

# Population ecology and conservation of beetles and pseudoscorpions living in hollow oaks in Sweden

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## Abstract

*Population ecology and conservation of beetles and pseudoscorpions living in hollow oaks in Sweden.*— This paper aims at giving a summary of recent research on the habitat requirements and population structure of beetles and pseudoscorpions living in old, hollow oaks in Sweden. An inventory of old oaks in pasture woodlands revealed that the species richness of beetles is higher at sites that are originally open and are still grazed. The trees in these plots are preferred for two reasons: they are more sun-exposed and have a larger trunk diameter. Many species are harmed by forest regrowth and, thus, to preserve the rarer saproxylic fauna it is important to continue the management of areas with old oaks. In four of thirteen species (*Osmoderma eremita*, *Tenebrio opacus*, *Elater ferrugineus* and *Larca lata*), the occupancy per tree were found to be significantly positively correlated with the number of trees in the stand. This finding is noteworthy as there is little scientific evidence available to support that saproxylic beetles suffer from habitat fragmentation. The population dynamics were investigated on a certain study species, *O. eremita*. The results suggest that the individuals of each tree could be seen as a local population, and the populations in all occupied trees in a stand together form a metapopulation.

Key words: Saproxylic, Tree hollows, Habitat fragmentation, *Osmoderma eremita*, Microclimate.

## Resumen

*Ecología de poblaciones y conservación de escarabajos y pseudoescorpiones que habitan en robles huecos en Suecia.*— Este trabajo pretende ofrecer un resumen de investigaciones recientes sobre los requerimientos de hábitat y la estructura de las poblaciones de escarabajos y pseudoescorpiones que viven en viejos robles huecos en Suecia. Un inventario de viejos robles situados en pastos de zonas boscosas reveló que existe mayor riqueza de especies de escarabajos en lugares originalmente abiertos y que todavía se utilizan para el pasto. Los árboles situados en estos terrenos son preferidos por dos razones: están más expuestas a los rayos del sol y el diámetro del tronco es mayor. Muchas especies sufren los perjuicios del recrecimiento del bosque, por lo que para preservar la fauna saprofita más rara es importante proseguir con la gestión de las áreas pobladas por robles viejos. En cuatro de trece especies (*Osmoderma eremita*, *Tenebrio opacus*, *Elater ferrugineus* y *Larca lata*) se encontró que la ocupación por árbol estaba correlacionada positivamente y de forma significativa con el número de árboles de la zona. Este hallazgo es notable dado que existen pocas evidencias científicas disponibles que apoyen que los insectos saprofitos sufran fragmentación del hábitat. Se estudia la dinámica de población de una especie determinada del estudio, *O. eremita*. Los resultados sugieren que los individuos de cada árbol pueden considerarse como poblaciones locales y que las poblaciones de todos los árboles ocupados de una zona próxima constituyen metapoblaciones.

Palabras clave: Saprofitos, Agujeros en los árboles, Fragmentación del hábitat, *Osmoderma eremita*, Microclima.

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## Introduction

In the temperate zone of Europe, old-growth deciduous forests have declined to a very small fraction of their original extent (HANNAH et al., 1995). Up until the nineteenth century, old trees were also widespread in pasture woodlands and wooded meadows, but abandoned management and changes of land use have severely reduced these habitats (e.g. KIRBY & WATKINS, 1998; NILSSON, 1997). This has caused old deciduous trees to become very scarce and, therefore, many species dependent on this habitat seem to be confined to small remnants with no possibility for dispersal between the populations (e.g. HARDING & ROSE, 1986; SPEIGHT, 1989).

When deciduous trees age, hollows with wood mould often form in the trunks. Trunk hollows begin to develop in trees when they are 150 years old (SPEIGHT, 1989). Wood mould is loose wood colonized by fungi, often with remains from bird nests and insects. Trunk hollows with wood mould harbour a specialized fauna mainly consisting of beetles, flies, mites and pseudoscorpions. In Sweden, large oaks (*Quercus* spp.) sustain the most diverse saproxylic fauna associated with wood mould in tree hollows (PALM, 1959).

Due to changes in land use, the fauna associated with old oaks faces several changes. In Sweden, old oaks predominantly occur in pasture woodlands, and as a consequence of ceased management, many of these have become closed forests. As a result, the microclimate in the trees may have changed. In addition, the available habitat has decreased at many localities, as old oaks have either been felled or died due to competition from undergrowth vegetation. Moreover, the distance between stands has increased. Two hundred years ago, stands with old oaks occurred contiguously over wide areas in southern Sweden, but during the 19<sup>th</sup> century most of these were cut down (ELIASSON & NILSSON, 1999). At present, stands with old oaks form small and isolated islands in a sea of managed forests and agricultural fields. In combination with a lower number of stands available for colonization and fewer dispersing individuals of species dependent on old oaks, it is expected that the connectivity between stands has severely decreased.

