-157.

Didham, R.K., Ghazoul, J., Stork, N.E., Davis, A.J. 1996. Insects in fragmented forests: a functional approach. Trends in Ecology and Evolution 11: 255-260.

Duelli, P. 1997. Biodiversity evaluation in agricultural landscapes: An approach at two different scales. Agriculture, Ecosystems and Environments 62: 81-91.

Elton, C.S. 1966. Dead and dying wood: the pattern of animal communities. John Wiley & Sons Inc. New York.

Harding, P. & Rose, F. 1986. Pasture woodlands in lowland Britain. A review of their importance for wildlife conservation. Inst. Terr. Ecology/Huntingdon.

Hengeveld, R. 1986. Insect conservation and biological processes. Proceedings of the 3rd European Congress on Entomology: 449-452.

Heydemann, B. 1982. Der Einfluss der Waldwirtschaft auf die Ökosysteme aus zoologischer Sicht. Waldwirtschaft und Naturhaushalt (Deutscher Rat für Landespflege) 40: 926-944.

Hilt, M. & Ammer, U. 1994. Totholzbesiedelnde Käfer im Wirtschaftswald - Fichte und Eiche im Vergleich. Forstwissenschaftliches Centralblatt 113: 245-255.

Hutson, M.A. 1978. Associations with vertebrates, their nests, roosts and burrows. In: Stubbs, A.E. & Chandler, P. (eds.). A Dipterist's handbook. The Amateur Entomologist 15. pp 134-151.

Johnson, M.L. & Gaines, M.S. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annual Reviews in Ecology and Systematics 21: 449-480.

Jones, C.G., Lawton, J.H., Shachak, M. 1994. Organisms as ecosystem engineers. Oikos 69: 373-386.

Kaila, L., Martikainen, P., Punttila, P., Yakovlev, E. 1994. Saproxylic beetles (Coleoptera) on dead birch trunks decayed by different polypore species. Annales Zoologici Fennici 31: 97-107.

Korpel, S. 1995. Die Urwälder der Westkarpaten. Fischer Verlag, Stuttgart, Jena, New York.

Lawton, J.H. 1995. Population dynamic priciples. In: Lawton, J.H. & May, R.M. (eds.). Extinction rates. Oxford University Press, Oxford. pp 147-163.

Leibundgut, H. 1993. Europäische Urwälder: Wegweiser zur naturnahen Waldwirtschaft. Verlag Paul Haupt, Berlin und Stuttgart.

McCarthy, B. & Bailey, R.1994. Distribution and abundance of coarse woody debris in a managed forest landscape of the central Appalachians. Canadian Journal of Forest Research: 245: 1317-1329.

Maser, C. & Trappe, J. 1984. The seen and unseen world of the fallen tree. USDA, General Technical Report GTR-PNW-164.

Nilsson, S. & Baranowski, R. 1997. Habitat predictability and the occurrence of wood beetles in old-growth beech forests. Ecography 20: 491-498.

Noss, R.F. & Csuti, B. 1997. Habitat fragmentation. In: Meffe, G.K. & Carroll, C.R. (eds). Principles of conservation biology. 2nd edition. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts. pp 269-304.

Økland, B. 1996. Unlogged forests: important sites for preserving the diversity of Mycetophilids (Diptera: Sciaroidea). Biological Conservation 76: 297-310.

Oliver, I., Beattie, A.J., York, A. 1998. Spatial fidelity of plant, vertebrate, and invertebrate assemblages in multiple-use forest in Eastern Australia. Conservation Biology 12: 822-835.

Rauh, J. 1993. Naturwaldreservate in Bayern. Band 2. Schriftenreihe Naturwaldreservate in Bayern. IHW-Verlag.

Saunders, D., Hobbs, R., Margules, C. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5: 18-32.

Scherzinger, W. 1996. Naturschutz im Wald. Ulmer Verlag, Stuttgart.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Nature and environment Series No. 42. Strasbourg.

Thomas, J.A. 1994. Why small cold-blooded insects pose different conservation problems to birds in modern landscapes. Ibis 137: S112-S119.

Warren, M.S. & Key, R.S. 1991. Woodlands: past, present potential. In: Collins, N.M. & Thomas J.A. (eds). The conservation of insects and their habitats. Academic Press, London. pp 160-212.

I Saproxylic Insect Diversity of Beech: Limbs are Richer than Logs

KARIN SCHIEGG

Abstract - Dead wood of larger dimensions is thought to be ecologically more important than dead wood of smaller dimensions such as limbs. I tested the hypothesis that logs host more saproxylic insect species than fallen dead limbs by comparing species richness, diversity and species abundance distributions of saproxylic Diptera and Coleoptera reared from logs and limbs of beech *Fagus sylvatica*. In both insect groups, limbs hosted more species and a higher diversity than logs. The species abundance distributions of Diptera and Coleoptera did not differ, indicating that the habitat rather than taxonomic relations determined relative species abundances. This view is supported by the fact that the species having emerged from logs, displayed a lognormal species abundance distribution but not those having emerged from limbs. This indicates that limbs and logs may harbour different communities of saproxylic insects. Activities for maintaining and enhancing forest biodiversity must include the preservation of dead timber of all sizes.

Introduction

A aim of modern conservation biology is to provide the scientific basis for conservation strategies. Practical conservation efforts, however, are often based on traditional beliefs and paradigms that have not been questioned. For instance, the importance of dead wood (coarse woody debris) in forest ecosystems has repeatedly been stated (e.g. Elton 1966; Maser & Trappe 1984; Kirby 1992; Kaila et al. 1994; Haase et al. 1998), but actions undertaken to increase the volume of dead wood in managed forests only focus on pieces of larger dimensions, which are thought to be ecologically more valuable than smaller pieces (Rauh 1993; McCarthy & Baily 1994). The argument goes that only snags (i. e. standing dead trees) and logs (fallen dead trees) can be used as shelters or nesting sites for birds and mammals. Furthermore, limbs are considered inappropriate for the development of saproxylic insects because of their stronger microclimatic fluctuations (Boddy 1983). Consequently, fallen limbs on the forest floor often are removed. Saproxylic insects form the largest and probably most vulnerable group among all the dead wood species. As yet no study has focused on the significance of dead wood dimensions for this group, though some authors have included dead wood pieces of smaller dimensions in their studies (Schmitt 1992; Rauh 1993, Hilt & Ammer 1994; Kleinevoss et al. 1996; Haase et al., 1998). I tested the hypothesis that logs host more saproxylic insect species than limbs by comparing species diversity and abundance distribution of saproxylic Diptera and Coleoptera breeding in logs and limbs. The results have practical implications for forest management strategies aiming at the maintenance and promotion of biodiversity in forests.

Methods

Study area

The study was carried out in the forest reserve of Sihlwald (47°15'; 8°33') on a NE-facing slope 10 km south of Zurich, Switzerland. The entire forest covers 10 km^2 and is dominated by beech *Fagus sylvatica* and spruce *Picea abies*, followed by ash *Fraxinus excelsior* and fir *Abies alba*. Dead wood averages out at 6.3 m^3 ha^{-1} and consists mainly of logs of beech and spruce (own unpubl. data). I selected 14 study plots similar to each other in terms of exposition, stand structure and age as well as tree species composition.

Data collection

Insects were collected using eclectors which are also called 'extraction cylinders' (Økland 1996) or 'emergence traps' (Irmler et al. 1996, Hövemeyer 1999). This trap type has been developed by Funke (1971) and resembles the Owen's trap (Owen 1989, 1992). Due to the tent-like construction of eclectors, pieces of dead wood can be enclosed to rear saproxylic insects. Emerging insects are attracted by the attached collecting vials which are the only source of light in the trap. This principle has been used successfully in various studies on saproxylic insects (Schmitt 1992; Hilt & Ammer 1994; Kleinevoss et al. 1996). I developed a modified eclector type, which can also be used on fallen dead wood in contact with the forest floor (Chapter 4). Four eclectors were installed in each of the 14 sites, two containing a part of a log (diameter at the smaller end > 20 cm, L = 1.5 m, log eclectors) and two containing limbs (diameter at both ends 5-10 cm, L = 1.0-1.5 m, limb eclectors), giving 28 traps of each type, 56 in total. The limbs were collected from the forest floor within 10 m around the traps and they did not posses side branches. I measured the length and diameter of each piece of dead wood and calculated the surface area and volume enclosed in each trap. Only dead beech wood at a medium stage of decay (presence of insect holes, bark partly loose) was considered to minimise between trap variation due to other factors than dead wood volume. The collecting vials were filled with a 2 % formaldehyde solution and emptied monthly from April - November 1996. All specimens of Diptera and Coleoptera were identified to species level by various specialists except for Psychodidae, Chironomidae, Cecidomyiidae, and Phoridae.

Species classification

All species were classified whether to be obligate saproxylic, facultative saproxylic, or independent of dead wood. Facultative saproxylic species are those that may also breed in decaying matter other than dead wood. Only saproxylic and facultative saproxylic species were included in the analyses. As eclectors are highly specific traps, I assumed that the inclusion of facultative saproxylics would cause an error so small as to be negligible. All classifications were based on McAlpine (1981), Freude et al. (1964-1983); Koch (1989-1992), Smith (1989), and on information given by the specialists who identified the species. In context with the promotion of dead wood in commercial forests, foresters often fear the outbreak of potentially hazardous species, so-called forest pests. I classified a beetle species as a potential forest pest, when it was recorded by Schwenke (1982) as having caused considerable damage to forest stands. Koch (1989-1992) gives information about the diet of all beetle species known from Central Europe. Based on this reference, I categorised each beetle species whether to be predatory (i. e. feeding mainly on other living arthropods, see also Hammond 1997) or not. Koch (1989-1992) also divides Central European beetle species into stenotopic, eurytopic and ubiquistic species (see also Rauh 1993) and I classified each species according to these categories. Ecological literature on saproxylic Diptera still is sparse, I could therefore only divide this group into predatory and non-predatory species, based on data given by McAlpine et al. (1981), Schwenke (1982), and Smith (1989). Species that were collected only from limbs or only from logs were called exclusive species. The data from each trap were pooled over the year.

Diversity measurements

As no insect community can be sampled completely, it is desirable to have at least an estimate of how many species are actually there. To estimate true species richness, I fitted the data to a truncated lognormal distribution following the maximum likelihood method devised by Cohen (1961) and described by Magurran (1988). Goodness of fit was tested by a χ^2-test (Magurran 1988). Diversity was measured with the Shannon index (Lloyd et al. 1968) and Fisher's α (Fisher et al. 1943). The first index was chosen because it is very popular and can therefore be used for comparative purposes. Fisher's α is also widely used, has a good discriminant ability and is less biased by the abundance of the commonest species than the Shannon index (Magurran 1988). It can be applied even if the underlying distribution does not follow a log series (Taylor 1978).

Results

Dead wood volume and surface

To compare the species numbers between limbs and logs, equal amounts of limbs and logs should be considered. However, it depends on the ecology of each species, whether this "amount" is measured as dead wood surface or volume. I therefore checked whether species richness was dependent on either dead wood surface area or dead wood volume by using regression analysis. As there was not enough variation in these two parameters within the traps, I used the differences between limb and log eclectors of a site in surface area and volume, respectively, as independent variables. The dependent variable was the difference in species richness between the two trap types. I found a significant, positive relationship both for Diptera ($R^2 = 0.21$; $p = 0.03$; $n = 28$) and for Coleoptera ($R^2 = 0.17$; $p = 0.04$; $n = 28$) when volume was used as independent variable. Neither for Diptera ($R^2 = 0.04$; $p = 0.31$; $n = 28$), nor for Coleoptera ($R^2 = 0.12$; $p = 0.09$; $n = 28$) such a relationship could be established using surface area as the independent variable. I therefore compared the assemblages on the basis of equal volumes. As dead wood volume in the log eclectors (mean ± SD: 0.168 m^3 ± 0.061 m^3) was on average four times greater than in the limb eclectors (0.041 m^3 ± 0.007 m^3), I pooled the data of four randomly selected limb eclectors and chose one log eclector with a volume as close as possible to the summed volume of the four limb eclectors. I repeated this procedure seven times until all 28 limb eclectors and seven log eclectors were considered, which resulted in a total dead wood volume of 1.15 m^3 for each trap type.

The species collected

A total of 426 species of (facultative) saproxylic Diptera (30'095 individuals) and 228 species of (facultative) saproxylic Coleoptera (4'906 individuals) were collected. Table 1 gives an overview about the three most abundant species in all samples and in each ecological category.

Table 1a. The three most abundant species and *number of individuals* of Diptera in the log and limb eclector samples (samples pooled over the year).

	logs	**limbs**
all species	Bradysia fungicola (Winnertz 1967); *3463*	Forcipomyia pseudonigra sp. n.; *1105*
	Scatopsciara calamophila Frey 1948; *1649*	Scatopsciara calamophila Frey 1948; *964*
	Camptochaeta minutula (Bukowski & Lengersdorf 1936); *1432*	Scatopsciara nacta (Johannsen 1912); 946
predators	Medetera acanthura Negrobov & Thuneberg 1970; *78*	Medetera abstrusa Thuneberg 1955; 57
	Euthyneura myrtilli Macquart 1836; *58*	Oedalea austroholmgreni, Chvála 1981; 46
	Tachypeza nubila (Meigen 1804) *55*	Rhamphomyia gibba (Fallén 1916); 38

The most abundant dipteran species in the limb samples, the Ceratopogonid *Forcipomiya pseudonigra* sp. n. is a species new to science (Delécolle in prep.). Whereas the dipteran samples are dominated only by representatives of the families *Ceratopogonidae* and *Sciaridae* (Table 1a), the log samples in Coleoptera contain mostly specimens of *Cisidae*, *Scolytidae* and *Lymexylonidae*, and the limb samples specimens of *Staphylinidae* and *Latridiidae* (Table 1b). The identity of the most abundant species in all categories clearly differs between the log and limb samples.

Table 1b. The three most abundant species and *number of individuals* of Coleoptera in the log and limb eclector samples (all samples together and in each ecological category. pot pest = potential pest species.

	logs	**limbs**
all species	Octotemnus glabriculus (Gyllenhal 1827); *579*	Leptusa fumida (Erichson 1839); *209*
	Xyleborus dispar (Fabricius 1792); *421*	Aridius nodifer (Westwood 1839); *177*
	Hyleocoetus dermestoides (Linné 1761); *277*	Proteinus brachypterus (Fabricius 1792); *122*
pot. pests	Xyleborus dispar (Fabricius 1792); *421*	Anobium costatum Aragona 1830; *23*
	Ptilinus pectinicornis (Linné 1758); *13*	Hedobia imperialis (Linné 1767); *6*
	Rhagium mordax (Degeer 1775); *5*	Strangalia maculata (Poda 1761); *6*
predators	Rhizophagus dispar (Paykull 1800); *83*	Denticollis linearis (Linné 1758); *67*
	Gabrius splendidulus (Gravenhorst 1802); *69*	Gabrius splendidulus (Gravenhorst 1802); *30*
	Rhizophagus nitidulus (Fabricius 1798); *43*	Rhizophagus perforatus Erichson 1845; *23*
stenotopic	Rhizophagus nitidulus (Fabricius 1798); *43*	Orchesia undulata Kraath 1853; *33*
	Bolitochara mulsanti Sharp 1875; *27*	Ptenidium intermedium Wankow 1869; *30*
	Liodopria serricornis (Gyllenhal 1813); *24*	Catops subfuscus Keller 1846; *25*
eurytopic	Octotemnus glabriculus (Gyllenhal 1827); *579*	Leptusa fumida (Erichson 1839); *209*
	Xyleborus dispar (Fabricius 1792); *421*	Aridius nodifer (Westwood 1839); *177*
	Hyleocoetus dermestoides (Linné 1761); *277*	Denticollis linearis (Linné 1758); *67*
ubiquistic	Proteinus brachypterus (Fabricius 1792); *50*	Proteinus brachypterus (Fabricius 1792); *122*
	Anotylus sculpturatus (Gravenhorst 1860); *13*	Proteinus macropterus (Gyllenhal 1806); *51*
	Epuraea biguttata (Thunberg 1784); *4*	Anotylus sculpturatus (Gravenhorst 1860); *47*

Numerical comparisons

The limbs significantly surpassed the logs in total species richness and in the number of individuals, both in Diptera and Coleoptera (Mann-Whitney U-Test; $n = 7$; $p < 0.05$; Table 2). These differences were not caused by the selection of the seven log eclectors. Most relationships did not change even when all log eclectors were considered, containing four times the dead wood volume of the limb eclectors (Table 2).

Table 2. Number of species and individuals collected from both $1.15 m^3$ of logs and limbs. In parentheses: numbers obtained when all log eclectors (total volume = $4.66\ m^3$) are considered.

	Diptera		**Coleoptera**	
	logs	**limbs**	**logs**	**limbs**
species	167 (305)	347	70 (153)	182
individuals	3165 (14'552)	15'441	737 (2'620)	2'286

In Coleoptera, the limb samples yielded significantly more potential pest and predatory species than the log samples (Mann-Whitney U-Test; $n = 7$; $p < 0.01$) also when the significance level was adjusted for the number of tests performed (significance level $p = 0.017$; Sokal & Rohlf 1995). In Diptera, limbs also yielded significantly more predatory species than logs (Mann-Whitney U-Test; $n = 7$; $p < 0.05$). Furthermore, limbs and logs differed with regard to the number of stenotopic, eurytopic and ubiquistic Coleoptera species (Friedman non-parametric two-way ANOVA, after Zar 1984, $H = 17.28$; $p < 0.01$; $n = 7$; Fig. 1) which was caused by the limb samples yielding in each category more species than the log samples (Mann-Whitney U-Test; $n = 7$; $p < 0.01$; significance level adjusted to $p = 0.017$, see above). It seems that the dominance of the limb samples was mainly due to the number of eurytopic and ubiquistic species (Fig. 1).

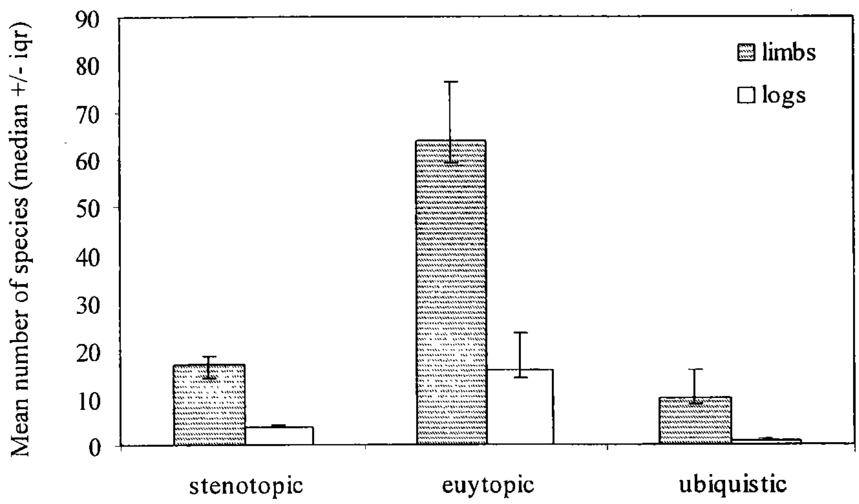

Figure 1. Mean number of stenotopic, eurytopic and ubiquistic beetle species obtained from limbs and logs. Given are medians ± interquartile ranges. n= 7.

Significantly more species were collected exclusively from limbs than from logs, both in Diptera and Coleoptera (Mann-Whitney U-Test; $n = 7$; $p < 0.05$; Table 3). In Table 4 the three most abundant exclusive species of Diptera and Coleoptera are given.

Table 3. Number of exclusive and shared species collected from both 1.15m^3 of logs and limbs.

	logs	limbs	shared
Diptera	25	119	142
Coleoptera	13	73	57

Table 4. The three most abundant species collected exclusively from logs and limbs. In parentheses: number of individuals; number of traps the species occurred.