There is a general opinion that many beetles associated with old oaks are threatened (e.g. EHNSTRÖM & WALDÉN, 1986; WARREN & KEY, 1991). However, it appears that prior to the present study, no quantitative studies had been carried out on the saproxylic invertebrates living in old, hollow oaks. The beetle fauna of Scandinavia and Britain is probably the best known in the world, but even here data on the habitat requirements of saproxylic beetles are built on the personal experience of entomologists, and not on quantitative data (e.g. HYMAN, 1992; JONSELL et al., 1998). In Sweden, the classical and most cited work on saproxylic beetles was written

by PALM in 1959, before the concepts of island biogeography and metapopulations were introduced (HANSKI & SIMBERLOFF, 1997), and statistical tools such as logistic regression became a standard method (HOSMER & LEMESHOW, 1989).

The aim of this paper is to provide a summary of research carried out by myself and colleagues on the habitat requirements and population structure of beetles and pseudoscorpions associated with old oaks. The habitat characteristics were studied, both at per tree and per stand level, in order to understand the pattern of habitat occupancy and to make suggestions about habitat management. Studies on the habitat occupancy and dispersal rates were conducted in order to reveal the population structure of certain species. This is important for nature conservation, as the population structure determines at which spatial scale habitat patch size and isolation become critical for long-term survival.

### Factors possibly affecting the saproxylic fauna

Studies on the saproxylic fauna associated with tree hollow could principally be divided into four levels as described below. The order is hierarchical, as studies at one level require knowledge on the levels described earlier.

#### Localities and their species composition

In Sweden, the description of old oaks in nature inventories has tended to be poor. However, an inventory method recently devised by N. Jansson and K. Antonsson takes the successional stage of the oaks into consideration (RANIUS et al., 2001) and, in the province where this study was performed (Östergötland), documentation has improved enormously over the past few years (e.g. ANTONSSON & WADSTEIN, 1991; JANSSON, 1998; SANDELL, 1999; RANIUS et al., 2001).

For most localities with old oaks in Sweden, the number of old trees has not been assessed, and the only data available related to the conservation values are records of species (mainly beetles and/or lichens) which have been found there. It is only recently that these records have been summarized and species lists compiled (NILSSON, 2001). Unfortunately, information on sampling efforts is rare, but such data are crucial if reliable comparisons between localities are to be made (RANIUS & JANSSON, in press).

In our studies, data on the occupancy per tree have been collected for saproxylic beetles and pseudoscorpions. The localities have indirectly been described in the analyses of the relation between occupancy and habitat quality and density.

#### Habitat requirements

There are two main reasons for investigating the habitat requirements of threatened species. First,

any changes in the habitat may constitute a threat to the fauna, and therefore should be avoided. Secondly, such studies provide information on where the species could be present, which is necessary for more detailed studies on, for example, metapopulation ecology and the influence of historical events.

Studies with quantitative methods on saproxylic beetles in other habitats indicate that their occurrence may be influenced by decay type (ARAYA, 1993), moisture (DAJOZ, 1980; NILSSON, 1997a) and decay stage of the dead wood (SIITONEN & SAARISTO, 2000), temperature (KELNER-PILLAULT, 1974), trunk diameter (SIITONEN & SAARISTO, 2000; JONSELL et al., 2001) and sun exposure (KAILA et al., 1997; JONSELL et al., 2001; SVERDRUP-THYGESON & IMS, 2002). Swedish species associated with hollow oaks are to some extent considered by KELNER-PILLAULT (1974) and DAJOZ (1980) in their studies on beech trees. These authors found the daily temperature and the type of wood mould to be important factors for the beetles in tree hollows. In Sweden, the habitat requirements of saproxylic beetles, including those in tree hollows, were studied by PALM (1959) with data from his own observations, but without quantitative analyses. He described saproxylic beetles regarding preferred tree species, preferences for sun exposure or shading, and which part of the tree they inhabit.

For some insect species, especially butterflies, more detailed studies on, for example, habitat utilization and individual survival of the larvae have provided an understanding of the autecology of the species, and this has enhanced conservation efforts (e.g. THOMAS, 1991; PULLIN, 1995). The larvae of most saproxylic beetles live in rotten wood, and the conditions of their microhabitat can therefore not usually be examined in detail in the field without destroying their habitat. Thus, it is often only the adults which are studied. Information on the habitat requirements consequently becomes generally less detailed for saproxylic beetles compared with butterflies.

The influence of current management, original canopy cover and tree size on the beetle fauna were examined in one of our studies (RANIUS & JANSSON, 2000). These habitat variables were studied because cessation of management of pasture woodlands has caused the habitats containing old sun-exposed trees to decrease in favour of more closed woods. This might be detrimental to the saproxylic fauna, since it is generally held among entomologists that beetles associated with old oaks prefer sun-exposed trees (e.g. PALM, 1959; GÄRDENFORS & BARANOWSKI, 1992). However, there is a lack of quantitative data to support this view (but see LOTT, 1999).

Furthermore, easily measurable characteristics of the oak trees were correlated with the presence/absence of some study species (eleven beetle species and two pseudoscorpion species which are easily surveyed by wood mould

sampling) (RANIUS & WILANDER, 2000; RANIUS, 2000, 2002a). This approach was based on the assumption that there is a correlation between the measured characteristics of the oaks and the conditions which directly affect the fauna. Because the characteristics are easy to measure, they are potentially useful when trees suitable for certain species are to be identified in the field.