	Diptera	Coleoptera
logs	Athypophthalmus inustus (MEIGEN 1804); (219; 16)	Liodopria serricornis (GYLLENHAL 1813) (24; 2)
	Corynoptera brevichaeta MOHRIG & ANTONOVA 1978; (120; 13)	Letoplectus spinolae (AUBÉ 1844) (9; 2)
	Athypophthalmus machidai (ALEXANDER 1921); (93; 15)	Cychramus variegatus (HERBST 1792) (5; 3)
limbs	Mycomya occultans (WINNERTZ 1863); (49; 2)	Bythinus burrelli DENNY 1825 (12; 7)
	Boletina trispinosa EDWARDS 1913 (39; 1)	Proteinus ovalis STEPHENS 1834 (10; 2)
	Trichosia morio (FABRICIUS 1794); (31; 7)	Philonthus fimetarius (GRAVENHORST 1802) (12; 3)

Both in Diptera and Coleoptera higher species diversity was found in the limb than in the log samples (Table 5). The differences of the Shannon indices were tested using a modified t-test specially designed for this purpose (Hutcheson 1970) and proved to be significant ($t_{Diptera} = 23.67$; $t_{Coleoptera} = 4.54$; $n = 7$; $p < 0.05$ in both cases, Table 5). After testing the Shannon index, I applied a jack-knife procedure to the Shannon indices and Fisher's α according to Magurran (1988), which improved the estimate of diversity and enabled standard errors to be calculated (Zahl 1977).

Table 5. Jack-knifed estimate of diversity of the log and limb inhabiting assemblages of Diptera and Coleoptera obtained from 1.15m^3 of both logs and limbs. Standard errors are given in parentheses.

	Diptera		Coleoptera	
	logs	**limbs**	**logs**	**limbs**
Shannon	3.21 (0.13)	4.02 (0.00)	2.28 (0.60)	4.30 (0.00)
Fisher's α	37.57 (1.46)	74.95 (1.02)	18.68 (1.27)	56.83 (1.11)

Species-abundance distributions

The calculation of species abundance distributions allows for detecting community-specific patterns and fitting parametric models for estimating species richness. As the aim of the procedures applied here was to describe the species abundance distribution of the assemblages gathered from limbs and logs rather than to compare them numerically, I used the complete data set that was not corrected for the different amounts of the volumes sampled. Additionally, the fit of any model depends on the number of species involved (Pielou 1975) which renders it advisable to include as many species as possible. The rank abundance distributions (abundance of each species plotted on a logarithmic scale against the species' rank in order from the most to the least abundant species) of the log and the limb inhabiting species were virtually identical both for Diptera and Coleoptera (Fig. 2).

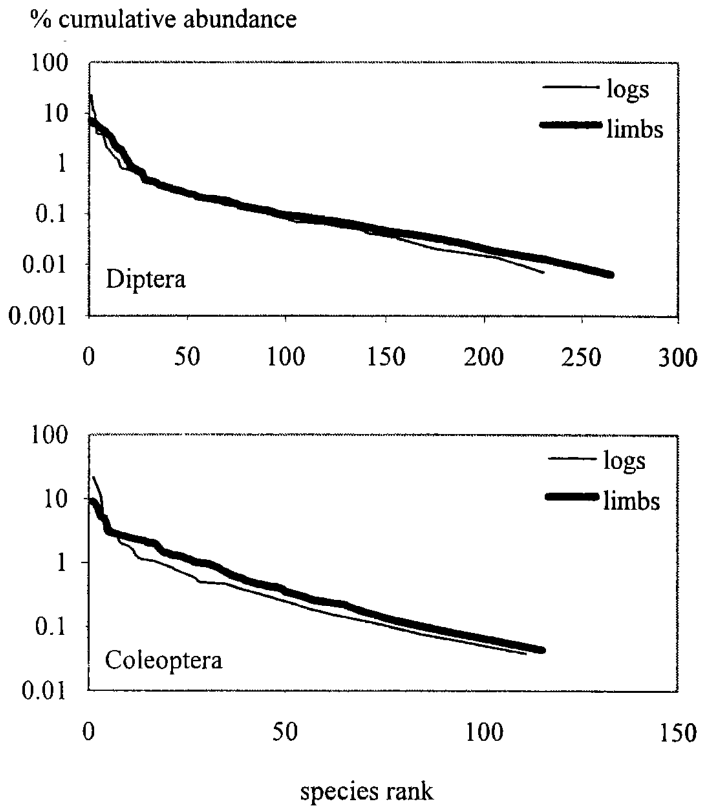

Figure 2. Rank-abundance distributions of Diptera and Coleoptera having emerged from logs and limbs.

The log data did not differ significantly from a truncated lognormal distribution in both Diptera ($\chi^2 = 5.8$; df = 8; $p > 0.20$;) and Coleoptera ($\chi^2 = 11.9$; df = 7; $p > 0.10$). The limb data could not be described by any parametric model creating patterns similar to those obtained empirically. The deviations from a truncated lognormal distribution were not large and arose only from one abundance class, the second highest in Diptera ($\chi^2 = 27.2$; df = 8; $p < 0.01$) and the lowest in Coleoptera ($\chi^2 = 19.0$; df = 7; $p < 0.01$). An estimate of total species richness was therefore theoretically only reliable for the data of the log eclectors.

Some authors have considered a graphic inspection to be sufficient to decide whether an empirical distribution follows a predicted pattern (Lambshead & Platt 1985; Hughes 1986). So I also calculated the estimated species richness also for the limb data as the estimated and observed patterns did not differ substantially (Table 6). The estimated species richness in Diptera was about 25 % higher in the logs and 27 % higher in the limbs than the observed species richness. In Coleoptera, the estimate was 15 % higher in the logs and 18%

in the limbs. Still more species were predicted for limbs than for logs although the data have not been corrected for the different amounts of volume sampled.

Table 6. Observed and estimated number of species (truncated lognormal model) reared from log and limbs. In parentheses: the underlying distribution deviated significantly from a truncated lognormal distribution.

	Diptera		Coleoptera	
Number of species	**logs**	**limbs**	**logs**	**limbs**
Observed	305	347	153	182
Estimated	406	(444)	179	(222)

Discussion

Species richness in limbs

The overall dominance of limbs in terms of species richness and diversity found in this study is unexpected and only partly in line with the findings of other authors working in similar habitats: Schmitt (1992) collected more rare but fewer exclusive species from limbs than from logs of beech, and in the study of Hilt & Ammer (1994), dead wood of smaller dimensions hosted more rare species and more exclusive species in spruce, but the opposite was true in oaks *Quercus sp.*. These results reflect the different tree species, diameters and volumes investigated, but indicate clearly that the significance of dead wood diameter for saproxylic insects varies among tree species. Limbs collected from the forest floor are supposed to have a higher moisture content than logs (Boddy 1983) and their bark is rougher and more often covered by lichens than the bark of logs, at least in beech (own obs.), which was the tree species I focused on. These factors have been shown to enhance the abundance of wood dwelling insects (Wallace 1953; Dajoz 1980; Petterson et al. 1995). Furthermore, the rotting process of limbs, and therefore the colonisation by saproxylic insects, usually starts before they break off, and so a limb lying on the forest floor may also contain species occurring in the canopy. To summarise, the more species rich and diverse fauna of limbs is likely to be caused by their heterogeneous surface and the variety of environmental conditions to which they are exposed.

Saproxylic insects are among the most endangered insect groups, at least in Europe (Speight 1989). The question thus arises whether many species specialising on logs have already become extinct whereas 'limb species' have been more likely to survive in the times of intensive management when only dead wood of smaller diameter - if any- was left in the forests. At least in Coleoptera, the dominance of the limb assemblages was most pronounced in eurytopic and ubiquistic species giving no evidence that particularly specialised species were absent in logs indicating their extinction. On the other hand, the number of exclusive species in logs was considerably lower than in limbs. A comparative study in a primeval forest would be promising to solve this question. However, the dominating presence of beetle species that are not specialised on particular environmental conditions in the limb samples could also be caused be the fluctuating microclimate of limbs. Species confined to more narrow niches may not be able to cope with the large changes in moisture or temperature that often take place in dead wood of smaller diameters. Augmenting the amount of dead limbs in managed forests is therefore a promising strategy to enhance overall biodiversity. As limbs hosted both more potential pest species and predatory species, neither group is promoted disproportionally when the number of dead limbs is increased.

Dead wood volume

Eclectors provide a unique opportunity for collecting arthropods in the field directly from their breeding substrate. The samples need not to be transported in the laboratory which may result in the loss of vagile species (Hammond 1997). The species abundances obtained by eclectors most likely reflect the natural patterns, because they are not affected by the species' behaviour or by weather conditions which may bias data obtained by intersection or pitfall traps (Siitonen 1994). However, as Irmler et al. (1996) have pointed out, the data may be difficult to quantify in relation to the breeding substrate, as each species uses a different (and mostly unknown) proportion of it. I found a significant positive relationship between dead wood volume, but not between surface area and species richness. It seems, therefore, that volume defined the amount of substrate relevant for the insects more adequately than surface area. This agrees with the results of Väisänen et al. (1993), who found that even the species richness of beetles living in the subcortical zone of trunks was better explained by dead wood volume than surface area.

Species abundance distribution and estimation of true species richness

The abundance distributions both of Diptera and Coleoptera are characterised by their large proportion of species being represented by only few individuals, which in fact is typical for 'hyperdiverse' communities (Magurran 1988). The resemblance of the curves displayed by the dipteran and the coleopteran data suggests that the populations of both groups are controlled by similar forces. Ecological factors are therefore more important than taxonomic relationships in shaping the relative abundance of saproxylic species.

The use of parametric models to explain patterns of species-abundance distributions has been intensively debated (Hughes 1986), but most authors agree on their advantages for comparative purposes (Magurran 1988). So far as I am aware, this is the first time that the species abundance distributions of saproxylic insects have been described. Kaila et al. (1994) state that the species abundance distributions of saproxylic beetles collected with window traps to resemble a log series, but do not give any data. In the present study, the pattern obtained by the log eclectors followed a truncated lognormal distribution, but this model did not reflect the data from the limb eclectors. Most collections with large numbers of taxonomically related species can be described by a lognormal distribution (Sugihara 1980). Whether the deviation of the limb data indicate the existence of distinct communities that are specialised breeders in limbs cannot be investigated further with my data, for instance by considering only the exclusive species. The fit of any model depends on the number of species involved (Pielou 1975), so the use of subsamples would not provide any further insights. The estimate of the true species richness by the truncated lognormal model suggests an undersampling of 26 % of the dipteran species and 17 % of the beetles. However, the estimation of true species richness does not change the ratio between logs and limbs established earlier.

Conclusions

At a first glance, the richness of the limb fauna is surprising, as dead wood of larger dimensions has always been claimed to be of 'greater ecological value' than limbs, branches or twigs (McCarthy & Baily 1994). There is of course no doubting the importance of snags and logs for the forest ecosystem, because many cavity-nesting species need dead wood of larger dimensions, and logs also harbour a considerable number of exclusive insect species. However, the label 'ecologically valuable' is often based on our knowledge of vertebrates, whereas insects are usually overlooked (Thomas 1994). In fact, invertebrates are powerful indicators of habitat quality due to the close and precise relationships of some species with their environment. Investigations into the invertebrate fauna may be more representative of overall biodiversity than conventional plant and vertebrate surveys (Oliver et al. 1998). Thus, when rating the 'ecological value' of dead wood dimensions for forest biodiversity, the saproxylic fauna must not be omitted.

To summarise, this study shows that a considerable part of saproxylic Diptera and Coleoptera breeds in dead limbs and, with its large number of species, contributes significantly to biodiversity in forests. Efforts to conserve dead wood should no longer focus only on logs and snags, but must also include smaller pieces of dead wood.

Acknowledgements - I would like to thank G. Pasinelli, W. Suter, and P. Duelli for their comments on the manuscript. Many thanks are also due to the various experts who identified the species collected during this study and the Swiss National Science Foundation for financial support (Grant No. 31-45'911.95).

References

Boddy, L. 1983. Microclimate and moisture dynamics of wood decomposing in terrestrial ecosystems. Soil Biology and Biochemistry 15: 149-157.

Cohen, A.C., Jr. 1961. Tables for maximum likelihood estimates: singly truncated and singly censored samples. Technometrics 3: 535-541.

Dajoz, R. 1980. Ecologie des insects forestières. Gauthier-Villars, Paris.

Elton, C.S. 1966. Dead and dying wood: the pattern of animal communities. Wiley & Sons Inc., New York.

Fisher, R.A., Corbet, A.S., Williams, C.B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology 12: 42-58.

Freude, H., Harde, K.W., Lohse, G. A. 1964-1983. Die Käfer Mitteleuopas, Band 1-11. Goecke & Evers, Krefeld.

Haase, V., Topp, W., Zach, P. 1998. Eichen-Totholz im Wirtschaftswald als Lebensraum für xylobionte Insekten. Zeitschrift für Ökologie und Naturschutz 7: 137-153.

Hammond, H.E.J. 1997. Arthropod diversity from Populus coarse woody material in North-Central Alberta: A review of taxa and collecting methods. The Canadian Entomologist 129: 1009-1033.

Hilt, M. & Ammer, U. 1994. Totholzbesiedelnde Käfer im Wirtschaftswald - Fichte und Eiche im Vergleich. Forstwissenschaftliches Centralblatt 113: 245-255.

Hövemeyer, K. 1999. Diversity patterns in terrestrial dipteran communities. Journal of Animal Ecology 68: 400-416.

Hughes, R.G. 1986. Theories and models of species abundance. American Naturalist 128: 879-899.

Hutcheson, K. 1970. A test for comparing diversities based on the Shannon formula. Journal of Theoretical Biology 29: 151-154.

Irmler, U., Heller, K., Warning, J. 1996. Age and tree species as factors influencing the populations of insects living in dead wood (Coleoptera, Diptera: Sciaridae, Mycetophilidae). Pedobiologia 40: 134-148.

Kaila, L., Martikainen, P., Punttila, P., Yakovlev, E. 1994. Saproxylic beetles (Coleoptera) on dead birch trunks decayed by different polypore species. Annales Zoolocici Fennici 31: 97-107.

Kirby, K. J. 1992. Accumulation of dead wood - a missing ingredient in coppicing? In: Buckley, G.P. (ed.). Ecology and management of coppice woodland. Chapman & Hall, London. pp 99-112.

Kleinevoss, K., Topp, W., Bohac, J. 1996. Buchen-Totholz im Wirtschaftswald als Lebensraum für xylobionte Insekten. Zeitschrift für Ökologie und Naturschutz 5: 85-95.

Koch, K. 1989-1992. Die Käfer Mitteleuropas. Ökologie. Goecke & Evers. Krefeld.

Lambshead, J. & Platt, H.M. 1985. Structural patterns of marine benthic assemblages and their relationships with empirical statistical models. In: Gibbs, P.E. (ed.). Proceedings of the 19th European Marine Biology Symposium, Plymouth, 1984. Cambridge University Press, Cambridge. pp 371-380.

Lloyd, M., Zar, J.H., Karr, J.R. 1968. On the calculation of informational-theoretical measures of biodiversity. American Midland Naturalist 79: 257-272.

Magurran, A.E. 1988. Ecological diversity and its measurement. Chapman & Hall, London.

Maser, C. & Trappe, J. 1984. The seen and unseen world of the fallen tree. USDA, General Technical Report GTR-PNW-164.

McAlpine, J.F., Peterson, B.V., Snewell, G.E., Teskey, H.J., Vockeroth, J.R., Wood, D.M. 1981. Manual of Nearctic Diptera. Volume 1-3. Monograph No 27. Canadian Governement Publication Centre, Quebec.

McCarthy, B. & Bailey, R. 1994. Distribution and abundance of coarse woody debris in a managed forest landscape of the central Appalachians. Canadian Journal of Forest Research 245: 1317-1329.

Økland, B. 1996. A comparison of three methods of trapping saproxylic beetles. European Journal of Entomology 93: 195-209.

Oliver, I., Beattie, A.J., York, A. 1998. Spatial fidelity of plant, vertebrate, and invertebrate assemblages in multiple-use forest in Eastern Australia. Conservation Biology 12: 822-835.

Owen, J. A. 1989. An emergence trap for insects breeding in dead wood. British Journal of Entomology and Natural History 2: 65-67.

Owen, J. A. 1992. Experience with an emergence trap for insects breeding in dead wood. British Journal of Entomology and Natural History 5: 17-20.

Petterson, R.B., All, J.P., Renhorn, K.-E., Esseen, P.-A., Sjornberg, K. 1995. Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. Biological Conservation 74: 57-63.

Pielou, E.C. 1975. Ecological diversity. Wiley & Sons Inc., New York.

Rauh, J. 1993. Naturwaldreservate in Bayern. Band 2. Schriftenreihe Naturwaldreservate in Bayern. IHW-Verlag.

Schmitt, M. 1992. Buchen-Totholz als Lebensraum für xylobionte Käfer. Waldhygiene 19: 97-191.

Schwenke, W. 1982. Die Forstschädlinge Europas. Volumes 2 and 4. Paul Parey, Hamburg, Berlin.

Siitonen, J. 1994. Decaying wood and saproxylic Coleoptera in two old spruce forests: a comparison based on two sampling methods. Annales Zoologici Fennici 31: 89-95.

Smith, K.G.V. 1989. An introduction to the immature stages of British flies. Handbook for the identification of British insects. Volume 10, Part 14. Royal Entomological Society, London.

Sokal, R.R. & Rohlf, F.J. 1995. Biometry. 3rd ed. Freeman and Company, New York.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Nature and environment Series No. 42. Strasbourg.

Sugihara, G. 1980. Minimal community structure: an explanation of species abundance patterns. American Naturalist 116: 770-778.

Taylor, L.R. 1978. Bates, Williamson, Hutchinson - a variety of diversities. In: Mound, L., & Warloff, A.N. (eds.). Diversity of insect faunas: 9th Symposium of the Royal Entomological Society. Blackwell, Oxford. pp 1-18.

Thomas, J.A. 1994. Why small cold-blooded insects pose different conservation problems to birds in modern landscapes. Ibis 137: S112-S119.

Väisänen, R., Biström, O., Heliövaara, K. 1993. Sub-cortical Coleoptera in dead pines and spruces: is primeval species composition maintained in managed forests? Biodiversity and Conservation 2: 95-113.

Wallace, H.R. 1953. The ecology of the insect fauna of pine stumps. Journal of Animal Ecology 22: 154-171.

Zahl, S. 1977. Jack-knifing an index of diversity. Ecology 58: 907-913.

Zar, J.H. 1984. Biostatistical analysis. Prentice Hall, New Jersey.

II Habitat Fragmentation in Saproxylic Diptera and Coleoptera: Scaling Dead Wood Volume and Connectivity

KARIN SCHIEGG

Abstract - Habitat fragmentation is a central problem in conservation biology and the scale at which fragmentation effects are investigated strongly influences the results obtained. A promising approach is scaling down fragmentation effects to the critical resource of a species or a community. For saproxylic insects, a habitat can be considered as fragmented, when the nearest piece of dead wood is beyond the travel distance of an individual insect. This is likely to be the case in managed forests, where dead wood is sparse. I tested the hypothesis that at a local level, increasing dead wood volume and connectivity led to an increase of species diversity of saproxylic insects. This relationship was investigated within 50 m, 100 m, 150 m, and 200 m of the collecting sites. Diversity was best explained by dead wood connectivity at the 150 m level, whereas dead wood volume was only of secondary importance. Thus, habitat fragmentation is expressed for saproxylic insects within forests by the distribution of single dead wood pieces. Dead wood further than 150 m from the collecting site did not influence species diversity which confirms the often suggested poor mobility of many saproxylic species.