#### Influence of the spatial distribution of the habitat

In nature conservation it is important to understand the mechanisms that are influencing populations living in a fragmented habitat. There are two theoretical concepts related to this problem: the concept of island biogeography (MACARTHUR & WILSON, 1967), and the metapopulation concept (e.g. HANSKI & GILPIN, 1997). The main distinction between these theories is that island biogeography deals with the number of species per habitat patch, whereas the metapopulation concept deals with the presence/absence of one species at a time.

The island biogeography concept is useful when studying an assemblage of species which have similar habitat requirements, and therefore experience habitat islands in a similar way. Island biogeography focuses on species richness and extinction rates, but is not useful in identifying those species that are the most threatened (DOAK & MILLS, 1994; ROSENZWEIG, 1995).

Metapopulation models can generate predictions about the probability for a species to survive in patchy landscapes with different sizes and densities of habitat patches (HANSKI & GILPIN, 1997). Therefore, the metapopulation concept is expected to be useful when making conservation plans for single species. In contrast to island biogeography, the occupancy pattern could be linked to dispersal rate, population dynamics within the habitat patches and population genetics of the particular species of study. Thus metapopulation studies can give a deeper understanding of the processes behind the observed pattern of habitat occupancy.

A metapopulation was originally described as a set of populations where local extinctions and recolonizations occur (LEVINS, 1969, 1970). In a habitat network inhabited by a metapopulation there are both occupied and empty habitat patches. Metapopulations are characterized by "turn-overs", which are the changes in the habitat occupancy over time, resulting from colonizations and extinctions taking place in different patches. The most straightforward way to recognise that a set of populations conform to a metapopulation is to document turn-overs, which have been done for several species (e.g. HANSKI, 1994; HARRISON et al., 1988; KINDVALL & AHLÉN, 1992; MOILANEN et al., 1998). However, for many species, it is impossible to achieve reliable evidence of whether metapopulation dynamics are of importance with this method and therefore other approaches are used.

Snapshot studies on the habitat occupancy yield a pattern that is influenced by the extinction–recolonization processes, and thus correlate with the metapopulation dynamics. In such studies, the colonization ability is reflected in the relation of habitat occupancy to between-patch isolation, and the extinction risk is reflected in the relation to patch size (LOMOLINO et al., 1989). Surveys of this kind can be used as a first step to assess whether the habitat occupancy is consistent with a metapopulation model, but to ascertain which population processes the observed pattern is resulting from, further studies on population dynamics and dispersal are required. Such studies should include assessments of the population size, population variability and its synchrony, and dispersal rates (HANSKI et al., 1995). In a metapopulation the habitat is divided into separate patches each possibly sustaining a local population that is so small it is vulnerable to extinction. There is some dispersal between patches, which, however, is so limited that the immigration has an insignificant influence on the dynamics of existing local populations. Recolonizations should be possible, but are so rare that a local population may become extinct without immediate recolonization taking place (HANSKI & GILPIN, 1997).

The influence of the spatial distribution of the habitat among saproxylic invertebrate species has mainly been studied in a beetle living in polypores, *Bolitophagus reticulatus* (NILSSON, 1997b; MIDTGAARD, 1996). The studies on *B. reticulatus* have been carried out on several spatial scales, from fruiting bodies of polypores to forest stands, but an approach with each tree viewed as a habitat patch seems to have been the most useful (RUKKE & MIDTGAARD, 1998; NILSSON, 1997b).

In this paper the influence of spatial distribution of the habitat was studied in eleven beetle species and two pseudoscorpion species. The population ecology and dispersal of one beetle, *Osmoderma eremita* (RANIUS, 2001; RANIUS & HEDIN, 2001) was also examined. Computer modelling was used to test whether the results from these studies were consistent with the pattern obtained from a snapshot presence/absence inventory (RANIUS & HEDIN, in press).

For invertebrates associated with tree hollows, metapopulation dynamics might be important on at least two different scales. First, each hollow tree could be viewed as a habitat patch, potentially sustaining a local population. As such, the local populations in an assemblage of trees may be interconnected to a metapopulation. Second, hollow trees are usually aggregated in assemblages, each with a potential population which is distributed between one or several trees. These populations may be more or less connected by dispersal and together form a metapopulation at a larger scale.

## History

The patterns of occupancy are not only a response of the current situation, but might also be related to historical events. These include changes in the climate and the distribution of the habitat, which might generate relict distributions of species that have limited abilities to cope with the current conditions. This is particularly important for species which have a restricted dispersal and are associated with a habitat that has recently changed its distribution. It has therefore been suggested that saproxylic species with a restricted colonization ability should be confined to sites with continuous occurrence of suitable trees over time, as colonization of newly created habitat patches is slow (NILSSON & BARANOWSKI, 1997). In consistence with this, there are studies which indicate that species richness of saproxylic insects is positively correlated with historical continuity (NILSSON & BARANOWSKI, 1997; ALEXANDER, 1998; JONSELL & NORDLANDER, 2002). However, because none of these studies have included any quantification of habitat amount and quality at present, it is impossible to draw any conclusions about the casual relationship between species richness and historical factors *per se* from these studies (see also NORDÉN & APPELQVIST, 2001). Regarding species inhabiting large, living trees (as in NILSSON & BARANOWSKI, 1997; ALEXANDER, 1998) there is probably often positive correlation between historical continuity and present habitat quality (because stands with unbroken continuity should, on average, contain a larger number of trees which are older, and therefore larger and with larger amounts of wood mould). Moreover, of these three studies, ALEXANDER (1998) alone uses historical data to identify sites with continuity. To use other, indirect evidence for historical continuity increases the interference between continuity and other characteristics of the stand that may affect the fauna. It is reasonable that historical continuity is important for the saproxylic fauna, at least at some geographical scale, but this is obviously difficult to test empirically.