Introduction

Habitat fragmentation has been postulated to be one of the major threats to biodiversity (Harris and Silva-Lopez 1992). Numerous studies have demonstrated the negative effects of reduced patch size and increased isolation for a variety of taxa (see Saunders et al. 1991; Noss & Csuti 1997 for reviews). Early studies mainly focused on birds (Klein 1989; Andrén 1994), but recently, arthropods have received more attention (e.g., Ås 1993; Wiens et al. 1997; Burke & Goulet 1998; Zabel & Tscharntke 1998). Ecological theory predicts that species occurring in stable habitats have low dispersal abilities and are therefore more vulnerable to habitat fragmentation than species adapted to unstable environments (Johnson & Gaines 1990; Noss & Csuti 1997). Additionally, habitat fragmentation is generally expected to be of greater significance for habitat specialists than for generalists (Lawton 1995).

Saproxylic insects are closely associated with the stable conditions in old-growth forests and are thus suspected to have limited dispersal abilities (Warren & Key 1991; Nilsson & Baranowski 1998). Most species are confined to particular microhabitats depending on stage of decay or moisture content of the dead wood (Speight 1989; Warren & Key 1991). Speight (1989) considered habitat loss and isolation to be the major causes of the high proportion of endangered species in this group, but the effects of habitat fragmentation on insect diversity are only poorly understood (Didham et al. 1996). Nilsson and Baranowski (1997) found major differences in the fauna of wood beetles due to past human disturbances and Økland (1996a) demonstrated temporal continuity of dead wood to influence positively the number of saproxylic mycetophilids (Diptera, Mycetophilidae). These results indicate that removal of dead wood is followed by long-lasting changes in the saproxylic community and that recolonisation of habitats by saproxylic insects occurs only at a low rate, if at all. In contrast, Ås (1993) found no differences in diversity of wood living beetles between small and large fragments of deciduous forest within a large coniferous forest. He concluded that the fragments had no distinct border to the surrounding forests, leading to an interchange of species. However, habitat fragmentation for saproxylic insects may be working also on a much smaller scale than on the level of forest patches. The smallest scale at which a species responds to patch structure is its 'grain' (Kotliar & Wiens 1990). The grain of sampling is often used by convention, without considering the ecological relations in which the focal organisms may be involved (Kareiva & Anderson 1988). At the level of an individual saproxylic insect, a habitat is fragmented when the nearest suitable piece of dead wood is beyond its travel distance. A 'habitat patch' can therefore be considered as a piece of dead wood and consequently, 'patch size' should be translated as 'volume of a piece of dead wood' and 'patch connectivity' as 'connectivity of dead wood pieces'.

I tested the hypothesis that increasing dead wood volume and connectivity led to an increase in species diversity of saproxylic insects. Additionally, I explored at which scale level species diversity and composition was influenced by dead wood volume and connectivity. This level depends on the mobility of saproxylic species and is therefore essential to know for developing conservation strategies for these species.

Methods

Study area

The study was carried out in the forest reserve Sihlwald (47°15'; 8°33') covering 10 km^2 at a NE-oriented slope, 10 km south of Zurich, Switzerland. The dominating tree species are beech *Fagus sylvatica* and spruce *Picea abies*, followed by ash *Fraxinus excelsior* and fir *Abies alba*. I selected 14 circular plots (r = 200 m) which differed in the amount of dead wood present but were similar with respect to exposition and slope. The plot centres, where the insect traps were placed, were at least 600 m apart to minimise dependence of the catches. Stand structure, age, and tree species composition did not differ between the plots within a range of about 20 m around the plot centres.

Insect sampling

Insects were collected using trunk-window traps (Kaila 1993) and eclectors (Funke 1971). Trunk-window traps consisted of a transparent plastic plate (30 x 45 cm) attached above a 30 cm wide plastic funnel. A 0.3 l collecting container with 4 % formaldehyde solution and some drops of a detergent to lower surface tension was mounted below the funnel. The trap was fixed on a piece of dead wood with the lower end about 1 m above ground. This method has been successfully used in various Scandinavian studies (Kaila 1993; Siitonen 1994; Økland et al. 1996; Kaila et al. 1997) and yields high numbers of saproxylic species. I placed four trunk-window traps within a range of 10 m in the centre of each study plot, resulting in 56 traps in total. They were emptied every second week from April - September in 1996 and 1997.

Eclectors are also called 'extraction cylinders' (Økland 1996b) or 'emergence traps' (Irmler et al. 1996). They enclose pieces of dead wood to rear saproxylic insects which are attracted after emergence by the attached collecting vials, which are the only source of light within the trap. This principle has been applied successfully in various studies on saproxylic insects (Schmitt 1992; Hilt & Ammer 1994; Kleinevoss et al. 1996; Haase et al., 1998). I developed a modified eclector type, which can also be used on fallen dead wood in contact with the forest floor. Four eclectors were installed in each of the 14 sites, two containing a part of a log (⌀ at the smaller end > 20 cm, L = 1.5 m, log eclectors) and two containing limbs (⌀ at both ends 5-10 cm, L = 1.0-1.5 m, limb eclectors), resulting in 28 traps of each type, 56 in total. The limbs were collected from the forest floor within 10 m around the traps. Total dead wood volume enclosed in the trap was for logs on average 0.168 m^3 (+/-

SD 0.061 m^3) and for limbs 0.041 m^3 (+/-0.007 m^3), respectively. Only dead wood of beech at a medium stage of decay (presence of insect holes, bark partly loose) was considered. The collecting vials were filled with a 2 % formaldehyde solution and emptied monthly from April 1996 - November 1997, but only once from November 1996 - April 1997. The limb eclectors could only be operated in 1996. All specimens of Diptera and Coleoptera were identified to species level by various specialists. I had to omit all catches of Psychodidae, Chironomidae, Cecidiomyidae, and Phoridae, and also all Diptera collected by trunk-window traps during August and September 1997 due to identification problems and time restrictions.

All species were classified whether to be obligate saproxylic or facultative saproxylic. The latter means that the species may also breed in other decaying matter. In Coleoptera, only obligate saproxylic species were included in the analyses, whereas in Diptera the facultative saproxylics were considered as well, because a reliable distinction was not possible, as literature on this subject is sparse. All classifications were based on McAlpine (1981), Koch (1989-1992), Smith (1989), and on information given by the specialists who identified the species. The data were treated for each trap type separately and pooled over the collecting period.

Dead wood volume and connectivity

In winter 1997/98, each of the 14 study plots was searched for dead wood pieces (minimum length = 1 m; ∅ at the smaller end > 20 cm). Each piece was numbered and its position recorded on a 1:5000 map. Diameter at both ends and length of lying pieces were measured. For standing dead trees, diameter was measured about 20 cm above ground and height was estimated. Diameter at the top was approximated using species-specific regression equations derived from the lying objects sampled. With these measures, I calculated the volume of each piece. Pieces less than 5 m apart were considered to have the same location. I calculated for each plot the sum of dead wood volume, and three indices of dead wood connectivity: (1) Nearest neighbour distance (NN, Diggle 1983) as mean distance of randomly selected dead wood pieces to their nearest piece. I used a random number table to select the pieces, and no distance was measured twice. Selection was stopped when over 90 % of all pieces were considered. The average of all distances was used as index. (2) Proximity index (PX, Whitcomb et al. 1981): This index is recommended for the analysis of spatial patterns of metapopulations (Hargis et al. 1998). It is calculated as NN, but instead of averaging nearest neighbour distances, the ratio of the patch size of the nearest neighbour and the nearest neighbour distance is used. I considered patch size to be the volume of a dead wood piece. However, the volumes of the dead wood pieces in my study area did not vary much, so PX would not contain considerably more information than NN. As a consequence, I modified the index as follows: I randomly selected five dead wood pieces within each quarter of a study plot with all pieces being at least 40 m apart, resulting in 20 pieces per study plot. The ratio between volume and distance of all pieces within 20 m of the 20 selected pieces was summed. The average of these sums was considered as index. (3) Circle (C, after Buckland et al. 1993): I placed five circles (r = 20 m) within each quarter of a study plot, which gave totally 20 circles per plot. The circles were placed randomly but overlaps were avoided. The volume of all dead wood pieces was summed and the average volume of all 20 circles was considered as index. For all index calculations, I excluded points further than 190 m from the study plot centre to avoid edge effects (Buckland et al. 1993). The three indices differ in the weight given to dead wood volume: NN does not include volume at all, PX is based on the ratios of volumes and distances, and C only includes randomly selected volumes. Following the suggestion of McGarigal & Marks (1995), I calculated the variance of each index as a measure of dispersion. As the variances of NN and C were all small, I only used the variance of PX (PXvar) in the further analyses. Dead wood volume and all four indices of connectivity (NN, PX, PXvar and C) were calculated on four scale levels, namely within the next 50, 100, 150, and 200 m of the study plot centre (Fig. 1).

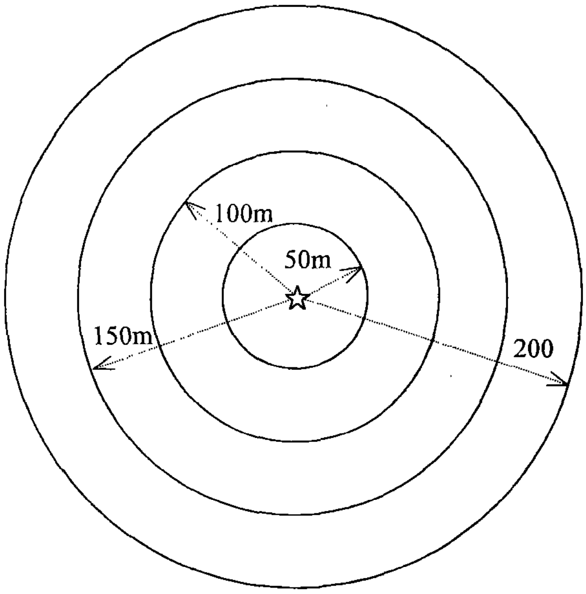

Fig. 1. A study plot divided into the four scale levels. ☆ = position of the traps.

Statistics

The relationship between species richness or diversity (measured by Fisher's α, Fisher et al. 1943) and the habitat parameters was investigated exploratively using backward stepwise regression (p to remove = 0.15, SYSTAT 7.0) with dead wood volume and the four connectivity indices (NN, PX, PXvar, and C) as independent variables. Sample size was the number of sites ($n = 14$). Assumptions of regression were checked using residual analyses and models were improved by removal of outliers when absolute t-values $\gg 2.0$ and tolerance < 0.20 (Wilkinson 1996). Fisher's α was chosen because it is widely used, has a good discriminant ability and is less biased by the abundance of the commonest species than the Shannon index (Magurran 1988). It can be applied even if the underlying distribution does not follow a log series (Taylor 1978). I investigated the influence of the dead wood volume and connectivity on species composition and abundance by Canonical Correspondence Analysis (CCA, ter Braak 1986, Jongman et al. 1995) using the programs CANOCO 4.0 and CANODRAW 2.0 (ter Braak & Šmilauer 1998). CCA is a multivariate technique for relating species composition and abundance to underlying environmental gradients. In this form of ordination, the axes are linear combinations of the environmental variables (direct gradient analysis). Significance of the axes was tested using a Monte Carlo permutation test with 500 randomisations.

Results

Species richness and diversity

A total of 2020 dead wood pieces, mainly logs of beech and spruce, were sampled. Their volume averaged $6.3 m^3 ha^{-1}$ and ranged from $48.6 m^3$ to $157.9 m^3$ per plot. The mean nearest neighbour distance was 14 m (200 m level) and a clumped distribution of dead wood occurred mostly along small streams. Table 1 summarises the number of species and individuals as well as species diversity obtained in each trap type.

Table 1. Number of species (individuals) and diversity (Fisher's α) collected by eclectors and trunk-window traps (trunk-window t.). In Coleoptera, only obligate saproxylics, in Diptera obligate and facultative saproxylics are considered.

		log eclectors (1996 & 1997)	**limb eclectors (1996)**	**trunk-window t. (1996 & 1997)**
Diptera	species	387 (36'232)	348 (15'543)	511 (3'643)
	Fisher's α	60.5	63.2	161.8
Coleoptera	species	80 (3'349)	65 (797)	166 (13'643)
	Fisher's α	14.7	16.7	26.6

More than 20 species of Diptera were new to science and 185 new to Switzerland (Haenni 1997; Merz 1997; Delécolle & Schiegg 1998; Dempewolf & Schiegg 1998; Otto & Schiegg in press; Chapter 4). The species numbers obtained by the different trap types in each site were weakly correlated. The only significant association was found between the species numbers of Diptera and Coleoptera collected by the limb eclectors (Spearman rank correlation, $r_S = 0.48$, $p < 0.05$, $n = 14$). Stepwise regressions of species richness and diversity on dead wood volume and the four indices of connectivity (NN, PX; PXvar, C) were performed for all scale levels (50 m, 100 m, 150 m, 200 m) separately. In Diptera, only dead wood connectivity on the 150 m scale was significantly related to species richness or diversity (Table 2).

Table 2. Resulting significant models from stepwise regressions of species richness (log transformed) and diversity of Diptera on dead wood volume and connectivity. Abbreviations: C150 = Circle connectivity index at the 150 m level, PXvar150 = PX connectivity index variance at the 150 m level.

Regression equations	**R^2**	**p**	**n**
log eclectors			
log (number of species) = 4.64+0.07∗C150	0.3952	0.03	12
limb eclectors			
log (number of species) = 4.41+0.07∗C150	0.3414	0.04	13
trunk-window traps			
log (number of species) = 5.43+1.20∗PXvar150	0.2823	0.05	14

A similar pattern was observed in Coleoptera. Again, dead wood connectivity at the 150 m level almost exclusively remained in the regression models (Table 3). Diversity of beetles reared from logs was the only variable that was influenced significantly by at least one of the chosen habitat parameters at all scale levels.

Table 3. Resulting significant models from stepwise regression of species richness and diversity of Coleoptera on dead wood volume and connectivity. Abbreviations: vol50; vol150 = dead wood volume at the 50 m and 150 m level, respectively, NN100; NN150 = nearest neighbour connectivity index at the 100 m and 150 m level, C150 = Circle connectivity index at the 150 m level.

Regression equations	R^2	p	n
log eclectors			
number of species = 12.62+0.16*vol150	0.4716	0.02	12
Fisher's α = 5.51+0.25*vol50	0.3921	0.02	13
Fisher's α = 15.82-0.49*NN100	0.3563	0.02	14
Fisher's α = 15.74-0.43*NN150	0.2958	0.04	14
Fisher's α = 17.26-0.56*NN200	0.2819	0.05	14
limb eclectors			
number of species = 14.50+1.18*C150	0.5550	0.04	14
trunk-window traps			
number of species = 73.35+1.27*NN150	0.4089	0.02	13

When another stepwise regression on coleopteran diversity was performed over all four scale levels using the previously significant parameters (i. e. volume50, NN100, NN150, and NN200, Table 3) as independent variables, only NN150 was selected.

Species composition

In the CCA procedures, dead wood volume and the four indices of dead wood connectivity were related as environmental factors for each scale level separately to the species abundance matrices of each trap type. In Diptera, CCA revealed significant relations between species composition and the environmental factors at the 50 m level for the log data and at the 200 m level for the limb data (Table 4). No significant pattern could be detected in the samples gathered by trunk-window traps.

Table 4. The first two canonical axes of CCA (Diptera). Eigenvalues given in parentheses. %var = represented percentage variance of the explainable variance of the species-environment relationship. Coeff = Correlation coefficient between the environmental variables and the first and second axis.

	Logs, 50 m level		**Limbs, 200m level**	
	axis1	*axis2*	*axis1*	*axis2*
eigenvalues	0.42	0.14	0.33	0.21
%var	53.2	18.0	31.6	20.6
Factor	*Coeff 1*	*Coeff 2*	*Coeff 1*	*Coeff 2*
NN	0.07	-0.34	0.53	-0.25
PX	-0.02	0.04	-0.18	-0.21
PXvar	-0.21	-0.13	-0.06	0.45
C	0.49	0.15	-0.16	0.13
Vol	0.09	0.55	-0.21	-0.01
p(axis1)	0.03		0.08	
p(all axes)	0.59		0.02	

The composition of the species reared from logs was mainly explained by C, which correlated most with the first axis, whereas the second axis was significantly influenced by dead wood volume. In the limb species, NN had the highest correlation coefficient with the first axis, followed by volume. PXvar contributed most to the position of the second axis, of which, however, the explanatory power was quite low. The higher order axes did not explain considerably more of the variance and were thus not considered here.

In Coleoptera, only the species data gathered by the log eclectors could be significantly related to the environmental factors by CCA. Species composition could be explained by dead wood volume and connectivity on the 100 m, 150 m, and the 200 m level (Table 5).

Table 5. The first two canonical axes of CCA (Coleoptera). %var = represented percentage variance of the explainable variance of the species-environment relationship. Coeff = Correlation coefficient between the environmental variables and the first and second axis.

	100m		**150m**		**200m**	
	axis1	*axis2*	*axis1*	*axis2*	*axis1*	*axis2*
eigenvalues	0.67	0.33	0.68	0.39	0.73	0.47
%var	46.0	22.5	45.7	26.2	44.7	28.6
Factor	*Coeff 1*	*Coeff 2*	*Coeff 1*	*Coeff 2*	*Coeff 1*	*Coeff 2*
NN	-0.68	-0.37	-0.27	-0.19	-0.30	-0.22
PX	0.19	0.64	-0.37	0.51	-0.45	0.33
PXvar	0.42	0.54	0.08	0.83	0.09	0.73
C	0.26	0.60	-0.14	-0.25	-0.02	-0.44
Vol	0.25	0.77	-0.15	0.47	0.30	0.30
p(axis1)	0.02		0.03		0.01	
p(all axes)	0.04		0.05		0.01	

The first CCA axes were mostly determined by the indices NN and PX at all scale levels, whereas dead wood volume was only influential on the second axis on the 100 m level. As around 70 % of the explainable variance was represented by the first two axes, the higher order axes did not contribute considerably to the total variance represented and were therefore not considered for the interpretations. Again, dead wood connectivity was the determining factor, whereas dead wood volume only played a minor role.

Discussion

Within-forest fragmentation

Ecological mechanisms operate at different spatial scales and linking the information gathered at these scales is a central problem in ecology and mainly in conservation biology (Wiens 1989; Hansson et al. 1995). In saproxylic insects, several authors chose a large scale approach and compared the saproxylic beetle assemblages between forests or forest patches with different amounts of dead wood (Rauh & Schmitt 1991; Siitonen 1994; Siitonen & Martikainen 1994; Kaila et al. 1997) and mostly found positive relations between species richness and dead wood density. Others included spatial aspects in their studies (Siitonen 1994; Økland 1996b; Økland et al. 1996). These investigations revealed that the influence of dead wood density on saproxylic beetles increased with increasing spatial scale of recording (from 0.1 ha to 4 km^2), whereas at a local level of some m^2 no such relationships could be found. It seems therefore that at the local level, species richness does not depend primarily on the amount of dead wood present, but rather on dead wood connectivity, as it has been demonstrated in this study. Low connectivity of dead wood pieces must therefore be regarded as within-forest fragmentation, causing reduced numbers and diversity of saproxylic insect species. Beside poor dispersal abilities, the high substrate specificity of most saproxylic insects (Paulus 1980; Warren and Key 1991) may additionally render this group vulnerable to isolation (Chapter 3). In sites with high dead wood connectivity, a species is more likely to find the type of dead wood that it is specialised on, than in sites with isolated dead wood pieces.

Species composition was only marginally influenced by dead wood volume, but more markedly by dead wood connectivity. As in CCA the identity of the species is important, the results could have been blurred by the inclusion of the facultative saproxylic species of Diptera. Nevertheless, it can be hypothesised that the species that depend most on dead wood connectivity are extinct in the study forest, because it has been intensively managed for centuries and has become a forest reserve only recently. As a consequence, the species assemblages in sites with high dead wood connectivity differ only slightly from those with low connectivity.