The effect of historical events on the fauna were not studied in our studies. Our study areas seem to have a similar history, and over wide areas there was a large, relatively contiguous occurrence of old oaks in the eighteenth century (ANONYMOUS, 1749). History therefore probably influences fauna in a similar way within all our study areas, although there may have been large differences between sites.

## Study species

In the study of the habitat requirements of species, the aim was to examine as many saproxylic beetles and pseudoscorpions living in tree hollows as possible. In a metapopulation

study a certain species must be selected. As rare and common species differ in their ecology, a threatened species should be studied if the results are to be useful in conservation work (JONSSON et al., 2001). The population ecology of *O. eremita* was chosen for many reasons. It is endangered throughout its range (LUCE, 1996), but occurs comparatively frequently in our study areas in Östergötland (e.g. RANIUS, 2002a). It therefore seemed that *O. eremita* could be abundant in suitable localities but was sensitive to fragmentation. In addition, *O. eremita* has a high priority in the European Union Habitat Directive (LUCE, 1996). It consequently receives attention from conservationists and studies are required to increase the understanding of its occurrence and preservation. A recent study shows that *O. eremita* is useful as an indicator of other threatened saproxylic beetles, as to a large extent they occur in the same trees and sites (RANIUS, 2002b). There are also practical advantages with studying *O. eremita*: it is comparatively easy to infer its presence/absence, both with pitfall traps and by searching for fragments of dead adults. By mark–release–recapture it is possible to obtain a sample size large enough for estimating population sizes and dispersal rates.

## Methods

### Survey methods

Ideally, surveys of saproxylic beetles reveal the occurrence of larvae developing within the tree. To observe the larvae is normally impossible without destroying the habitat, so other measures of habitat occupancy must be used. In the present studies, three main methods were applied to assess the saproxylic fauna (fig. 1): 1. Trapping by window traps set in hollow trees near the entrance hole; 2. Trapping by pitfall traps set in tree hollows with wood mould; 3. Searching for living and dead individuals in wood mould samples.

These three methods are complementary, as each of them is efficient to catch certain types of species (RANIUS & JANSSON, 2002). Window traps collect flying and, regarding pseudoscorpions, also phoretic individuals. This method collected the highest number of species. Nevertheless, several species restricted to tree hollows are rarely caught with this method (RANIUS & JANSSON, 2002). Pitfall traps collect individuals walking on the surface of the wood mould, these mainly being species that develop in the tree hollows. Some species could be sampled by searching for them in the wood mould. This is the best method for surveying pseudoscorpions, and also for some beetle species from which fragments of dead adults are frequently found in the wood mould. This is the fastest and cheapest method, and therefore

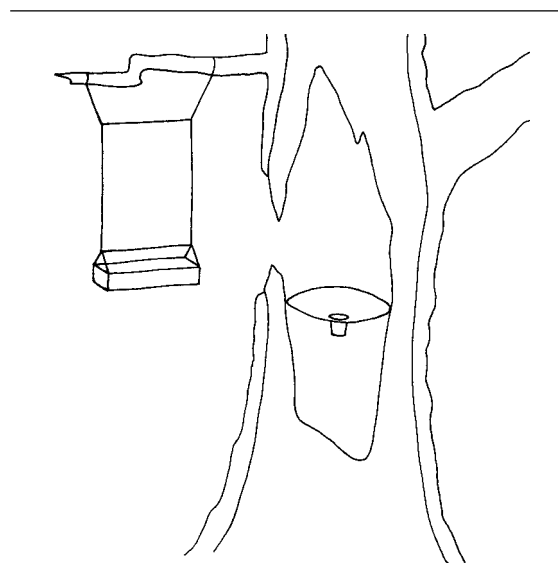


Fig. 1. Two kinds of traps used to collect beetles in tree hollows. Pitfall traps were plastic cups placed in the tree hollows with the opening level with the wood mould surface. Window traps consisted of a 30 x 40 cm<sup>2</sup> wide transparent plastic plate with a tray underneath.

*Fig. 1. Dos tipos de trampas usadas para recolectar escarabajos en los huecos de los árboles. Las trampas eran recipientes de plástico situados en los agujeros de los árboles con el lado abierto modelado en madera y orientado hacia la superficie. Las trampas ventana consistían en unas placas de 30 x 40 cm<sup>2</sup> de plástico transparente con una bandeja debajo.*

suitable if presence/absence data from a larger number of trees are required.