Scaling within-forest fragmentation

The positive effects of dead wood connectivity on species richness and diversity could be demonstrated nearly exclusively on the 150 m level, both for Diptera and Coleoptera and for all trap types. Dead wood connectivity on a range smaller than 150 m around the traps was not related to species richness and diversity. This range may be too small to offer the variety of dead wood types needed to enhance species richness, so some highly specialised species may be lacking. On the other hand, the plots with a radius of 200 m may have been too large to demonstrate the influences of dead wood connectivity or volume on species richness and diversity. As connectivity indices are based on averages, a plot highly connected at the 150 m level can have a lower connectivity index at the 200 m level (when only few dead wood pieces are found between 150 and 200 m) and vice versa. Thus, when working on the grain of saproxylic species, habitat features further than 150 m seem to be too far to influence species richness and diversity significantly. The range of 150 m could be interpreted as an approximation of mean 'home range' of saproxylic Diptera and Coleoptera, which confirms the poor mobility suggested by some authors (Speight 1989; Warren & Key 1991; Nilsson & Baranowski 1998). It cannot be excluded, however, that the relations described here may be different in forests with other amounts or distributions of dead wood.

Depending on insect group and trap type analysed, different connectivity indices explained species richness and diversity most accurately. Different trap types sample slightly different parts of the saproxylic community, which may also result in weak intercorrelations between samples of different trap types as in this study. With eclectors, insects can be collected directly from their breeding substrate and the species abundances obtained in this way most likely reflect the natural patterns (Siitonen 1994). Trunk-window traps measure flight activity abundances reflecting the species that are present or just cross the collecting site. Each assemblage seems to contain species with slightly different habitat requirements and it is therefore even more remarkable that dead wood connectivity at the 150 m level was favoured so clearly.

Conclusions

The SLOSS debate, whether single large or several small reserves of the same total area will contain more species, has been a major controversy in conservation biology for the last two decades (see Saunders et al. 1991; Rosenzweig 1995 for reviews). When scaling down this question to the grain of saproxylic insects, the answer is, that 'several small' is preferable to 'single large', as patch connectivity (connectivity of dead wood pieces) rather than patch size (dead wood volume) explained species richness best. So far, recommendations for the preservation of saproxylic insects have been based only on the amount of dead wood that should be left in forests (Hilt & Ammer 1994), but without any comments on the spatial arrangement (Simberloff 1999). In my study forest, the plots with the highest dead wood connectivity had mean nearest neighbour distances of 6-12 m and the average dead wood density was only slightly above the average of Central European managed forests. I postulate therefore, that a significant increase of saproxylic species could be achieved in managed forests, when the mean distance between two neighbouring dead wood pieces with ∅ > 20 cm were not more than 12 m. Scaling down fragmentation effects to the critical resource of a species or a community is a promising approach to develop conservation strategies. It is important to consider how an individual animal perceives its environment, because it is the individual's level at which population dynamics are determined (Clemons & Buchholz 1997). Results gathered at the local level must be linked to results obtained at larger scales to answer the questions posed by theory and practice.

Acknowledgements - I thank the many colleagues that helped me with dead wood recording and the Swiss National Science Foundation for the financial support of this study (Grant 31-45911.95). The comments of Gilberto Pasinelli and Josef Senn greatly improved the manuscript.

References

Andrén, H. 1994. Effects of habitat fragmentation on birds an mammals in landscapes with different proportions of suitable habitat: A review. Oikos 71: 355-366.

Ås, S. 1993. Are habitat islands islands? Woodliving beetles (Coleoptera) in deciduous forest fragments in boreal forests. Ecography 16: 219-228.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L. 1993. Distance sampling. Chapman & Hall, London.

Burke, D. & Goulet, H. 1998. Landscape and area effects on beetle assemblages in Ontario. Ecography 21: 472-479.

Clemons, J.R., & Buchholz, R. 1997. Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge.

Delécolle, J.-C., & Schiegg, K. 1998. Contribution à l'étude des Cératopogonidés de Suisse. I. Révision et redescription des espèces paléarctiques du genre Ceratoculicoides Wirth & Ratanaworabhan, 1971. (Diptera, Ceratopogonidae). Bulltin de la Societé Entomologique de la France 103: 273-286.

Dempewolf, M. & Schiegg, K. 1998. Pipunculid flies collected in the forest reserve Sihlwald ZH (Diptera, Pipunculidae): Three species new to Switzerland. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 71: 111-114.

Didham, R.K., Ghazoul, J., Stork, N.E., Davis, A.J. 1996. Insects in fragmented forests: a functional approach. Trends in Ecology and Evolution 11: 255-260.

Diggle, P.J. 1983. Statistical analysis of spatial patterns. Academic Press, London.

Fisher, R.A., Corbet, A.S., Williams, C.B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology 12: 42-58.

Funke, W. 1971. Food and energy turnover of leaf-eating insects and their influence on primary production. Ecological Studies 2: 81-93.

Haase, V., Topp, W., Zach, P. 1998. Eichen-Totholz im Wirtschaftswald als Lebensraum für xylobionte Insekten. Zeitschrift für Ökologie und Naturschutz 7: 137-153.

Haenni, J.-P. 1997. Scatopsidae (Diptera) nouveaux pour la faune de Suisse. (Contribution à la connaisance des Scatopsidae de Suisse. IV). Bulletin de la Société neuchâteloise des Sciences naturelles 120: 121-124.

Hansson, L., Fahrig, L., Merriam, G. 1995. Mosaic landscapes and ecological processes. IALE Studies in Landscape Ecology 2. Chapman & Hall, London.

Hargis, C.D., Bissonette, J.A., David, J.L. 1998. The behavior of landscpae metrics commonly used in the study of habitat fragmentation. Landscape Ecology 13: 167-186.

Harris, L.D. & Silva-Lopez, G. 1992. Forest fragmentation and the conservation of biological diversity. In: Fiedler, P.L. & Jain, S.K. (eds). Conservation biology: the theory and practice of nature conservation, preservation, and management. Chapman & Hall, London, pp 197-237.

Hilt, M. & Ammer, U. 1994. Totholzbesiedelnde Käfer im Wirtschaftswald - Fichte und Eiche im Vergleich. Forstwissenschaftliches Centralblatt 113: 245-255.

Irmler, U., Heller, K., Warning, J. 1996. Age and tree species as factors influencing the populations of insects living in dead wood (Coleoptera, Diptera: Sciaridae, Mycetophilidae). Pedobiologia 40: 134-148.

Johnson, M.L. & Gaines, M.S. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annual Reviews in Ecology and Systematics 21: 449-480.

Jongman, G.H.G., ter Braak, C.J.F., van Tongeren, O.F.R. 1995. Data analysis in community and landscape ecology. Cambridge University Press.

Kaila, L. 1993. A new method for collecting quantitative samples of insects associated with decaying wood or wood fungi. Entomologica Fennica 29: 21-23.

Kaila, L., Martikainen, P., Punttila, P. 1997. Dead trees left in clear-cut benefit saproxylic Coleoptera adapted to natural distrurbances in boreal forest. Biodiversity and Conservation 6: 1-18.

Klein, B.C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. Ecology 70: 1715-1725.

Kleinevoss, K., Topp, W., Bohac, J. 1996. Buchen-Totholz im Wirtschaftswald als Lebensraum für xylobionte Insekten. Zeitschrift für Ökologie und Naturschutz 5: 85-95.

Kareiva, P. & Anderson, M. 1988. Spatial aspects of species interactions: the wedding of models and experiments. In: Hastings, A. (ed). Lecture notes in biomathematics: community ecology. Springer Verlag, Berlin. pp 38-54.

Koch, K. 1989-1992. Die Käfer Mitteleuopas. Ökologie. Goecke und Evers. Krefeld.

Kotliar, N. & Wiens, J. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59: 253-260.

Lawton, J.H. 1995. Population dynamic principles. In: Lawton, J.H. & May, R.M. (eds). Extinction rates. Oxford University Press, Oxford. pp 147-163.

Magurran, A.E. 1988. Ecological diversity and its measurement. Chapman & Hall, London.

McAlpine, J.F., Peterson, B.V., Snewell, G.E., Teskey, H.J., Vockeroth, J.R., Wood, D.M. 1981. Manual of Nearctic Diptera. Volume 1-3. Monograph No 27. Canadian Governement Publication Centre, Quebec.

McGarigal, K. & Marks, B. 1995. FRAGSTATS: Spatial analysis program for quantifying landscape structure. USDA Forest Service Gen. Tech. Rep. PNW-GTR-351.

Merz, B. 1997. Die Micropezidae (Diptera) der Schweiz. Mitteilungen der Schweizerischen Entomologischen GeseslIschaft 70: 93-100.

Nilsson, S.G. & Baranowski, R. 1997. Habitat predictability and occurence of wood beetles in old-growth beech forests. Ecography 20: 491-498.

Noss, R.F. & Csuti, B. 1997. Habitat fragmentation. In: Meffe, G.K. & Carroll, C.R. (eds). Principles of conservation biology. 2nd edition. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, pp 269-304.

Økland, B. 1996a. Unlogged forests: important sites for preserving the diversity of Mycetophilids (Diptera: Sciaroidea). Biological Conservation 76: 297-310.

Økland, B. 1996b. A comparison of three methods of trapping saproxylic insects. European Journal of Entomology 93: 195-209.

Økland, B., Bakke, A., Hågvar, S., Kvamme, T. 1996 What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodiversity and Conservation 5: 75-100.

Otto, C.-J. & Schiegg, K. In press. Chironomidae (Diptera) collected in the forest reserve Sihlwald ZH. Mitteilungen der Schweizerischen Entomologischen Gesellschaft.

Paulus, H.F. 1980: Einige Vorschläge für Hilfsprogramme unserer gefährdeter Käfer. Natur und Landschaft 55: 28-32.

Rauh, J. & Schmitt, M. 1991. Methodik und Ergebnisse der Totholzforschung in Naturwaldreservaten. Forstwissenschaftliches Centralblatt 110: 114-127.

Rosenzweig, M. 1995. Species diversity in space and time. Cambridge University Press, Cambridge.

Saunders, D., Hobbs, R., Margules, C. 1991. Biological consequences of ecosystem fragmentation: A review. Conservation Biology 5: 18-32.

Schmitt, M. 1992. Buchen-Totholz als Lebensraum für xylobionte Käfer. Waldhygiene 19: 97-191.

Siitonen, J. 1994. Decaying wood and saproxylic Coleoptera in two old spruce forests: a comparison based on two sampling methods. Annales Zoologici Fennici 31: 89-95.

Siitonen, J. & Martikainen, P. 1994. Occurrence of rare and threatened insects living on decaying populus tremula: a comparison between Finnish and Russian Karelia. Scandinavian Journal of Forest Research 9: 185-191.

Simberloff, D. 1999. The role of science in the preservation of forest biodiversity. Forest Ecology and Management 115: 101-111.

Smith, K.G.V. 1989. An introduction to the immature stages of Brithish flies. Handbook for the identification of British insects. Volume 10. Part 14. Royal Entomological Society, London.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Nature and environment Series No. 42. Strasbourg.

Taylor, L.R. 1978. Bates, Williamson, Hutchinson - a variety of diversities. In: Mound, L. & Warloff, A.N. (eds). Diversity of insect faunas: 9th Symposium of the Royal Entomological Society. Blackwell, Oxford. pp 1-18.

ter Braak, C.J.F. 1986. Canonical Correspondance analsysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.

ter Braak, C.J.F. & Šmilauer, P. 1998. CANOCO. Software for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis (version 4). Centre for Biometry Wageningen (Wageningen, NL) and Microcomputer Power (Ithaca NY, USA).

Warren, M.S. & Key, R.S. 1991. Woodlands: past, present potential. In: Collins, N.M. & Thomas, J.A. (eds). The conservation of insects and their habitats. Academic Press, London. pp 160-212.

Whitcomb, R.F., Robbins, C.S., Lynch, J.F., Whitcomb, B.L., Klimkiewicz, M.K., Bstrak, D. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. In: Burgess, R.L. & Sharpe, D.M. (eds). Forest island dynamics in man-dominated landscape. Springer Verlag, New York. pp 125-205.

Wilkinson, L. 1996. Systat for Windows: Statistics. SPSS Inc.

Wiens, J.A. 1989. Spatial scaling in ecology. Functional Ecology 3: 385-397.

Wiens, J.A., Schooley, R.L., Weeks, R.D. 1997. Patchy landscapes and animal movements: do beetles percolate? Oikos 78: 257-264.

Zabel, J. & Tscharntke, T. 1998. Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially? Oecologia 116: 419-425.

III Are there saproxylic beetle species characteristic for high dead wood connectivity?

KARIN SCHIEGG

Abstract - Saproxylic beetles have been shown to be vulnerable to within-forest fragmentation expressed as large distances between single dead wood pieces (low dead wood connectivity). From samples of a two-year study of saproxylic beetles, species that were characteristic for sites with high dead wood connectivity were identified by Canonical Correspondence Analysis, the method of Dufrêne and Legendre (IndVal) and by considering the species occurring exclusively in sites with high dead wood connectivity. These species mainly differed from the other species by their high habitat specificity. Hence, there are species-specific responses of saproxylic beetles to the spatial arrangement of dead wood. High dead wood connectivity must be achieved in managed forests to sustain particularly vulnerable species.

Introduction

The fragmentation of formerly continuous habitats due to human land alterations is a central issue in conservation biology and has provoked a large variety of investigations into species responses to habitat loss and insularisation (see Soulé 1986; Saunders et al. 1991; Andrén 1994; Walters 1998 for reviews). Generally, large-bodied, poorly dispersing species confined to particular, stable habitat types are considered as prone to extinction due to habitat fragmentation, although empirical evidence is scant (Morrison et al. 1998). Several authors have reviewed traits related to high risks of extinction in general (e. g., Flessa et al. 1986; Gaston 1994), but as Didham et al. (1998a) point out, studies that contrast species by traits that confer susceptibility or resilience to fragmentation are rare and mostly deal with vertebrates (e. g., Diamond 1984; Bright 1993; Hager 1998). Notable exceptions are the studies of Didham et al. (1998a) and Didham et al. (1998b) who found that rarity and population variability of leaf-litter beetles in tropical forests were significant predictors of vulnerability to forest fragmentation, and that zoophagous beetle species were more extinction prone than other species. Saproxylic beetles are suspected to suffer from habitat loss and fragmentation of populations due to the removal of dead wood in managed forests (Speight 1989; Warren & Key 1991; Ås 1993; Kaila et al. 1994). Saproxylic species are species that are dependent during some part of their life-cycle on dead or dying wood, wood-inhabiting fungi or on the presence of other saproxylic species (Speight 1989).

For saproxylic beetles, habitat fragmentation can be expressed at a local scale as large distances between dead wood pieces (low dead wood connectivity). Chapter 2 demonstrates that sites with high connectivity of dead wood pieces have more species and higher diversity of saproxylic Diptera and Coleoptera than sites with clumped dead wood distributions. It is assumed in the present study, that species characteristic for sites with high dead wood connectivity are sensitive to within-forest fragmentation expressed as high distances between dead wood pieces. Some authors argue that most saproxylic species are specialists and only poorly mobile, especially large ones (Warren & Key 1991; Nilsson & Baranowski 1997). But as no study has focused on life-history traits which may render saproxylic insects sensitive to fragmentation, the ultimate causes (*sensu* Simberloff 1986) why this group should be particularly vulnerable to isolation effects, remain speculative.

Saproxylic beetle species, that are characteristic for sites with high dead wood connectivity, are extracted from samples collected in sites with a gradient from low to high dead wood connectivity. In a next step, biological traits of these species are compared with the traits of species which do not depend on high dead wood connectivity. Learning more about the attributes that render species vulnerable to fragmentation allows to predict better their responses to environmental alterations and to understand the underlying patterns of fragmentation-induced changes in biological communities.

Methods

Study area and insect sampling

The insects were sampled in the forest reserve Sihlwald (47°15'; 8°33') covering 10 km^2 at a NE-exposed slope, 10 km south of Zurich, Switzerland. The reserve was established in 1994, but the forest has previously been managed in some areas for centuries. Dead wood averages out at 6.3 m^3 ha^{-1}. The dominating tree species are beech *Fagus sylvatica* and spruce *Picea abies*, followed by ash *Fraxinus excelsior* and fir *Abies alba.* I selected 14 study plots between 500-800 m asl. that were similar to each other with respect to exposition, stand structure and age as well as tree species composition.

In the centre of each site, four trunk-window traps (Kaila 1993) and four eclectors (modified after Funke 1971) were placed. Two eclectors of a site contained logs (log eclectors), the other two limbs (limb eclectors), collected within 10 m around the trap. Only dead wood of beech, *Fagus sylvatica*, at a medium stage of decay (presence of insect holes, bark partly lose) was used. The traps were operated from April - September in 1996 and 1997, the limb eclectors only in 1996. All specimens of Coleoptera were identified to species level by various specialists.

Dead wood sampling and connectivity indices

In each of the 14 sites, I searched for dead wood pieces (minimum length = 1 m; ∅ at the smaller end > 20 cm), within 150 m around the traps. Each piece was numbered and its position recorded on a 1:5000 map of the area. Pieces less than 5 m apart were recorded as having the same position. For lying pieces, diameter at both ends and length was measured. For standing dead trees, diameter was measured about 20 cm above ground and height was estimated. Diameter at the top was approximated using tree species-specific regression equations derived from the lying objects sampled. Measuring connectivity with several metrics simultaneously is advantageous for the understanding of spatial processes (Rogers 1993; McGarigal & McComb 1995; Ritters et al. 1995). I calculated therefore the volume of each piece and subsequently three indices of dead wood connectivity for each plot: 1. Nearest neighbour distance (NN, Diggle 1983) as mean distance of randomly selected dead wood pieces to their nearest piece. I used a random number table to select the pieces, and no distance was measured twice. Selection was stopped when over 90% of all pieces were considered. 2. Proximity index (PX, modified after Whitcomb et al. 1981): I randomly selected five dead wood pieces within each quarter of a study plot with all pieces being at least 40 m apart from each other, resulting in 20 pieces per study plot. The ratios between volume and distance of all pieces within 20 m of the 20 selected pieces were summed. The average of these 20 sums yielded PX. 3. Circle (C, after Buckland et al. 1993): I placed five circles (r = 20 m) within each quarter of a study plot, giving totally 20 circles per plot. The circles were placed randomly without overlapping. The volume of all dead wood pieces was summed and the average volume of all 20 circles per plot was considered as index C. Following McGarigal & Marks (1995), I calculated the variance of each index as a measure of dispersion. As the variances of NN and C were all small, I only used the variance of PX (PXvar) in the further analyses.

Extraction of species characteristic for high dead wood connectivity

The data obtained by each trap type (trunk-window trap, log eclector, limb eclector) were analysed separately by three different methods to extract the species characteristic for high dead wood connectivity.

(1) Canonical Correspondence Analysis (CCA)

Canonical Correspondence Analysis (CCA, ter Braak 1986; 1995) is a multivariate technique for relating species composition and abundance to underlying environmental gradients. The axes calculated by the analysis are linear combinations of the environmental variables (direct gradient analysis) and the species are ordinated along these axes according to their abundances. Thus, species preferences are characterised by their position on the axes (Marshall & Elliott 1997; Spitzer et al. 1997; Didham et al. 1998a). I performed a CCA for each of the data sets obtained by the three trap types, using the four connectivity indices (NN; PX; PXvar and C) as environmental variables. I considered the last five species at the end of axis 1, pointing into the direction of increasing dead wood connectivity, as characteristic for high dead wood connectivity. All calculations were done using CANOCO 4.0 (ter Braak & Šmilauer 1998), significance of the axes was tested with a Monte Carlo permutation test with 500 permutations and only significant ordinations ($p \leq 0.05$) were considered.

(2) Indicator value method

The indicator value method developed by Dufrêne and Legendre (1997) is a new approach to identify indicator species for *a priori* established groups of samples. The indicator value of a species *i* in group *j* is calculated by multiplying its group specificity (A_{ij}) with its group fidelity (B_{ij}). A_{ij} is the mean abundance of the species *i* in the sites of group *j* relative to its abundance in all groups considered. B_{ij} is the relative frequency of occurrence of species *i* in the sites of group *j*:

$A_{ij} = \text{NIndividuals}_{ij} / \text{NIndividuals}_i$

$B_{ij} = \text{Nsites}_{ij} / \text{Nsites}_j$

$\text{IndVal} = A_{ij} \times B_{ij} \times 100$

The resulting indicator value (IndVal) is expressed as percentage of perfect indication (when all individuals of a species are found only in one of the *a priori* established groups and when the species occurs in all sites of that group). I ranked the 14 study plots according to each of the four connectivity indices and the average rank was used to divide the plots into three groups: highly connected (5 sites), medium connected (4 sites) and poorly connected (5 sites). The significance of the indicator values was assessed by a randomisation test (Dufrêne & Legendre 1997). The species that were assigned to be significant indicators of the highly connected group ($p \leq 0.05$), were considered as characteristic for high dead wood connectivity.