### Study areas

The surveys of beetles and pseudoscorpions were all out in Bjärka-Säby and its surroundings, in Kättilstad, and in Sankt Anna, all situated in the province of Östergötland, southeastern Sweden (fig. 2). Bjärka-Säby and its surroundings is one of the few remaining landscapes in Northern Europe with a high density of old oaks (RANIUS et al., 2001). In this area, there are two cores with particularly high densities of old oaks, Sturefors and Bjärka-Säby, and a third stand, Brokind, which also has a much higher density of oaks than the surrounding landscape. Therefore, investigations were carried out in these stands in order to

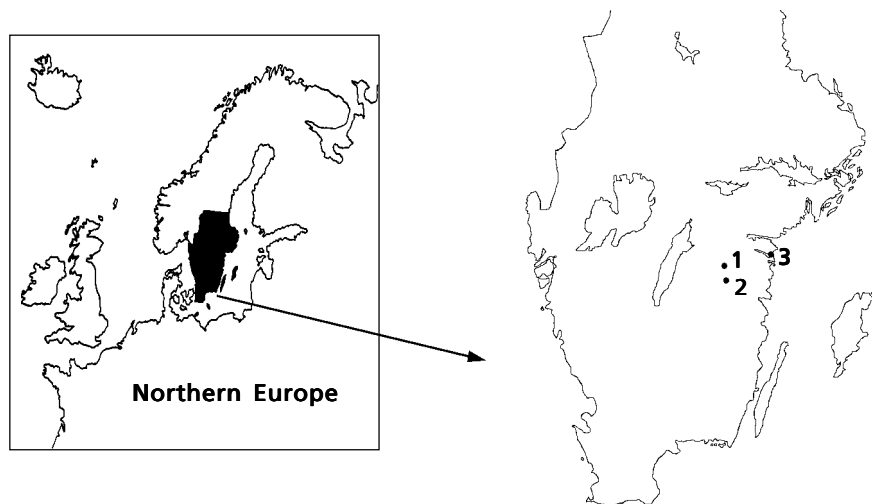


Fig. 2. Study areas in the province of Östergötland, Sweden: 1. Bjärka-Säby; 2. Kättilstad; 3. Sankt Anna.

*Fig. 2. Áreas de estudio en la provincia de Östergötland, Suecia: 1. Bjärka-Säby; 2. Kättilstad; 3. Sankt Anna.*

examine the situation for the fauna in large stands with high densities of hollow oaks.

Kättilstad is an ideal area for examining the effect of habitat fragmentation, because the physical characteristics of the oaks and the climate is similar to Bjärka-Säby, but the assemblages of hollow oaks are much smaller (RANIUS, 2000). Samplings were also carried out in Sankt Anna (RANIUS & WILANDER, 2000; RANIUS, 2002), which is situated on the coast, and therefore has a climate somewhat different from the other areas. There is a wide variation of hollow oaks within Sankt Anna, as there is one large island containing many old oaks with large girths, and several small islands further off the shore, with rather thin, slowly growing, old oaks.

## Results and discussion

### Species composition

The species lists in RANIUS & JANSSON (2000) and RANIUS & WILANDER (2000) are two of the first published with measures on occupancy/tree for saproxylic beetles and pseudoscorpions. With the use of pitfall and window traps 120 saproxylic beetle species which normally inhabit old oaks were found and identified (RANIUS & JANSSON, 2000). Among these species, 40% were on the Swedish red list (EHNSTRÖM et al., 1993). Seven pseudoscorpion species were found in wood

mould samples from the hollow oaks (RANIUS & WILANDER, 2000). Data on recorded species can obviously not be regarded as an unbiased measure of species richness, as it is affected by the sampling method (RANIUS & JANSSON, 2002). However, as our methods are always standardized, our results are always comparable between sites. To our knowledge only one other comparable study has been published, and this was on saproxylic beetles in trunk hollows of beech trees (NILSSON & BARANOWSKI, 1997). The number of species per tree was lower in their study, probably at least partly because a less efficient sampling method was used.

### Habitat quality

The species richness of saproxylic beetle species was higher in plots that were originally open and were still grazed (RANIUS & JANSSON, 2000). The trees in these plots were preferred for two reasons: they are more sun-exposed and have a larger trunk diameter (figs. 3, 4). Grazed, and therefore more open stands, contained more saproxylic beetle species than those affected by forest regrowth, probably because increased sun exposure makes the microclimate warmer (RANIUS & JANSSON, 2000). In grazed land, the habitat is more open not just because of grazing itself, but also because shrubs and young trees are cut to increase grass growth. The preference for sun-