(3) Exclusive species

Finally, those species that occurred exclusively in the five highly connected plots (see indicator value method) were selected as characteristic for high dead wood connectivity.

The three methods are based on different aspects of the species data. As none of them will give a complete picture of the species characteristic for high dead wood connectivity, I lumped the species indicated as characteristic for high dead wood connectivity together and searched then for common biological traits.

Biological traits

Ecological information was compiled for each species collected in collaboration with F. Köhler, (Koleopterologisches Forschungsbüro), Bornheim, Germany, and J. Rusch, Altdöbern, Germany, two of the most acknowledged experts of the ecology of Central European beetles. Their data bases on beetle ecology refer mostly to Horion (1941-1974; 1951), Horion (1951), Freude et al. (1964-1983), Koch (1989-1992), Köhler (1996), and Köhler & Klausnitzer (1998). Only saproxylic species were included in the analyses. The selection of the traits considered here was directed by their relevance for susceptibility to fragmentation effects as well as by the amount of information available for all species of this study. Each species was rated according to its habitat specificity as stenotopic or having broader habitat requirements following the classification provided by Koch (1989-1992). Next, I considered dead, deciduous wood and wood mould as rare dead wood types and therefore classified the species whether to be associated with these types of dead wood or not. The density of dead, deciduous wood present in the study area was significantly lower than of dead, coniferous wood (Schiegg unpubl.). *Bibloporus bicolor* (DENNY 1825) for instance, was recorded as stenotopic species confined to wood mould and *Rhizophagus perforatus*, ERICHSON 1845, as eurytopic and associated with dead, deciduous wood. Furthermore, the species were grouped according to their diet into mycetophages (e. g., *Octotemnus glabriculus* (GYLLENHAL 1827)), xylophages (e. g., *Ptilinus pectinicornis* (LINNÉ 1758)), xylomycetophages (specialists on ambrosia fungi living inside wood, e. g., *Hylis foveicollis* (THOMSON 1847)) and zoophages (e. g., *Rhinosimus planirostris* (FARBRICIUS 1787)). Phytophagous species and those with unknown diet were summarised as 'other' (4 % of 175 species). All species that have been observed as flying adults in the field three months per year or less (Köhler, unpubl.) were considered to have a short mobile phase. Unfortunately, no information on this trait was available for 17 % of the species but as I regarded it as particularly important, I included this category despite this limitation. The most abundant species with a short mobile phase was *Denticollis linearis* (LINNÉ 1758). Finally, all species that were included in the Red List of Germany (Geiser 1998) where regarded as threatened, as the Swiss Red List for Coleoptera only contains few selected families (Brancucci 1994; Marchi 1994).

The next step was to contrast the traits of the species indicated by the different methods as characteristic for high dead wood connectivity (hereafter called 'characteristic species') with the traits of the species not indicated by any method (hereafter called 'remaining species'). I tested whether the proportion of species with particular biological attributes differed, when the characteristic species and the remaining species were compared (χ^2-2x2 table tests of independence, Sokal & Rohlf 1995). The species obtained by the three trap types were pooled for these tests.

Results

Out of 175 species initially considered, 30 species were extracted by at least one of the three methods to be characteristic for high dead wood connectivity (see appendix for a detailed species list). Different species were indicated by the three methods. Only three species were obtained by two methods to be characteristic, namely *Euplectus fauveli* GUILLEBEAU 1888, *Cis lineatocribratus* MELLIE 1848, and *Strangalia aurulenta*, (FABRICIUS 1792) and none species was indicated by all three methods (Fig.1).

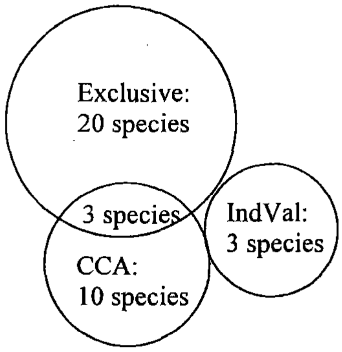

Fig. 1. The species numbers obtained by the three approaches. IndVal = Indicator value method; CCA = method based on Canonical Correspondence Analysis, exclusive = species occurring exclusively in highly connected sites.

Table 1 gives an overview about the attributes and number of species obtained by each method.

The indicator value method yielded only three species with significant indicator values: *Anisotoma orbicularis* (HERBST 1792), *Euplectus brunneus* (GRIMM 1841) and *Dryocoetes autographus* (RATZEBURG 1837), which did not have any particular traits in common. As three was to low a number of species to be tested, I performed the χ^2-2x2 table tests of independence only with the other two approaches.

The CCA method included only species collected by log eclectors and trunk-window traps, as no significant ordination was possible for the data obtained by the limb eclectors. The first axis (Eigenvalue 0.68; % variance explained 51.4; $p = 0.01$) of the ordination of the log eclector data was determined by the variable PX, whereas PXvar contributed most to the position of the first axis (Eigenvalue 0.15; % variance explained 57.7; $p = 0.05$) in the ordination of trunk-window trap data. As a tendency, the CCA approach yielded a higher proportion of species associated with wood mould ($\chi^2 = 2.78$; $p = 0.09$; df = 1) and more species were recorded as threatened than in the remaining species ($\chi^2 = 3.5$; $p = 0.06$).

The proportion of stenotopic species was markedly larger in the species occurring exclusively in highly-connected sites ($\chi^2 = 7.34$; $p = 0.01$; df = 1).

Overall, the characteristic species shared some traits, which tended to separate them from the remaining species (Table 1).

Table 1. The number of species indicated by each method as characteristic for high dead wood connectivity, grouped according to their biological attributes. Percentages are given in parentheses. Indval = Indicator value method; CCA = method based on Canonical Correspondence Analysis, exclusive = species occurring exclusively in highly connected sites; charact. = species indicated by at least one method to be characteristic for high dead wood connectivity, remaining = species not indicated by any method to be characteristic for high dead wood connectivity, all = all species included in this study. Note that the species numbers in the category 'habitat specificity' are not additive.

	indval		**CCA**		**exclusive**		**charact.**		**remaining**		**all**	
number of species	**3**		**10**		**20**		**30**		**145**		**175**	
habitat specificity												
stenotopic	1	(33.3)	2	(20.0)	15	(75.0)	18	(60.0)	62	(42.8)	80	(45.7)
wood mould	1	(33.3)	3	(30.0)	1	(5.0)	5	(16.7)	17	(11.7)	22	(12.6)
deciduous wood	1	(33.3)	4	(40.0)	10	(50.0)	14	(46.7)	56	(38.6)	70	(40.0)
diet												
mycetophagous	1	(33.3)	4	(40.0)	7	(35.0)	10	(33.3)	45	(31.0)	55	(31.4)
xylophagous	1	(33.3)	2	(20.0)	8	(40.0)	11	(36.7)	37	(25.5)	48	(27.4)
xylomycetophages	0	(0.0)	1	(10.0)	1	(5.0)	2	(6.7)	9	(6.2)	11	(6.3)
zoophagous	1	(33.3)	3	(30.0)	4	(20.0)	7	(23.3)	47	(32.4)	54	(30.9)
other	0	(0.0)	0	(0.0)	0	(0.0)	0	(0.0)	7	(4.9)	7	(4.0)
mobile phase												
1-3 months	0	(0.0)	4	(40.0)	9	(45.0)	12	(40.0)	40	(27.6)	52	(29.7)
> 3 months	3	(100.0)	6	(60.0)	9	(45.0)	16	(53.3)	79	(54.5)	95	(54.3)
unknown	0	(0.0)	0	(0.0)	2	(10.0)	2	(6.7)	26	(17.9)	28	(16.0)
threat												
threatened	0	(0.0)	5	(50.0)	7	(35.0)	9	(30.0)	34	(23.4)	43	(24.6)
safe	3	(100.0)	5	(50.0)	13	(65.0)	21	(70.0)	111	(76.6)	132	(75.4)

A slightly larger proportion of stenotopic species occurred in the characteristic than in the remaining species (χ^2 = 2.98; p =0.08; df = 1). The proportion of zoophages was only marginally lower in the characteristic than in the remaining species (χ^2 = 0.96; p = 0.33; df = 1) and the proportion of species with a short mobile phase larger (χ^2 = 1.83; p = 0.18; df = 1), these relations are not statistically significant. Body sizes of characteristic (Ø ± SD = 4.2 ± 0.4 mm) and the remaining species (4.0 ± 0.4 mm) were not significantly different (t-test; t = 0.16; p = 0.44).

Discussion

Methodology

The three methods used differed both in the number and in the identity of the species they extracted as characteristic for high dead wood connectivity. This finding illustrates that it is indispensable to use a combination of methods, when aiming at identifying species characteristic for particular habitat features. Three species were yielded by two methods as characteristic for high dead wood connectivity: *Euplectus fauveli*, GUILLEBEAU 1888, a small, stenotopic species occurring in wood mould and particularly in moist habitats. The species is widespread in Europe, but appears to occur only in low densities. Rauh (1993) reports it as indicator of mostly undisturbed forest stands. The second species was *Cis lineatocribratus*, MELLIE 1848, which is specialised on dead wood inhabiting fungi such as the Hoof fungus *Fomes fomentarius*. The species is recorded as endangered in the Red List of Germany (Geiser 1998). The third species was *Strangalia aurulenta*, (FABRICIUS 1792) a large, xylophagous species which as an adult needs pollen to feed on. *S. aurulenta* is stenotopic and only develops in dead, deciduous wood of large diameters. This species is rarely encountered and rated as heavily endangered in the Red List of Germany (Geiser 1998). Speight (1989) lists *S. aurulenta* as 'species useful in identifying forests of international importance to nature conservation'. Overall, all these three species have traits which are suspected to render them sensitive to fragmentation effects. In the following section, I briefly discuss the advantages and limitations of the methods used:

CCA - Canonical Correspondence Analysis has the restriction that it basically requires unimodal species response curves (Palmer 1993; ter Braak 1995). Though this technique is robust against violations of this assumption (ter Braak & Prentice 1988), it is inappropriate for extremely short gradients, where species abundances appear as monotonic functions of the environmental gradients (ter Braak & Prentice 1988; ter Braak 1995). To view the last five species of a gradient as characteristic, as in this study, is somewhat arbitrary. Alternatively, the species scores may be grouped by cluster analysis (Carey et al. 1995); however, it then has to be decided how many clusters should be formed (Milligan & Cooper 1985). For an investigation where the very end of a gradient is of interest, the clusters include too many sites which makes meaningful comparisons difficult.

Indicator value method - This method proposed by Dufrêne and Legendre (1997) is a new approach combining a species relative abundance with its relative frequencies of occurrence in various groups of sites and it has been successfully used in other studies (Borcard & Vaucher-von Ballmoos 1997; Rambo & Muir 1998). In this study, the results are somewhat ambiguous and difficult to interpret as only three species were considered to be significant indicators of highly connected sites. To achieve a high and therefore significant indicator value, a species must occur with high frequency in a particular group of sites only. Some potentially characteristic species may have been just too rare in the samples considered here to be rated as indicative for high dead wood connectivity.

Exclusive species - To discuss the traits of species occurring only in a particular group of samples can give a quick and rough impression, whether there are any differences to the species in the other groups. The traits of the species that occurred only in the highly connected sites agreed fairly well with what was hypothesised to be typical for species characteristic for high dead wood connectivity. On the other hand, this procedure is not selective enough to exclude species that were sampled just by chance in the highly connected group. *Dasytes plumbeus* (MÜLLER 1776) and *Eucnemis capucina* AHRENS 1812, most probably are such species, as they are both widespread and common in Europe and do not have any specialised habitat requirements (Koch 1998-1992).

Biological traits of species characteristic for high dead wood connectivity

Habitat specificity - The proportion of stenotopic species was significantly larger in the characteristic than in the remaining species. Species occupying narrow niches and those confined to rare habitat types are particularly sensitive to habitat fragmentation (Lawton 1995), except for species specialised on edge habitats (e. g., Cappucino & Root 1992; Roland 1993). Stubbs (1972) estimated that for very specialised saproxylic species, only 1% of potential substrate is suitable for colonisation by these species. Wood mould, for instance, is encountered only in dead wood types that are sparse in commercial forests, namely in the final decay stages, as well as in cavities and hollow trees (Rauh 1993). Nilsson & Baranowski (1997) argue that hollows are extremely stable habitats, suitable for the colonisation by beetles for more than hundred years. They conclude that species depending on wood mould must be even less mobile than other saproxylic species because they found fewer species in hollow trees in stands that had previously been managed compared to unmanaged zones. In this study, the CCA method yielded a slightly higher proportion of species associated with wood mould which may support the evidence of increased vulnerability to fragmentation of these species.

Diet - The proportion of zoophages within the characteristic species was nearly 20 % though not significantly lower than in the remaining species. Species at high trophic levels often are found to be particularly vulnerable to fragmentation effects (Pimm & Lawton 1977; Kareiva 1987; Kruess & Tscharntke 1994; Didham et al. 1998b). In contrast, other authors demonstrated that the proportion of species in different trophic categories remained constant when diversity fell due to fragmentation effects (Heatwole & Levins 1972; Mikkelson 1993). Predatory beetles are considered to be trophic generalists and are therefore likely to establish and persist easier than herbivores (Brinck 1948; Root 1973; Becker 1975), which may be a reason for the pattern observed in this study. Zoophagous saproxylic species may find their prey not only in particular dead wood types and consequently depend less on dead wood connectivity than non-predatory species.

Duration of mobile phase - Due to their mostly short life-spans, insects are generally time-limited dispersers (Dixon et al. 1987; Ward 1987). Consequently, the number of dead wood pieces that can be located and colonised, is restricted by the time available to travel between them. However, not only total life-span may limit the time for dispersal, but also the length of mobility periods. The proportion of species being mobile for short periods of time was slightly larger in the characteristic than in the remaining species, indicating that species dispersing only for short periods of time may depend particularly on high dead wood connectivity. This result must be handled with care, however, because no data were available for 17 % of all species.

Concluding remarks

Most parts of the study forest have been managed for centuries (Chapter 3). Hence, the species we observe today in this area are predominantly those that passed the bottle-neck of intensive forestry, as there is no reserve of a similar old-growth forest in the close vicinity as a source for immigration. The surviving species either had the genetic potential to cope with the reduced dead wood amounts or escaped in some way or another the changes in their environment. The latter are called 'old-growth' or 'relict' species (Alexander 1988; Speight 1989; Rauh 1993; Kaila et al. 1997; Niemlä 1997), which are only found in forests with long temporal and spatial continuity of dead wood. Such species did not occur in my samples except for *S. aurulenta*, which has been indicated by the CCA method and the method of exclusive species as characteristic for high dead wood connectivity. Some 'relict' species, however, may have never been present in the area due to the rather shady and humid conditions caused by the north-eastern exposition of the slope. The deficit in these 'old-growth' species may be one reason, why the differences between the characteristic and the remaining species did not appear more markedly. Another reason may be the lack of more detailed information of the species' ecology such as dispersal capacity. Nevertheless, it could be demonstrated that saproxylic beetle species differ in their response to within-forest fragmentation, with stenotopic species being more vulnerable than other species. Hence, among the traits considered here, mostly high habitat specificity contributes to susceptibility of saproxylic beetle species to fragmentation effects. This finding underlines the importance of leaving dead wood pieces distributed over the whole area of managed forests to support particularly vulnerable species and to facilitate recolonisation by regionally extinct species. This is one important step towards a forestry that 'sees a forest as a community of species rather than a wood factory' (Simberloff 1999).

Acknowledgements - I thank the Swiss National Science Foundation for the financial support of this study (Grant 31-45911.95) and Gilberto Pasinelli, Sari Pitkanen and Peter Duelli for their comments on the manuscript.

References

Alexander, K.N.A. 1988. The development of an index of ecological continuity for deadwood associated beetles. Antenna 12: 69-71.

Andrén, H. 1994. Effects of habitat fragmentation on birds an mammals in landscapes with different proportions of suitable habitat: A review. Oikos 71: 355-366.

Ås, S. 1993. Are habitat islands islands? Woodliving beetles (Coleoptera) in deciduous forest fragments in boreal forests Ecography 16: 219-228.

Becker, P. 1975. Island colonization by carnivorous and herbivorous Coleoptera. Journal of Animal Ecology 44: 893-906.

Borcard, D. & Vaucher-von Ballmoos, C. 1997. Oribatide mites (Acari, Oribatidae) of a primary peat-bog-pasture transition in the Swiss Jura mountains. Ecoscience 4: 470-479.

Brancucci, M. 1994. Rote Liste der gefährdeten Wasserkäfer (nur Hydradephaga) der Schweiz. In: Duelli, P. (ed.). Rote Listen der gefährdeten Tierarten in der Schweiz. Bundesamt für Umwelt, Wald und Landschaft (BUWAL), Bern. pp 60-63.

Bright, P.W. 1993. Habitat fragmentation - problems and predictions for British mammals. Mammal Review 23: 101-111.

Brinck, P. 1948. Coleoptera of Tristan de Cunha. Det Norske Videnskaps. Akademie, Oslo No.17.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L. 1993. Distance sampling. Chapman & Hall, London.

Cappucino, N. & Root, R.B. 1992. The significance of host patch edges to the colonization and development of *Corythucha marmorata* (Hemiptera: Tingidae). Ecological Entomology 17: 109-113.

Carey, P.D., Preston, C.D., Hill, M.O., Usher, M.B., Wright, S.M. 1995. An environmentally defined biogeographical zonation of Scotland designed to reflect species distributions. Journal of Ecology 83: 833-845.

Diamond, J.M. 1984. 'Normal' extinctions of isolated populations. In: Nietecki, M.H. (ed.). Extinctions. The University of Chicago Press, Chicago. pp 191-246.

Didham, R.K., Hammond, P.M., Lawton, J.H., Eggleton, Stork, P.N. 1998a. Beetle species responses to tropical forest fragmentation. Ecological Monographs 68: 295-323.

Didham, R.K., Hammond, P.M., Lawton, J.H., Eggleton, P. 1998b. Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. Philosphical Transactions of the Royal Society of London, Series B 353: 437-451.

Diggle, P.J. 1983. Statistical analysis of spatial patterns. Academic Press, London.

Dixon, A.F.G., Kindlmann, P., Leps, J., Holman, J. 1987. Why there are so few species of aphids, especially in the tropics. American Naturalist 129: 580 592.

Dufrêne, M. & Legendre, P. 1997. Species assembleges and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345-366.

Flessa, K.W. 1986. Causes and consequences of extinctions. In: Raup, D. M. & Jablonski, D. (eds.). Patterns and processes in the history of life. Springer-Verlag, Berlin. pp 235-258.

Freude, H., Harde, K., W., Lohse, G.A. 1964-1983. Die Käfer Mitteleuopas, Band 1-11. Goecke & Evers, Krefeld.

Funke, W. 1971. Food and energy turnover of leaf-eating insects and their influence on primary production. Ecological studies 2: 81-93.

Gaston, K.J. 1994. Rarity. Chapman & Hall, London.

Geiser, R. 1998. Rote Liste der Käfer (Coleoptera). In: Binot, M., Bless, R., Boye, P., Gruttke, H., Pretscher, P. (eds.): Rote Liste der gefährdeten Tiere Deutschlands. Schriftenreihe Landschaftspflege und Naturschutz 55: 168-230.

Hager, H.R. 1998. Area-sensitivity of reptiles and amphibians: are there indicator species for habitat fragmentation? Ecoscience 5: 139-147.