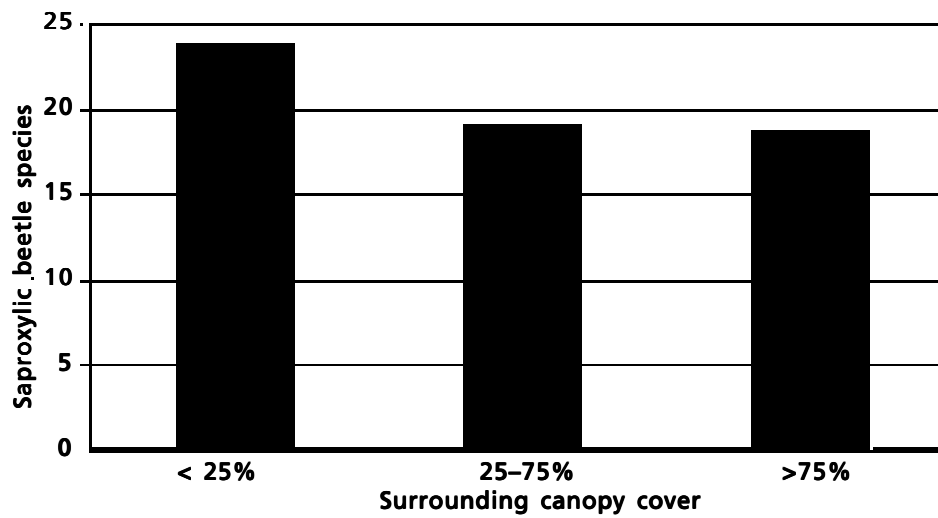


Fig. 3. Number of saproxylic beetles per tree, with the oaks divided into categories depending on surrounding canopy cover:  $n$  (< 25%, free-standing) = 21;  $n$  (25-75%, half-open) = 30;  $n$  (> 75%, shaded) = 39. (Data from RANIUS & JANSSON, 2000.)

Fig. 3. Número de escarabajos saprófitos por árbol, con los robles agrupados por categorías según la cubierta arbórea de los alrededores:  $n$  (< 25%, campo abierto, con árboles aislados) = 21;  $n$  (25-75%, árboles medio aislados) = 30;  $n$  (75%, sombreado) = 39. (Datos de RANIUS & JANSSON, 2000.)

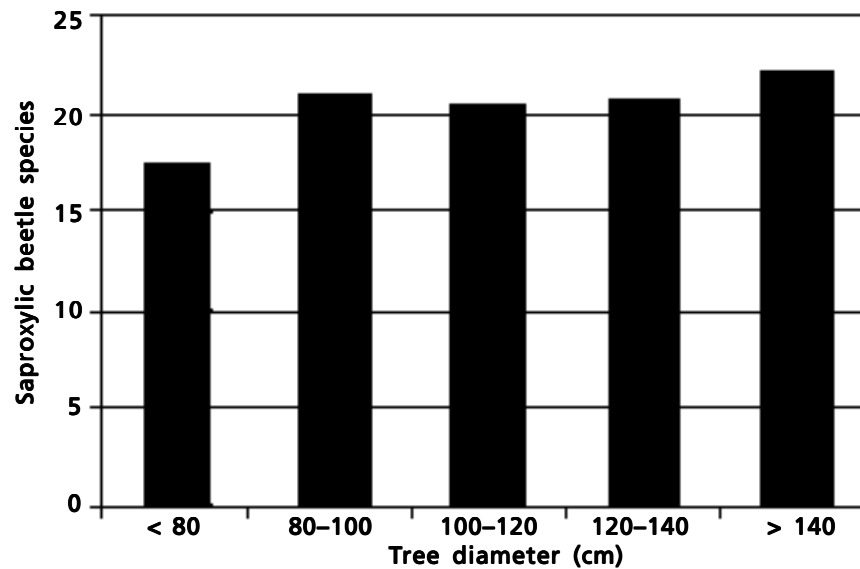


Fig. 4. Number of saproxylic beetles per tree, with the oaks divided into categories of different trunk diameter:  $n$  (< 80 cm) = 22;  $n$  (80-100 cm) = 12;  $n$  (100-120 cm) = 25;  $n$  (120-140 cm) = 13;  $n$  (> 140 cm) = 18. (Data from RANIUS & JANSSON, 2000.)

Fig. 4. Número de escarabajos saprófitos por árbol, con los robles agrupados por categorías según el diámetro del tronco:  $n$  (< 80 cm) = 22;  $n$  (80-100 cm) = 12;  $n$  (100-120 cm) = 25;  $n$  (120-140 cm) = 13;  $n$  (> 140 cm) = 18. (Datos de RANIUS & JANSSON, 2000.)

exposed oaks has been considered by several Swedish entomologists (PALM, 1959; GÄRDENFORS & BARANOWSKI, 1992; JONSELL et al., 1998), but Palm alone recorded the preferences for single species. The number of species preferring sun exposure and shade according to PALM (1959), is consistent with the present study, but his conclusions regarding single species disagree in part with our own (RANIUS & JANSSON, 2000). This difference can not be discussed further as quantitative data were not included in his report.

VERA (2000) has suggested that oaks are adapted to a landscape kept open by grazing of large herbivores (see also SVENNING, 2002). If this is true, it is reasonable that saproxylic beetles associated with oaks would also be evolutionarily adapted to such conditions (GÄRDENFORS & BARANOWSKI, 1992). However, it is difficult to test this hypothesis. First, many beetle species which we in Sweden regard as typical for old oaks may occur in any tree species if the microhabitat, for instance the quantity and quality of wood mould, is suitable. For instance, oak is by far the most important tree species for *O. eremita* in Sweden, while the beetle occurs in a large number of tree species in continental Europe (LUCE, 1996), perhaps mostly in beech (DAJOZ, 1980). Therefore, it is difficult to determine whether a species has adapted through evolution to oak or any other tree species only based on its preferences observed in Sweden today (cf. GÄRDENFORS & BARANOWSKI, 1992). Secondly, for most beetles in our study, Sweden constitutes the coldest region within their distribution area. Therefore, their preference for a warm microclimate may be a way to compensate for a colder climate in Sweden. Perhaps many of these beetle species are able to live in denser forests further south. This has been found for butterflies (THOMAS, 1993), but it is still an untested hypothesis for saproxylic beetles.