Heatwole, H. & Levins, R. 1972. Trophic structure stability and faunal change during recolonization. Ecology 53: 531-534.

Horion, A. 1941-1974. Faunistik der mitteleuropäischen Käfer. Vol. I-XII. Kernen, Stuttgart.

Horion, A. 1951. Verzeichnis der Käfer Mitteleuropas (Deutschland, Oesterreich, Tschechoslowakei) mit kurzen, faunistischen Angaben. Kernen, Stuttgart.

Kaila, L. 1993. A new method for collecting quantitative samples of insects associated with decaying wood or wood fungi. Entomologica Fennica 29: 21-23.

Kaila, L., Martikainen, P., Punttila, P. 1997. Dead trees left in clear-cut benefit saproxylic Coleoptera adapted to natural distrurbances in boreal forest. Biodiversity and Conservation 6: 1-18.

Kaila, L., Martikainen, P., Punttila, P., Yakovlev, E. 1994. Saproxylic beetles (Coleoptera) on dead birch trunks decayed by different polypore species. Annales Zoologici Fennici 31: 97-107.

Kareiva, P. 1987. Habitat fragmentation and the stability of predator-prey interactions. Nature 326: 388-390.

Koch, K. 1989-1992. Die Käfer Mitteleuopas. Ökologie. Goecke & Evers, Krefeld.

Köhler, F. 1996. Käferfauna in Naturwaldzellen und Wirtschaftswald. Vergleichende Untersuchungen im Waldreservat Kermeter in der Nordeifel. Schriftenreihe LÖBF/LAfAO (Recklinghausen) 6: 1-283.

Köhler, F. & Klausnitzer, B. 1998. Verzeichnis der Käfer Deutschlands. Entomologische Nachrichten und Berichte, Beiheft 4: 1-185.

Kruess, A. & Tscharntke, T. 1994. Habitat fragmentation, species loss and biological control. Science 264: 1581-1584.

Lawton, J.H. 1995. Population dynamic priciples. In: Lawton, J.H. & May, R.M. (eds.). Extinction rates. Oxford University Press, Oxford. pp 147-163.

Marchi, W. 1994. Rote Liste der gefährdeten Laufkäfer und Sandlaufkäfer der Schweiz. In: Duelli, P. (ed.). Rote Listen der gefährdeten Tierarten in der Schweiz. Bundesamt für Umwelt, Wald und Landschaft (BUWAL), Bern. pp 55-59.

Marshall, S. & Elliott, M. 1997. A comparison of univariate and multivariate numerical and graphical techniques for determining inter- and intraspecific feeding relationships in estuarine fish. Journal of Fish Biology 51: 526-545.

McGarigal, K. & Marks, B. 1995. FRAGSTATS: Spatial analysis program for quantifying landscape structure. USDA Forest Service Gen. Tech. Rep. PNW-GTR-351.

McGarigal, K. & McComb, W.C. 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. Ecological Monographs 65: 235-260.

Mikkelson, G.M. 1993. How do food webs fall apart? A study of changes in trophig structure during relaxation on habitat fragments. Oikos 67: 539-547.

Milligan, G.W. & Cooper, M.C. 1985. An examination of procedures for determining the number of clusters in a data set. Psychometrika 50: 159-179.

Morrison, M.L., Marcot, B.G., Mannan, R.W. 1998. Wildlife-habitat relationships. 2nd edition. The University of Wisconsin Press.

Niemelä, J. 1997. Invertebrates and boreal forest management. Conservation Biology 11: 601-610.

Nilsson, S.G. & Baranowski, R. 1997. Habitat predictability and occurrence of wood beetles in old-growth beech forests. Ecography 20: 491-498.

Palmer, M.W. 1993. Putting things in even better order. Ecology 74: 2215-2230.

Pimm, S.L. & Lawton, J.H. 1977. Number of trophic levels in ecologcial communities. Nature 268: 329-331.

Rambo, T.R. & Muir, P.S. 1998. Bryophyte species associations with coarse woody debris and stand ages in Oregon. The Bryologist 10: 366-376.

Rauh, J. 1993. Naturwaldreservate in Bayern. Band 2. Schriftenreihe Naturwaldreservate in Bayern. IHW-Verlag.

Ritters, K.H, O'Neill, R.V., Hunsaker, C.T., Wichkham, J.D., Yankee, D.H., Timmins, S.P., Jones, K.B., Jackson, B.L. 1995. A factor analysis of landscpae pattern and structure metrics. Landscape Ecology 10: 23-39.

Rogers, C.A. 1993. Describing landscapes: indices of structure. M. S. Thesis, Simon Fraser University, Burnaby, B. C.

Roland, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. Oecologia 93: 25-30.

Root, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (Brassica oleracea). Ecological Monographs 43: 95-124.

Saunders, D., Hobbs, R., Margules, C. 1991. Biological consequences of ecosystem fragmentation: A review. Conservation Biology 5: 18-32.

Simberloff, D. 1986. The proximate causes of extinction. In: Raup; D.M. & Jablonski; D. (eds.). Patterns and processes in the history of life. Springer-Verlag, Berlin. pp 259-276.

Simberloff, D. 1999. The role of science in the preservation of forest biodiversity. Forest Ecology and Management 115: 101-111.

Sokal, R. R. & Rohlf, F.J. 1995. Biometry. 3rd edn. Freeman and Company, New York.

Soulé, M.E. 1986. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Sunderland, Massachsetts.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Nature and Environment Series No. 42. Strasbourg.

Spitzer, K., Jaroš, J., Havelka, J., Lepš, J. 1997. Effect of small-scale disturbance on butterfly communities of an indochinese montane rainforest. Biological Conservation 80: 9-15.

Stubbs, A.E. 1972. Wildlife conservation and dead wood. Supplement of the Journal of the Devon Trust for nature Conservation. pp 1-18.

ter Braak, C.J.F. 1986. Canonical Correspondance analsysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.

ter Braak, C.J.F. 1995. Ordination. In: Jongman, R.H., ter Braak, C.J.F., van Tongeren, O.F.R. (eds.). Data analysis in community ecology. Pudoc, Wageningen, The Netherlands.

ter Braak, C.J.F. & Prentice, I.C. 1988. A theory of gradient analysis. Advances in Ecological Research 18: 217-313.

ter Braak, C.J.F. & Šmilauer, P. 1998. CANOCO. Software for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis (version 4). Centre for Biometry Wageningen (Wageningen, NL) and Microcomputer Power (Ithaca NY, USA).

Walters, J.R.1998. The ecological basis of avian sensitivity to habitat fragmentation. In: Marzluff, J.M. & Sallabanks, R. (eds.). Avian conservation: research and management. Island Press. pp 181-192.

Ward, S.A. 1987. Optimal habitat selection in time-limited dispersers. American Naturalist 129: 568-579.

Warren, M.S. & Key, R.S. 1991. Woodlands: past, present potential. In: Collins, N.M. & Thomas, J.A. (eds.). The conservation of insects and their habitats. Academic Press, London. pp 155-212.

Whitcomb, R.F., Robbins, C.S., Lynch, J.F., Whitcomb, B.L., Klimkiewicz, M.K., Bstrak, D. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. In: Burgess, R.L. & Sharpe, D.M. Forest island dynamics in man-dominated landscape. Springer Verlag, New York. pp 125-205.

Appendix

List of species characteristic for high dead wood connectivity in taxonomic order. CCA = method based on Canonical Correspondence Analysis; Indval = Indicator value method; exclusive = species occurring exclusively in highly connected sites; st = stenotopic; dw = associated with deciduous wood; wm = associated with wood mould; d = diet (mycetophagous (m); zoophagous (z); xylophagous (xl); xylomycetophagous (xm); other (o); dmp = duration of mobile phase < 3 months, RL = on the Red List of Germany.

	CCA	indval	exclusive	st	dw	wm	d	dmp	RL
Leidodidae									
Anisotoma orbicularis (Herbst 1792)		x			x		m		
Ptilidae									
Ptenidium turgidum Thomson 1855	x			x	x	x	m		x
Staphylindae									
Gyrophaena minima Erichson 1837			x				m		
Placusa tachyporoides (Waltl 1838)			x				z		
Pselaphidae									
Euplectus karsteni (Reichenbach 1816)	x			x		x	z	x	
Euplectus fauveli Guillebeau 1888	x		x	x		x	z	x	
Euplectus brunneus (Grimm 1841)		x		x		x	z	x	
Melyridae									
Dasytes plumbeus (Müller 1776)			x		x		z		
Trogositidae									
Nemosoma elongatum (Linné 1761)			x			x	z		
Elateridae									
Melanotus rufipes (Herbst 1784)			x		x		z		
Eucnemidae									
Eucnemis capucina Ahrens 1812	x			x	x	x	xm	x	x
Buprestidae									
Agrilus olivicolor Kiesenwetter 1857	x			x			xl		x
Clambidae									
Clambus nigrellus Reiter 1914			x	x			m		?
Nitidulidae									
Cryptarcha strigata (Fabricius 1787)			x	x	x		z		
Cryptophagidae									
Caenoscelis sibirica Reitter 1889			x	x	x		m	x	x
Atomaria wollastoni Sharp 1867	x			x			m	?	x
Endomychidae									
Endomychus coccineus (Linné 1758)	x						m		
Cisidae									
Cis lineatocribratus Mellie 1848	x		x	x			m		x
Cis bidentatus (Olivier 1790)			x				m		
Anobiidae									
Grynobius planus (Fabricius 1787)			x	x	x		xl	x	x
Episernus granulatus Weise 1887			x	x			xl	x	x
Anobium pertinax (Linné1758)	x						xl	x	
Melandryidae									
Anisoxya fuscula (Illiger 1798)			x	x	x		xm	x	x
Cerambycidae									
Tetropium castaneum (Linné 1758)			x	x			xl	x	

Appendix: continued

Cerambycidae (continued)	**CCA**	**indval**	**exclusive**	**st**	**dw**	**wm**	**d**	**dmp**	**RL**
Strangalia aurulenta (Fabricius 1792)	x		x	x	x		xl	x	x
Stenostola dubia (Laicharting 1784)			x		x		xl	x	
Scolytidae									
Hylesinus oleiperda (Fabricius 1792)			x	x	x		xl	x	
Xylechinus pilosus (Ratzeburg 1837)			x	x			xl	x	
Dryocoetes autographus (Ratzeburg 1837)		x					xl		
Xyleborus germanus (Blandford 1894)			x		x		m		

IV Diptera and Coleoptera collected in the Forest Reserve Sihlwald ZH

K. SCHIEGG, M. OBRIST, P. DUELLI, B. MERZ, K. C. EWALD

Abstract - We analysed an extensive data set of Diptera (953 species) and Coleoptera (699 species) collected by trunk-window traps and eclectors in the forest reserve Sihlwald (Kt. Zurich, Switzerland) in 1996 and 1997. The samples contained 186 species of Diptera new to the Swiss fauna and approximately 20 species of the same group new to science were found. Temporal variability among the samples was larger than spatial variability. Despite the unusually large collecting effort, several methods applied for estimating total species richness revealed undersampling of > 30 %. We therefore underline the necessity for using standardised sampling techniques which make different studies comparable and reduce sampling effort without considerable loss of information.

Introduction

Ecological studies of insects usually require extensive samples which frequently are analysed and published only partly. As a result, valuable background information about faunistically interesting species, phenological data or the efficiency of the traps used gets lost. Furthermore, it remains often unclear, which proportion of the focal community has been sampled. However, the latter aspect is important for further studies, as such data may be used as a guideline for choosing the adequate sampling strategy. Here we present a dataset from an ecological investigation into saproxylic Diptera and Coleoptera based on two year sampling with eclectors and trunk-window traps. We first describe a new eclector type and discuss the efficiency of the traps we used for this investigation. Second, we estimate total species richness using rarefaction curves (Simberloff 1972) and other parametric and nonparametric techniques (Magurran 1988; Colwell & Codington 1994). We then explore the effects of spatial and temporal variability on our collectings. Finally, we give a list of 105 species of Diptera new to Switzerland and not yet included in the Swiss Checklist (Merz et al. 1998).

Methods

Study area

The study was carried out in the forest reserve Sihlwald (47°15'; 8°33') at a NE-orientated slope 10 km south of Zurich, Switzerland. The entire forest covers 10 km^2 and is dominated by beech *Fagus sylvatica* and spruce *Picea abies*, followed by ash *Fraxinus excelsior* and fir *Abies alba*. Rainfall averages out at 1400 mm per year. We selected 14 study plots between 500-800 m asl. that were similar to each other with respect to exposition, stand structure and age as well as tree species composition.

Insect sampling

Insects were collected using eclectors ('extraction cylinders', Økland 1996; 'emergence traps' Irmler et al. 1996) and trunk-window traps (Kaila 1993). Due to the tent-like construction of eclectors, pieces of dead wood can be enclosed to rear saproxylic insects. Emerging insects are attracted by the attached collecting boxes which are the only source of light in the trap. The senior author developed an improved eclector type, which can be used on fallen dead wood in contact with the forest floor (Fig. 1).

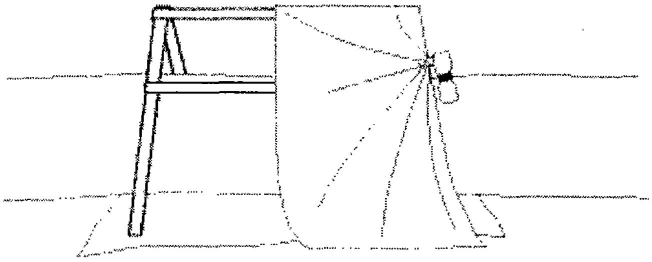

Fig. 1. A log eclector during installation.

Its construction is simple and it can be installed within one hour in the field. Material costs are low and the trap is suited for repeatable use. A major advantage are the simplified collecting boxes which can be exchanged within a few minutes. Four eclectors were installed in each of the 14 sites, two containing a part of a log (diameter at the smaller end > 20 cm, L = 1.5 m, log eclectors) and two containing branches (diameter at both ends 5-10 cm, L = 1.0-1.5 m, branch eclectors), giving 28 traps of each type, 56 in total. The collecting boxes were filled with a 2 % formaldehyde solution and emptied monthly from May - November 1996 and 1997. The branch eclectors were only operated in 1996. Additionally, four trunk-window traps (Kaila 1993) were installed in each plot (Fig. 2).

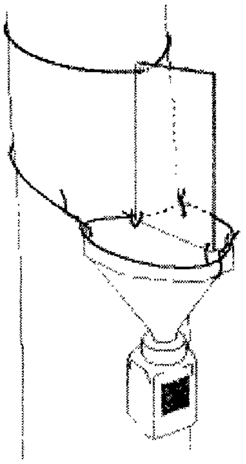

Fig. 2. A trunk-window trap

All traps were placed in the plot centre within a range of 10 m. Trunk-window traps consisted of a transparent plastic plate (30 x 45 cm) attached above a 30 cm wide plastic funnel. A 0.3 l collecting box with 4 % formaldehyde solution and some drops of a detergent to lower surface tension was mounted below the funnel. The trap was fixed on a piece of dead wood with the lower end about 1 m above ground. This method has been successfully used in various studies (Kaila 1993; Siitonen 1994; Økland et al. 1996; Hammond 1997; Kaila et al. 1997) and yields high numbers of saproxylic species. The small diameter of the collecting box prevents animals from drinking the formaldehyde solution and reduces evaporation. The only restriction is that falling leaves may clog up the opening of the collecting box in autumn. The trunk-window traps were active from April - September both in 1996 and 1997 and were emptied biweekly. All specimens of Diptera and Coleoptera were sorted out and identified to species level by various specialists except for Cecidiomyiidae. Chironomidae, Phoridae, Psychodidae and Sphaeroceridae which could be identified only partly due to identification problems. Additionally, we had to omit all samples of Diptera collected by trunk-window traps in August and September 1997 because of restrictions in time and money.

Estimating species richness

As no community can be sampled fully, one might be interested in how many species it actually contains. We applied the following three methods for estimating total species richness:

a) s/i functions (increasing number of species with increasing number of individuals)

Rarefaction curves (Simberloff 1972) usually are applied to reach a standardised estimate of the number of species collected with any given sampling effort, e. g., number of individuals (Colwell & Coddington 1994). However, these methods can also be used to extrapolate the number of species for a given, large number of individuals (Duelli 1997). We found empirically the following equation to describe the asymptotic function of the number of species per number of individuals:

$$N_s = \frac{\underline{N_s} * (1\text{-}\exp(-p1 * N_i^{p2}))}{(1 - \exp(-p1 * \underline{N_i}^{p2}))}$$

where

Ns = number of species caught with a given number of traps
Ni = number of individuals caught with a given number of traps
<u>Ns</u> (<u>Ni</u>) = total number of species (individuals) caught with all traps
p1 and p2 = function parameters

Applying this function to a sufficiently large dataset allows to estimate the number of species that would have been obtained if more individuals had been collected (e. g. 1 Mio. individuals, for a more detailed description see Duelli 1997).

b) Parametric models for estimating species richness

A community can be characterised by the abundance distribution of its species. These distributions usually are described in relation to four main models (Magurran 1988): the log normal distribution, the geometric series, the logarithmic series and MacArthur's broken stick model. We fitted our data to a truncated lognormal distribution following the maximum likelihood method devised by Cohen (1961) and described by Magurran (1988). Goodness of fit was tested by χ^2-test (Magurran 1988). We used the truncated lognormal model to calculate an estimate of total species richness.

c) Abundance-based estimators of species richness

Non-parametric models provide an alternative way to estimate total species richness (reviews in Colwell & Coddington 1994; Chadzon et al. 1998). We decided upon the abundance-based coverage estimator (ACE) developed by Chao et al. (1993) and Lee & Chao (1994). This estimator is based on those species with less than 11 individuals per sample, as it is suspected that undersampling occurs mostly in low abundance classes. All calculations were done using EstimateS Version 5.0 (Colwell 1997).

Reducing sampling effort?

Trunk-window traps are frequently used in investigations into saproxylic beetles, but the number of traps involved usually is smaller than in our study (Kaila 1993; Siitonen 1994; Kaila et al. 1997). The question arises, therefore, what consequences reduced sampling effort has. Based on our extensive data set obtained from 56 traps, we compared the number of beetle species we obtained in 1997 with the species numbers in subsamples of that year. The subsamples were formed by simulating reduced sampling effort: a) considering only two out of four traps per site, resulting in 14 sites and 28 traps, and b) considering only seven sites, resulting also in 28 traps. With this procedure, our subsamples differed only in the number of sites involved. The traps and sites to be included in the subsamples were selected randomly and this was repeated until the mean number of species stabilised (10 times).

Results

Number of species collected

Totally, 699 (29'690 individuals) species of beetles and 953 (61'866 individuals) species of Diptera were recorded. Of the latter, 186 species were new to Switzerland (Haenni 1997; Merz 1997; Delécolle & Schiegg 1998; Dempewolf & Schiegg 1998; Otto & Schiegg in press) and some of them have already been included in the Swiss Diptera Checklist (Merz et al. 1998). About 20 species were new to science (e.g. Delécolle & Schiegg 1999), most of them belonging to *Sciaridae* (Heller, pers. com.). The species new to Switzerland which have not yet been published, are given in the appendix and a complete list of species is available from P. Duelli upon request. No beetle species new to the Swiss fauna was found (Besuchet, unpubl.). As only a part of the specimens of the families Psychodidae, Chironomidae, Phoridae, and Sphaeroceridae were identified, we excluded these families in all tables and analyses, except for estimation of species numbers.

Table 1. Number of species collected by the three trap types. Diptera, trunk-window traps, 1997: data only April - July 31. Not included are the species of Cecidiomyiidae, Chironomidae, Phoridae, Psychodidae and Sphaeroceridae.

	log eclectors			**branch eclectors**	**trunk-window traps**			**all traps**
	1996	**1997**	**total**	**1996**	**1996**	**1997**	**total**	**total**
Coleoptera								
families	32	30	**40**	**38**	54	50	**58**	**61**
species	232	237	**328**	**265**	443	404	**581**	**699**
individuals	3'215	2'604	**5'819**	**2'901**	14'348	6'622	**20'970**	**29'690**
Diptera								
families	37	35	**41**	**45**	53	35	**55**	**59**
species	348	280	**441**	**415**	481	297	**595**	**879**
individuals	14'927	23'891	**38'818**	**17'000**	2'514	2'615	**5'129**	**60'947**

In Coleoptera, the eclectors yielded a total of 399 species, 116 (29.1 %) of which did not occur in the trunk-window traps. Alternatively, 298 of 581 species (51.3 %) were found exclusively in the trunk-window traps. In Diptera, 566 species were collected by eclectors and 322 (56.9 %) were not present in the trunk-window traps, which in turn contained 351 of 595 species (59.0 %) not occurring in eclectors (Tab. 1).

Trunk-window traps

In Coleoptera, 55.7 % of all species collected by trunk-window traps were sampled in both years (Fig. 3). Most species were present with only few individuals, only two species exceeded 5 % of relative abundance, namely *Xyleborus dispar*, (FABRICIUS, 1792), (39.2 % in 1996; 12.1 % in 1997) and *Atomaria diluta* ERICHSON, 1846, (5.0 % in 1997). Hence, the larger number of individuals in the coleopteran samples was mainly due to these two species.

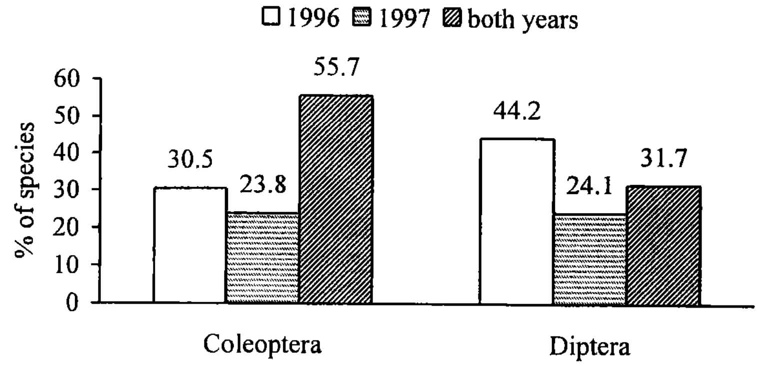

Fig. 3. Percentages of species collected by trunk-window traps exclusively in 1996 and 1997, and in both years.

As dipteran data from trunk-window traps in 1997 are only available from 7 May - 31 July, we only considered the data of this time span in 1996 for between year comparisons. There was a marked species turnover between 1996 and 1997, as only 31.7 % of the species were collected in both years (Fig. 3). Only Sciarids were present with relative abundances > 5 %: *Bradysia hilariformis* TUOMIKOWSKI, 1960 with 7.5 % in 1996 and 7.2 % in 1997, as well as *Scatopsciara calamophila* FREY, 1948 with 5.9 % in 1997 and *Bradysia fungicola* (WINNERTZ, 1967) with 6.1 % in 1997.

Spatial variability

When only the samples of half of the trunk-window traps active in 1997 were considered, still >75 % of all beetle species were recorded (Table 2), It was of no relevance whether the number of traps per site or the number of sites was reduced, neither the observed nor the estimated species numbers differed significantly from each other (Mann-Whitney U-test, df = 1, p > 0.1 in all cases). We did not use the ACE estimator here, as the collector's curve (cumulative number of species plotted against sampling effort, see below) did not reach an asymptote, making reliable estimation by a nonparametric procedure impossible.

Table 2. Number of beetle species (observed and estimated) obtained in all samples of the trunk-window traps of 1997 and in subsamples, where only half of the traps per site (traps) or half of the sites (sites) were considered. Given are mean numbers ± SD (10 randomisations). Si = species/individuals function; lognormal = estimate based on truncated lognormal distribution of species abundances.

method	all samples	subsamples	
observed		**traps**	**sites**
	404	312 ± 13.8	305 ±8.9
estimated			
Si	658	527 ± 41.9	526 ± 39.0
lognormal	605	465 ± 11.2	467 ± 11.8

Log eclectors

As the branch eclectors were operated only in 1996, we had to rely on log eclectors for between year comparisons. The collectings with interception traps in two consecutive years are temporally independent. In contrast, eclector samples of the second year can only contain species which have already been present in the first year, provided that the trap has not been displaced. Hence, the samples reflect the situation at the time when the trap was installed. Despite this potential limitation, over 20 % of the species sampled with log eclectors appeared only in the second sampling year, both in Diptera and in Coleoptera (Fig. 4).

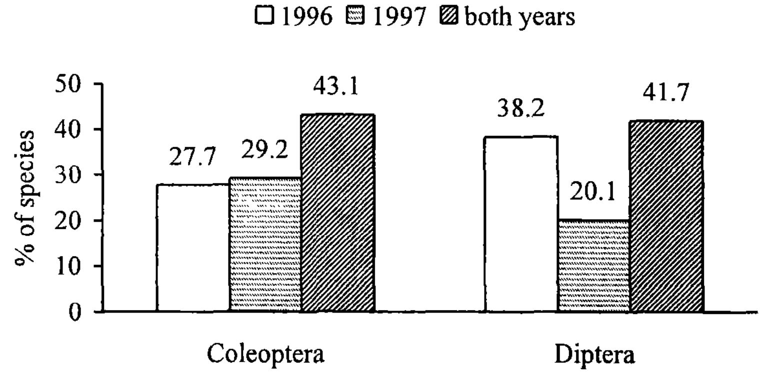

Fig. 4. Percentages of species collected by log eclectors exclusively in 1996 and 1997, and in both years.

In Coleoptera, 57 (17.4 %) and in Diptera 78 (17.7 %) species were more abundant in the second than in the first year. Regarding the samples of 1996 and 1997, the relative frequency of three species in Coleoptera and of four species in Diptera was > 5 %.

Estimated species numbers

Given the unusually large collecting effort of this study, one might suspect that further samples would not add a considerable number of species. However, Fig. 5 shows still increasing numbers of species both in Diptera and in Coleoptera when plotting them against sampling effort (collector's curve). The abundance-based coverage estimator of species richness (ACE) does also not reach an asymptote, indicating that considerably more plots should be sampled to obtain a flattened curve.

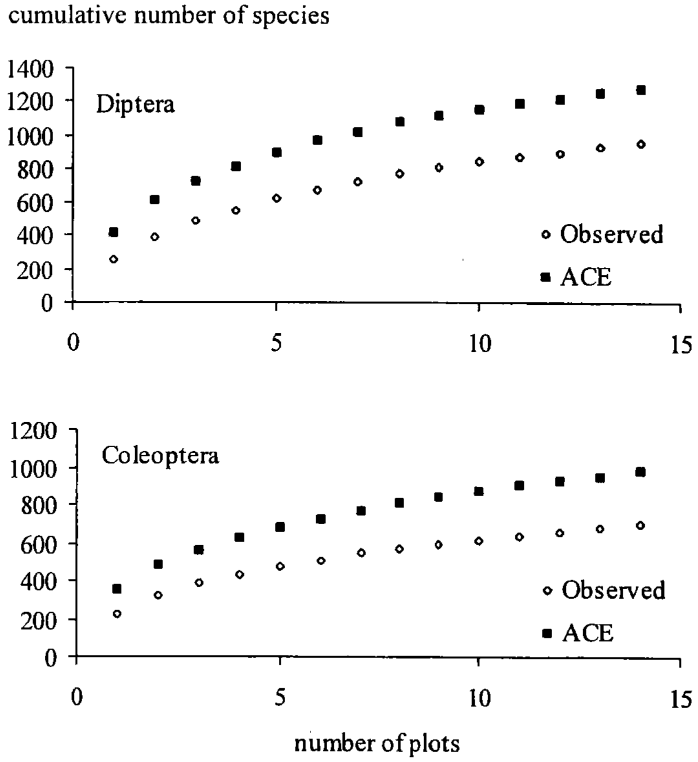

Fig. 5. Cumulative number of species against sampling effort. Data from all traps and both years pooled .

The species-abundance distribution did not deviate significantly from a truncated lognormal distribution, neither in Coleoptera ($\chi^2 = 9.97$; $p > 0.10$, $df = 7$) nor in Diptera ($\chi^2 = 7.23$; $p > 0.30$; $df = 7$). All three methods for estimating species richness revealed a clear undersampling of at least 39 % in Coleoptera and 30 % in Diptera (Table 3).

Table 3. Observed and estimated numbers of species. All traps pooled, data from 1996 and 1997. SI = species/individual function; lognormal = estimate based on truncated lognormal distribution of species abundances. ACE = abundance-based coverage estimator of species richness.

method	Coleoptera	Diptera
observed	953	699
estimated		
SI	1370	1612
lognormal	1145	1679
ACE	>983	>1278

Fig. 6 shows the contribution of each trap type to the total estimated species richness. The slope of the curve representing the trunk-window trap samples was steeper than of the curve originating from the eclector samples. This illustrates that more species were collected in low abundances by trunk-window traps. Furthermore, the curve of the trunk-window traps flattens earlier in the dipteran than in the coleopteran data, reflecting the higher species:individuals ratio of the dipteran samples stated earlier.

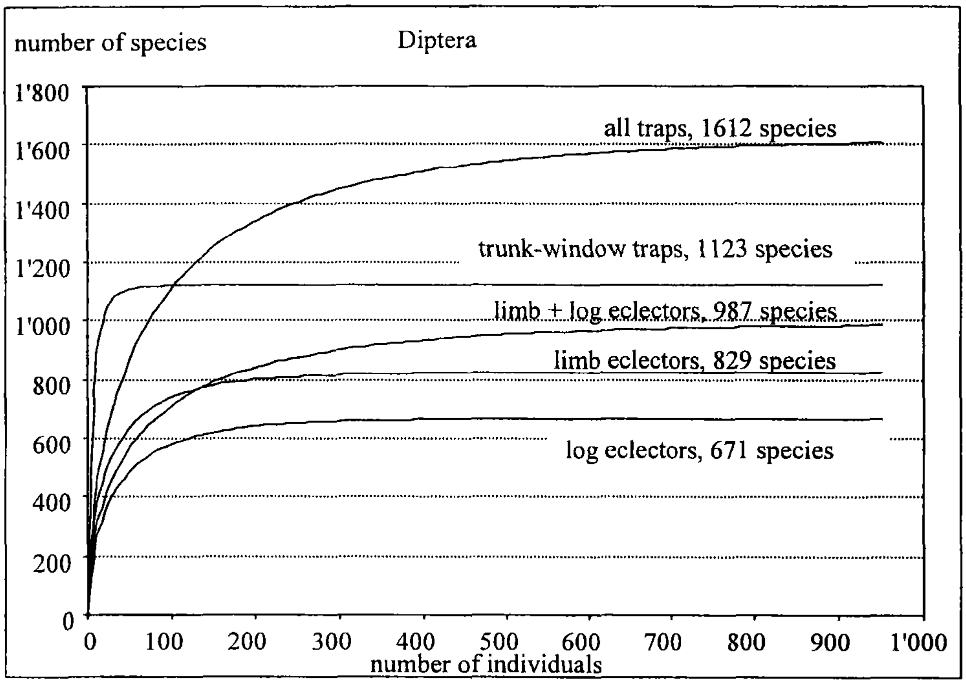

Fig. 6a. Extrapolated number of dipteran species per number of individuals (x1000) for each trap type.

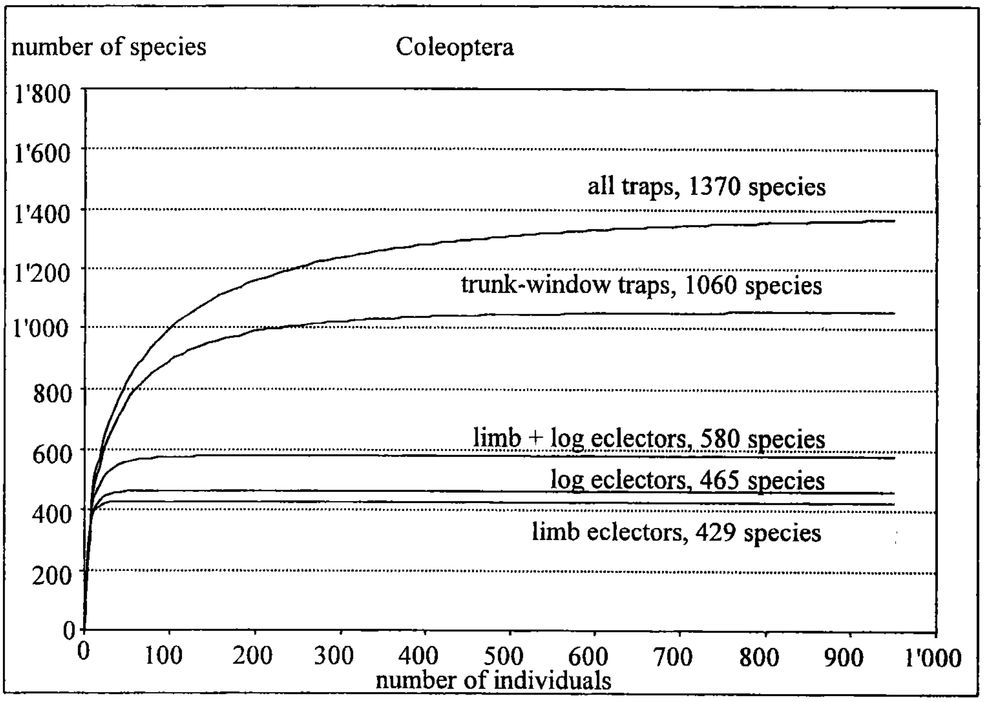

Fig. 6b. Extrapolated number of coleopteran species per number of individuals (x1000) for each trap type.

Discussion

Species new to Switzerland

Most species new to Switzerland belong either to Ceratopogonidae or Sciaridae. Both groups have received little attention in Switzerland and are therefore only poorly known (Menzel 1998; Szadziewski 1998). Some species of other families are common in neighbouring countries and could be expected to occur also in Switzerland (*Oedalea holmgreni* ZETTERSTEDT,1852: *Hemerodromia unilineata* ZETTERSTEDT 1842; *Phaonia mystica* (MEIGEN 1826)). Others are rare and only known from other parts of Europe (*Euthyneura halidayi* COLLIN 1926; *Oedalea oriunda* COLLIN 1961; *Rhamphomyia obscuripennis* MEIGEN 1830). The large number of dipteran species new to the Swiss fauna illustrates the sparse knowledge of this group, especially of species associated with forested habitats.

Trapping efficiency

Trunk-window traps yielded more species both in Diptera and in Coleoptera than eclectors. Beetles were present in much larger numbers in the trunk-window traps than Diptera (20'970 versus 5'129), which was mainly due to the frequent occurrence of *Xyleborus dispar* (FABRICIUS 1792) and *Atomaria diluta* ERICHSON 1846. Just the opposite relation was found in the eclectors, where Diptera were more abundant than Coleoptera (8'720 versus 55'818).

As all interception traps, trunk-window traps measure flight activities of the species present in the area (Hammond 1997). Hence, the collectings are biased towards active flyers and also contain species which accidentally cross the area. The species abundance distributions in samples gathered by eclectors in the first year are more likely to reflect the real patterns, but the species collected originate solely from the substrates enclosed. Thus, eclectors provide specific samples of high information quality, but interception traps give a better impression about the species present in an area. Further advantages and limitations of both trap types are discussed in Albrecht (1990), Schmitt (1992), Kaila (1993), Rauh (1993), Økland (1996) and Hammond (1997).

Interpretation of eclector samples

The collecting strategy of eclectors is based on the assumption that emerging insects are attracted by the light originating from the collecting boxes. Our data provide evidence that some species behave differently: First, we found > 20 % of all species only in the second year, both in Diptera and in Coleoptera, and for at least some of these species we know that their larval phase lasts less than one year (e.g. most Diptera). Second, 17 % of all species were more abundant in the second year than in the first, indicating that they may have been reproducing in the trap. We cannot exclude that some species may have entered the trap through openings created by mice, but we consider their quantity as negligible. It is possible that the attractivity of the light source within the trap is lowered for species which do not intend to disperse. Whether insects undertake migrational or trivial flights depends on intrinsic, as well as external factors such as photoperiod, ambient temperature and humidity, and varies between species and even within populations (Rankin & Burchsted 1992). Some saproxylic species of Ptilidae, for instance, produce wingless generations after successful colonisation of dead wood forming an inbreeding 'multiplication phase'. Winged adults appear only when the dead wood deteriorates forcing the population to find a new substrate (Hamilton 1978). Additionally, the microclimate within the trap is warmer and dryer than outside, so some species may adapt their dispersal strategy to the altered conditions.

Another confounding factor is the postponed dispersal of species, where only a part of a population emerges in a particular year. This strategy helps minimising the risk of entire populations to be wiped out in case of harsh weather conditions (Johnson 1969). The composition of the communities and phenological aspects must therefore be interpreted carefully when samples originate from eclectors. But despite these limitations, the following conclusions can be drawn here: First, species that were collected only in the first year must be predominantly those that intended to migrate before oviposition, and their larval phase lasts one year or less. Second, species that occurred only in the second year must have passed a larval phase lasting at least two years, and they also tended to migrate before reproduction. Finally, the larval phase of the species that were markedly more abundant in the second year than in the first, must be one year or less, and they tended to reproduce without or before migration.

How many species are there?

Our study demonstrates that even with our unusually large collecting effort, only a portion of the spectrum of species has been sampled. Ecological investigations implicitly assume that a representative sample of the community in focus has been obtained. Especially when the species are grouped into guilds, they should be represented in frequencies reflecting the conditions in the study area. Unfortunately, this basic assumption has never been tested, as this would require a nearly fully sampled community, which is almost impossible to achieve. Optimising the collecting strategies and developing statistical models to scale up the relations found in the samples are the only ways to gain an adequate insight into the communities of interest. Several authors elaborated methods for standardised sampling (e. g., Albrecht 1990; Duelli 1997) providing a basis for comparing the outcomings of different investigations, as well as reducing sampling effort without considerable loss of information. However, it depends on the habitat, which sampling strategy must be considered as optimal. Often, a trade-off has to be made whether to force spatial (= number of collecting sites) or temporal (= length of collecting periods) aspects of the study to obtain a maximum number of species. In our study, we observed high species turnover between the two sampling years, as for instance 44.2 % of all dipteran species collected by trunk-window traps were found only in 1996. On the other hand, a reduction in the number of traps of 50 % in one year resulted in the loss of about 25 % of the species, irrespective whether the number of traps per site or the number of sites was reduced. The same held true for estimations of total species richness, whether being done by applying the truncated lognormal distribution model or the extrapolation by rarefaction curves. Thus, the effect of between year variability was larger than of spatial heterogeneity. As we selected our study plots to be as similar to each other with regard to exposition, as well as stand structure and age, this result could be expected. Up to 66 % of the species were collected exclusively by one trap type, underlining that it is indispensable to combine several collecting methods to obtain a sample of the community appropriate to answer the questions of a study. We suspect that the use of additional trap types such as yellow water pans or malaise tents would lead to a considerable increase of the species recorded.