Many beetle species prefer larger trunks which may be because trees with a larger girth have more stable microclimate (RANIUS & JANSSON, 2000; fig. 4). The microclimate might affect the beetles directly (e.g. KELNER-PILLAULT, 1974), but it might also give rise to an indirect effect, as the microclimate influences which fungi species dominate and thus which kind of wood rot develops, and that affects the saproxylic fauna (ARAYA, 1993). Alternatively, it is the successional stage of the trunk that influences its suitability; because there are more species in larger trunks, it seems that most beetle species prefer trees of intermediate or late stages. During the decay of a living hollow trunk, the amount of wood mould is at first small but increases over time. The first hollows are usually formed when branches at a height of a few metres fall from the tree. The size of the entrance hole increases gradually, and later an entrance is often formed at ground level. For two pseudoscorpion species, a difference was found regarding preferences for these characteristics (RANIUS & WILANDER, 2000). *Larca lata* was exclusively

found in large trunks with large amounts of wood mould, whereas *Allochermes wideri* did not rely on these characteristics. Furthermore, the species tended to differ in their preferences concerning the height and size of the entrance. Hence, *L. lata* occurs predominantly in hollow oaks that are of a later successional stage than those that contained *A. wideri*.

The community of saproxylic invertebrates therefore seems to change during the successional decay of the living oak trunk. However, to be able to study this in more detail, further information on how and when oak trunks change during the succession is required. Therefore, it would be desirable if future research on invertebrates in old oaks included more studies also on the oaks themselves.

Our studies on habitat requirements provide some insight into how the fauna is influenced by canopy cover and the size and successional stage of the trunk. Furthermore, occupancy per tree of the study species was affected by characteristics that are related to the microclimate and the successional stage of the trunks, such as the amount of wood mould, and orientation and situation of the entrance hole (RANIUS & WILANDER, 2000; RANIUS 2002). However, these data are not sufficient to reliably predict whether individual trees contain particular species. The major reason for this is probably that the species are dependent on the nutrient supply and particular microclimate conditions, which are only partly reflected in the physical characteristics of the trees we have measured. Some laboratory studies on *O. eremita* have been conducted on the sensitivity to drought and freezing (DAJOZ, 1980; VERNON et al., 1996; 1997). However, it is difficult to link information achieved from this kind of studies with results from field studies. The main problem is that as it is impossible to study the particular place where the larvae live without disturbing the habitat, the nutrient supply and microclimate have never been examined in detail in the field.

Habitat occupancy in relation to the spatial structure of the habitat

In the beetles *Elater ferrugineus*, *Tenebrio opacus* and *O. eremita* and the pseudoscorpion *L. lata*, the occupancy per tree was positively correlated with the number of trees in the stand (fig. 5), whereas no such correlation was found for nine other species (RANIUS & WILANDER, 2000; RANIUS, 2002). This is one of the first studies that correlates the occupancy pattern of individual saproxylic invertebrate species with the spatial distribution of the habitat (but see also RUKKE & MIDTGAARD, 1998; KEHLER & BENDRUP-NIELSEN, 1999; KOMONEN et al. 2000). The positive correlation is consistent with what metapopulation ecologists refer to as Levin's rule (HANSKI & GILPIN, 1997). This means that the population in a stand would conform to a metapopulation and the level of