Acknowledgements - We thank the Swiss National Foundation for the financial support (Grant 31-45911.95 to K. C. Ewald, P. Duelli and W. Suter) and Verena Fataar (publication service WSL) for drawing the traps. Many thanks are due to all experts who determined the species included in this study, mainly the following persons: **Diptera:** P. Chandler, Berks, U.K. (Mycetophilidae); J.-C. Delécolle, Strassburg, F (Ceratopogonidae); M. Dempewolf, Bielefeld, D. (Pipunculidae); A. Glatthaar, Würenlos, CH (Simuliidae); A. Godfrey, Spilsby, U.K. (Anthomyiidae, Heleomyzidae); P. Grootaert, Brüssel, B (Hybotidae, Empididae); J.-P. Haenni, Neuchâtel, CH (Anisopodidae, Bibionidae, Scatopsidae); K. Heller, Kiel, D (Sciaridae); B. Merz (Clusiidae, Heleomyzidae, Lauxaniidae, Lonchaeidae, Sciomyzidae); L. Munari, Venedig, I (Sphaeroceridae); C.-J. Otto, Fahrenkrug, D (Chironomidae); M. Pollet, Brüssel, B (Dolichopodidae); A. Pont, Reading, UK (Muscidae, Fannidae); H.-G. Rudzinski, Schwanewede, D (Sciaridae, Calliphoridae); D. Simova-Tosic, Belgrad, Y (Tipulidae); A. Stark, Halle-Saale, D (Hybotidae, Empididae); J. Stary, Olomouc, CZ (Limoniidae); H.-P. Tschorsnig, Stuttgart, D (Rhinophoridae, Tachinidae); G. Weber, Braunschweig, D (Phoridae, Psychodidae). **Coleoptera**: S. Barbalat, Neuchâtel, CH (Buprestidae, Cerambycidae, Lucanidae, Scarabaeidae); J. Bohac, Budweis, CZ (Staphylinidae); H. Callot, Strassburg, F (Elateridae; Eucnemidae, Mycetophagidae, Pythidae); R. De Marchi, Winterthur, Switzerland (sorting the beetles to family level); B. Franzen, Köln, D (Clavicornia s. l.); P. Herger, Luzern, CH (Cholevidae, Melandryidae); D. Hölling, Bonn, D (Curculionidae); A. Kapp, Rankweil, OE (Clavicornia s. l., Pselaphidae, Staphylinidae); D. Kubisz, Krakau, PL (Anobiidae, Cantharidae, Lathrididae, Mordellidae, Scaphididae); M. Smolenski, Warschau, Polen (Staphylinidae); M. Varvara, Iasi, R (Carabidae, Chrysomelidae); M. Wanat, Wroclaw, PL (Clambidae, Scolytidae, Throscidae).

References

Albrecht, L. 1990. Naturwaldreservate in Bayern. Band 1. Schriftenreihe Naturwaldreservate in Bayern. IHW-Verlag.

Chadzon, R.L., Colwell, R.K., Denslow, J.S. Guariguata, M.R. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. In: Dallmeier, F. & Comiskey, J.A. (eds.). Forest biodiversity research, monitoring and modeling: Conceptual background and old world case studies. Parthenon Publishing, Paris. pp 285-309.

Chao, A., Ma, M.-C., Yang, M.C.K. 1993. Stopping rules and estimation for recapture debugging with unequal failure rates. Biometrika 80: 193-201.

Cohen, A.C., Jr.. 1961. Tables for maximum likelihood estimates: singly truncated and singly censored samples. Technometrics 3: 535-541.

Colwell, R.K. 1997. EstimateS: statistical estimation of species richness and shared species from samples. Version 5. User's guide and application published at: http://viceroy.eeb.uconn.edu/estimates.

Colwell, R.K. & Coddington J.A. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London B 345: 101-118.

Delécolle, J.-C. & Schiegg, K. 1998. Contribution à l'étude des Cératopogonidés de Suisse. I. Révision et redescription des espèces paléarctiques du genre Ceratoculicoides Wirth & Ratanaworabhan, 1971. (Diptera, Ceratopogonidae). Bulletin de la Société Entomologique de France 103: 273-286.

Delécolle, J.-C. & Schiegg, K. 1999. Contribution à l'étude des Cératopogonidés de Suisse II. Description de Brachypogon (s.str.) fagicola n. sp. (Diptera, Nematocera). Bulletin de la Société Entomologique de France 104: 31-34.

Dempewolf, M. & Schiegg, K.1998. Pipunculid flies collected in the Forest Reserve Sihlwald (Kt. Zürich) (Diptera: Pipunculidae): Three species new to Switzerland. Mitteilungen der Schweizerischen Entomologischen Geseslischaft 71: 111-114.

Duelli, P. 1997. Biodiversity evaluation in agricultural landscapes: an approach at two different scales. Agriculture, Ecosystems and Envirnoment 62: 81-91.

Haenni, J.-P. 1997. Scatopsidae (Diptera) nouveaux pour la faune de Suisse. (Contribution à la connaisance des Scatopsidae de Suisse. IV). Bulletin de la Société neuchâteloise des Sciences naturelles 120: 121-124.

Hamilton, W.O. 1978. Evolution and diversity under bark. In: Mound, L. A. & Waloff, N. (eds.). Diversity of insect faunas. Symposium of the Royal Entomological Society of London 9. pp 156-175.

Hammond, P. 1997. Arthropod Biodiversity from Populus coarse woody material in North-Central Alberta: a review of taxa and collection methods. The Canadian Entomologist 129: 1009-1033.

Irmler, U., Heller, K., Warning, J. 1996. Age and tree species as factors influencing the populations of insects living in dead wood (Coleoptera, Diptera: Sciaridae, Mycetophilidae). Pedobiologia 40: 134-148.

Johnson, C.G. 1969. Migration and dispersal of insects by flight. Methuen, London.

Kaila, L. 1993. A new method for collecting quantitative samples of insects associated with decaying wood or wood fungi. Entomologica Fennica 29: 21-23.

Kaila, L., Martikainen, P., Punttila, P. 1997. Dead trees left in clear-cut benefit saproxylic Coleoptera adapted to natural distrurbances in boreal forest. Biodiversity & Conservation 6: 1-18.

Lee, S.-M. & Chao, A. 1994. Estimating population size via sampling coverage for closed capture-recapture models. Biometrics 50: 88-97.

Magurran, A.E. 1988. Ecological diversity and its measurement. Chapman & Hall, London.

Menzel, F. 1998. Sciaridae. In: Merz, B., Bächli, G., Haenni, J.-P., Gonseth, Y. (eds.), Diptera Checklist. Fauna Helvetica 1. pp 126-130.

Merz, B. 1997. Die Micropezidae (Diptera) der Schweiz. Mitteilungen der Schweizerischen Entomologischen Geseslischaft 70: 93-100.

Merz, B., Bächli, G., Haenni, J.-P., Gonseth, Y. 1998. Diptera Checklist. Fauna Helvetica 1. 369 pp.

Økland, B. 1996. A comparison of three methods of trapping saproxylic beetles. European Journal of Entomology 93: 195-209.

Økland, B., Bakke, A., Hågvar, S., Kvamme, T. 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodiversity & Conservation 5: 75-100.

Otto, C.-J. & Schiegg, K. In press. Chironomidae (Diptera) collected in the forest reserve Sihlwald ZH. Mitteilungen der Schweizerischen Entomologischen Geseslischaft.

Rauh, J., 1993. Naturwaldreservate in Bayern. Band 2. Schriftenreihe Naturwaldreservate in Bayern. IHW-Verlag.

Rankin, M.A. & Buchsted, J.C.A. 1992. The cost of migration in insects. Annual Reviews in Entomology 37: 533-559.

Schmitt, M. 1992. Buchen-Totholz als Lebensraum für xylobionte Käfer. Waldhygiene 19: 97-191.

Siitonen, J. 1994. Decaying wood and saproxylic Coleoptera in two old spruce forests: a comparison based on two sampling methods. Annales Zoologici Fennici 31: 89-95.

Simberloff, D. 1972. Properties of the rarefaction diversity measurement. American Naturalist 106: 414-418.

Szadziewski, R. 1998. Ceratopogonidae. In: Merz, B., Bächli, G., Haenni, J.-P., Gonseth, Y. (eds.). Diptera Checklist. Fauna Helvetica 1. pp 102-104.

Appendix

dipteran species new to Switzerland.

Limoniidae
Ormosia rostrifera SAVCHENKO 1973
Psychodidae
Feuerborniella obscura (TONNOIR 1919)
Mormia nigripennis KERK 1971
Psychoda brevicornis TONNOIR 1940
Psychoda crassipennis TONNOIR 1940
Psychoda lobata TONNOIR 1940
Satchelliella palustris (MEIGEN1818)
Sycorax feuerborni JUNG 1954
Ceratopogonidae
Atrichopogon fuscus (MEIGEN 1804)
Atrichopogon setosipennis (KIEFFER 1911)
Bezzia fuliginata CLASTRIER 1962
Brachypogon babiogorensis SZADZIESKI 1994
Brachypogon fagicola (DELÉCOLLE 1999)
Brachypogon hudjakovi (REMM 1974)
Brachypogon nitidulus (EDWARDS 1921)
Ceratoculicoides havelkai WIRTH & GROGAN 1988
Ceratoculicoides tontoeguri (HAVELKA 1980)
Ceratopogon grandiforceps (KIEFFER 1913)
Culicoides achrayi Kettle & LAWSON 1955
Culicoides cameroni CAMPELL & PELHAM-CLINTON 1960
Culicoides dewulfi GOETGHEBUER 1936
Culicoides pseudoheliophilus CALLOT & KREMER 1961
Dasyhelea flaviventris (GOETGHEBUER 1910)
Dasyhelea malleola REMM 1962
Dasyhelea pallidiventris (GOETGHEBUER 1931)
Dasyhelea paludicola KIEFFER 1925
Dasyhelea saxicola EDWARDS 1929
Forcipomyia acanthophora REMM 1976
Forcipomyia borealis REMM 1966
Forcipomyia ciliata (WINNERTZ 1852)
Forcipomyia eques (JOHANNSEN 1908)
Forcipomyia picea (WINNERTZ 1852)
Forcipomyia tenuisquama KIEFFER 1924
Forcipomyia tibialis REMM 1961
Forcipomyia titillans (WINNERTZ 1852)
Kolenohelea calcarata (GOETGHEBUER 1920)
Palpomyia brachialis (HALIDAY 1833)
Palpomyia distincta (HALIDAY 1833)
Palpomyia lineata (MEIGEN 1804)
Mycetophilidae
Allodia pyxidiiformis ZAITZEV 1983
Allodia retracta PLASSMANN 1977

Mycetophilidae (continued)
Coelosia silvatica LANDROCK 1918
Mycomyopsis trilineata (ZETTERSTEDT 1838)
Neomycomya fimbriata (MEIGEN 1818)
Sciaridae
Bradysia affinis (ZETTERSTEDT 1838)
Bradysia fenestralis (ZETTERSTEDT 1838)
Bradysia giraudii (SCHINER 1864)
Bradysia hilaris (WINNERTZ 1867)
Bradysia lobulifera FREY 1948
Bradysia longicauda MOHRIG & MENZEL 1990
Bradysia lucida MOHRIG & MAMAEV 1989
Bradysia nervosa(MEIGEN 1818)
Bradysia quadrispina MOHRIG & KRIVOSHEINA 1982
Bradysia subaprica MOHRIG & KRIVOSHEINA 1989
Caenosciara alnicola TUOMIKOSKI 1957
Caenosciara lucifuga MOHRIG 1970
Camptochaeta dentata (BUKOWSKI & LENGERSDORF 1936)
Camptochaeta minutula (BUKOWSKI & LENGERSDORF 1936)
Camptochaeta praedentata (MOHRIG & MAMAEV 1987)
Corynoptera brevichaeta MOHRIG & ANTONOVA 1978
Corynoptera heteroclausa RUDZINSKI 1991
Corynoptera saetistyla MOHRIG & KRIVOSHEINA 1985
Corynoptera sphenoptera TUOMIKOSKI 1960
Corynoptera tetrachaeta TUOMIKOSKI 1960
Corynoptera trispina TUOMIKOSKI 1961
Cratyna egertoni (EDWARDS 1922)
Cratyna pernitida (EDWARDS 1915)
Cratyna perplexa (WINNERTZ 1867)
Dolichosciara flavipes (MEIGEN 1804)
Dolichosciara ornata (EDWARDS 1915)
Dolichosciara subflavipes (MOHRIG & MENZEL 1994)
Epidapus schillei (BÖRNER 1903)
Leptosciarella confusa MENZEL & MOHRIG 1997
Leptosciarella fuscipalpa (MOHRIG & MAMAEV 1979)
Leptosciarella melanoma MOHRIG & MENZEL 1990
Leptosciarella viatica (WINNERTZ 1867)
Leptosciarella yerburyi FREEMAN 1983
Lycoriella brevipila TUOMIKOSKI 1960
Lycoriella eflagellata TUOMIKOSKI 1961
Lycoriella mali (FITCH 1856)
Lycoriella micria MOHRIG & MENZEL 1990
Lycoriella minutula (BUKOWSKI & LENGERSDORF 1936)
Scatopsciara fluviatiliformis MOHRIG & MAMAEV 1987
Scatopsciara longispina MOHRIG & KRIVOSHEINA 1989

Appendix (continued)

Sciaridae (continued)
Trichodapus rhenanus (FRITZ 1983)
Trichosia flavicoxa TUOMIKOSKI 1960
Trichosia pulchricornis (EDWARDS 1925)
Trichosia trochanterata (ZETTERSTEDT 1851)
Xylosciara heptacantha TUOMIKOSKI 1957
Hybotidae
Anthalia schoenherri ZETTERSTEDT 1838
Euthyneura halidayi COLLIN 1926
Oedalea holmgreni ZETTERSTEDT 1852
Oedalea oriunda COLLIN 1961
Empididae
Hemerodromia unilineata ZETTERSTEDT 1842
Hilara abominalis ZETTERSTEDT 1838
Empididae (continued)
Hilara hirtipes COLLIN 1927
Hilara implicata COLLIN 1927
Rhamphomyia obscuripennis MEIGEN 1830
Dolichopodidae
Rhaphium ensicorne MEIGEN 1824
Rhaphium xiphias MEIGEN 1824
Teuchophorus nigricosta (VON ROSER 1840)
Anthomyiidae
Eutrichota frigida (ZETTERSTEDT 1845)
Mycophaga testacea GIMMERTHAL 1834)
Muscidae
Phaonia apicalis STEIN 1914
Phaonia mystica (MEIGEN 1826)

Curriculum vitae

name	Karin Schiegg
27.3.1968	Born in Zug, Kt. Zug, Switzerland.
1987	Matura Type B (Literargymnasium Rämibühl, Zurich, Switzerland).
1988-1994	Studies in Biology. Major: Zoology, minors: Geobotanics (ETH Zurich) and environmental sciences. Diploma (Masters): 'Parental traits, eggsize and nest temperatures in House sparrows (*Passer domesticus*)'. Supervisor: Prof. H.-U. Reyer, Zoological Institute of the University of Zurich. Temporal positions as scientific assistent in mathematics and zoology. Teacher in biology at the Berit-Schule für Arztgehilfinnen (1993-1995).
1995	Pilot project for PhD at the Chair for Nature and Landscape Protection, ETH Zurich and the Swiss Federal Institute for Forest, Snow and Landscape Research, WSL Birmensdorf. Writing application for PhD grant of the Swiss National Science Foundation.
1996-1999	PhD on 'Limiting factors of saproxylic insects: habitat relationships of an endangered ecological group', Prof. Dr. K.C. Ewald (Chair for Nature and Landscape Protection, ETH Zurich) and Prof. Dr. P. Duelli (WSL, Birmensdorf), supported by the Swiss National Science Foundation. Acquisition of grant of the Swiss National Science Foundation for a postodoc (Interrelations of habitat fragmentation, dispersal and inbreeding in the red-cockaded woodpecker: a simulation study using a spatially explicit individual-based model), at Virginia Polytechnic Institute and State University, Backsburg, Virginia (USA).

Publications

Reviewed journals

Delécolle, J.-C. & K. Schiegg. 1998. Contribution à l'étude des Cératopogonidés de Suisse. I. Révision et redescription des espèces paléarctiques du genre Ceratoculicoides Wirth & Ratanaworabhan, 1971 (Diptera, Ceratopogonidae). Bulletin de la Société Entomologique de France 103: 273-286.

Delécolle, J.-C. & K. Schiegg 1999. Contribution à l'étude des Cératopogonidés de Suisse II. Description de *Brachypogon (s.str.) fagicola n. sp.* (Diptera, Nematocera). Bulletin de la Société Entomologique de France 104: 31-34.

Delécolle, J.-C. & Schiegg, K. In press. Contribution à l'étude des Cératopogonidés de Suisse III. Description de trois espèces nouvelles appartenant au genre *Forcipomyia* Meigen (Diptera, Nematocera). Bulletin de la Société Entomologique de France.

Dempewolf, M. & K. Schiegg. 1998. Pipunculid flies collected in the Forest Reserve Sihlwald (Kt. Zürich), (Diptera: Pipunculidae): Three species new to Switzerland. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 71: 11-114.

Otto, C.-J. & , K. Schiegg. In press. Chironomidae (Diptera) collected in the Forest Reserve Sihlwald (Kt. Zürich): 21 species new to Switzerland. Mitteilungen der Schweizerischen Entomologischen Gesellschaft.

Schiegg, K. & L. Munari. In press. Sphaeroceridae (Diptera) collected in the Forest Reserve Sihlwald (Kt. Zürich). Mitteilungen der Schweizerischen Entomologischen Gesellschaft.

Schiegg, K., Obrist, M., Duelli, P., Merz, B., Ewald, K. C. In press. Diptera and Coleoptera collected in the Forest Reserve Sihlwald ZH. Mitteilungen der Schweizerischen Entomologischen Gesellschaft.

Other publications

Schiegg, K. 1998. Totholz bringt Leben in den Wirtschaftswald. Schweizerische Zeitschrift für Forstwesen 149: 784-794.

Schiegg, K. & B. Nievergelt. 1998. Rahmenbedingungen für eine ökosystemare Naturwaldforschung. Wissenschaftliche Kommission Naturlandschaft Sihwald.

Schiegg, K. In press. Ein wenig mehr Totholz - viel mehr Leben. Zürcher Wald.

Schiegg, K. In press. Leben im Totholz. Informationsblatt des Forschungsbereiches Landschaft. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, Birmensdorf.

Posters

Schiegg, K. 1994. Parental traits, eggsize and nest temperatures in House sparrows (*Passer domesticus*). Zoologia et Botanica, Swiss Society of Zoology and Swiss Society of Botany, Lausanne.

Schiegg, K. 1995. Limiting factors of saproxylic insects: habitat relationships of an endangered ecological group. Congress for PhD students (ZOEK), Zürich.

Schiegg, K. 1998/1999. Small but beautiful: Influence of dead wood dimensions on saproxylic insects. Swiss Academy of Sciences (SAS), Airolo and Congress for PhD students (ZOEK), Zürich. Award for the most attractive poster.

Talks

Scientific talks

Schiegg, K. 1997. Die Rolle von Totholz in Wirtschaftwäldern. 'Montagskolloquium', Section of wood sciences; ETH Zürich.
Schiegg, K. 1998. Influence of dead wood dimensions on species richness and diversity of saproxylic Diptera and Coleoptera. 4th World Diptera Congress, Oxford, U.K.
Schiegg, K. 1999. Habitat fragmentation in saproxylic Diptera and Coleoptera: scaling dead wood volume and connectivity. Zoologia et Botanica, Swiss Society of Zoology and Swiss Society of Botany, Zürich.
Schiegg, K. 1999. Enhancing biodiversity in forests: Species-centered and community based approaches. Postgraduate course on biodiversity in forests, Lausanne.
Schiegg, K. 1999. Habitatfragmentierung am Beispiel von Totholzinsekten. International Entomological Congress, Basel.
Schiegg, K. 1999. Limitierende Faktoren totholzlebender Dipteren und Käfer. Meeting on saproxylic insects, Bern.
Schiegg, K. 1999. Limitierende Faktoren totholzlebender Dipteren und Käfer - Habitatsbeziehungen einer gefährdeten ökologischen Gruppe. WSL Kolloquium, Birmensdorf.

Other talks

Schiegg, K. 1998. Totholz - ein Ort voller Leben. Entomological Society of Zurich, Zürich.
Schiegg, K. 1999. Die Förderung von Totholzinsekten in Wirtschaftswäldern. Kolloquium BUWAL, Bern.
Schiegg, K. 1999. Landschaftsindikatoren für Nachhaltigkeit. Jubiläumsfachtagung der Schweizerischen Vogelwarte Sempach "Wildtiere als Indikatoren für eine nachhaltige Entwicklung", Sempach.