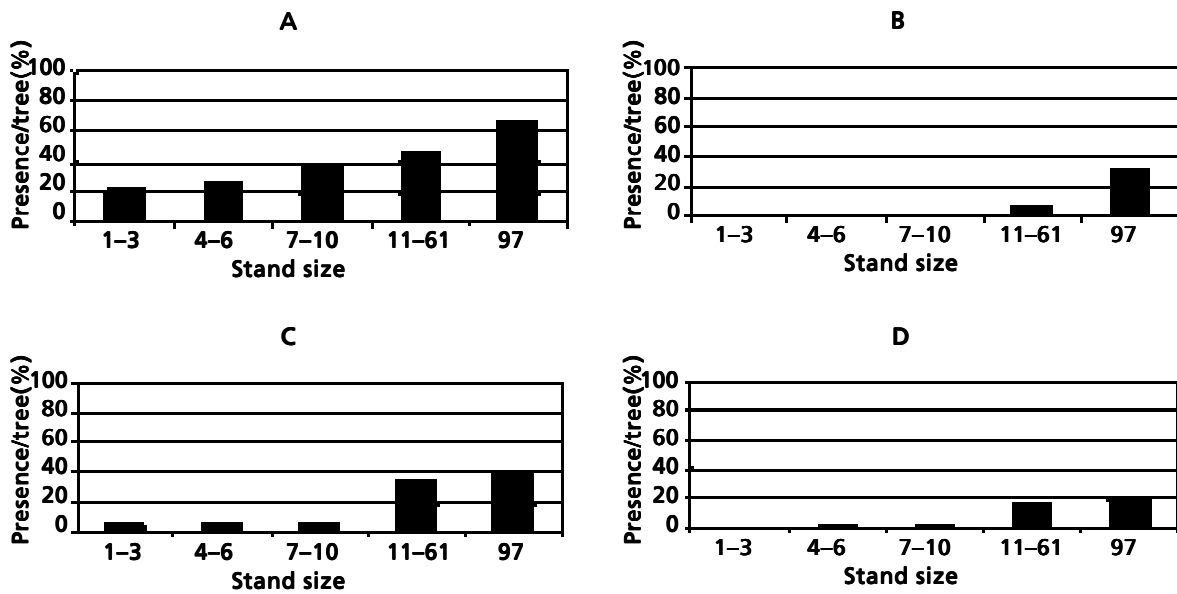


Fig. 5. Frequency of occurrence/tree of the beetles: *Osmoderma eremita* (A); *Elaterr ferrugineus* (B); *Tenebrio opacus* (C); and the pseudoscorpion *Larca lata* (D) in relation to stand size (beetle data from RANIUS, 2002). Only beetle species with significant correlation to stand size are presented here. Data on *Larca lata* is from the same inventory as the beetle data (RANIUS, 2002) and has not been published previously. Stand size is defined as the number of hollow oaks within a cluster with a distance of < 250 m from one hollow oak to another.

Fig. 5. Frecuencia de ocurrencia por árbol de los escarabajos: *Osmoderma eremita* (A); *Elaterr ferrugineus* (B); *Tenebrio opacus* (C); y del pseudoescorpión *Larca lata* (D) en relación con el tamaño de la zona (datos de escarabajos de RANIUS, 2002). Sólo se presentan especies de escarabajos con una correlación significativa con el tamaño de la zona. Los datos sobre *Larca lata* se han extraído del mismo inventario que los de los escarabajos (RANIUS, 2000) y no se han publicado anteriormente. Se define el tamaño de la zona como el número de robles con huecos dentro de un grupo con una distancia < 250 m de un roble a otro.

dispersal within the stand influences the occupancy per tree. A study on the dispersal of *O. eremita* gives support to this view as the dispersal rate was found to be low (RANIUS & HEDIN, 2001), while the dispersal of the other species has not been studied. LEVIN's (1970) model predicts that the fraction of occupied habitat patches increases with patch density and that there is a threshold patch density required for long-term persistence of the metapopulation. The number of empty but suitable patches would be constant for all persistent metapopulations and equal with the number of patches which are required for metapopulation survival. In studies on *O. eremita* (e.g. RANIUS & NILSSON, 1997), the habitat quality, especially the amount of wood mould, differed between trees. It could not be determined therefore whether individual trees were empty because they were less suitable or, as LEVIN's (1970) model presupposes, due to stochastic extinctions in suitable patches.

Furthermore, trees from which the species had become extinct in recent years might be recorded as occupied by the beetle species, as fragments were used to infer presence/absence, and these may remain for some time after extinction. The quantitative pattern, however, with increasing habitat occupancy in larger stands, is consistent with Levin's model.

For *O. eremita*, but not for the other species, the occupancy was also analysed at a larger spatial scale (RANIUS, 2000). The occupancy per stand was then found to be strongly associated with stand size and mean trunk diameter, but not with the density of neighbouring stands. This implies that the size of each stand, which affects extinction risks, is more important for occupancy than the potential for inter-stand dispersal. On this scale, the population seems to conform to a non-equilibrium, declining metapopulation (HARRISON & TAYLOR, 1997), subject to a higher rate of local extinctions than

colonizations (RANIUS & HEDIN, 2002).

Thus, the occupancy of *O. eremita* correlates to the amount of habitat in the immediate surroundings (within 250 m) but not on a larger scale (within 2,500 m). Studies on saproxylic beetles and flies in boreal forests have encountered the opposite pattern, with a stronger correlation with the density of habitat at scales of several km<sup>2</sup> in comparison to smaller scales (ØKLAND et al., 1996; ØKLAND, 1996).

In the present study area, *O. eremita* still occurs in almost all larger stands, but the occupancy pattern did not reveal any connectivity between these (RANIUS, 2000). This could be because the density of hollow oaks was historically much higher in this area than it is today. Over the last two centuries, old-growth oaks have severely declined in Sweden (ELIASSON & NILSSON, 1999). Currently, approximately 90% of the hollow oaks in Kättilstad are situated on land previously owned by the nobility (author's observation), which is approximately 60% of the land (THAM, 1855). In an inventory on land owned by other farmers and the church in 1749, several thousand oaks in Kättilstad were classified as "old and unusable" (ANONYMOUS, 1749), but very few old oaks can now be found there. Thus, most hollow tree stands were probably colonized by *O. eremita* long ago and, lately, the beetle has been confined to small stands without connectivity.

Four species were systematically absent from single trees and very small stands, probably because of extinctions from these stands (RANIUS & WILANDER, 2000; RANIUS, 2002). This is consistent with the underlying reasoning of the minimum viable metapopulation size (MVM) concept (HANSKI et al., 1996). MVM is an estimate of the minimum number of interacting local populations necessary for long-term survival of a metapopulation. Computer simulations on *O. eremita* show that its metapopulation dynamics are slow, in the sense that it may take centuries from the fragmentation of its habitat until their reduced metapopulations finally become extinct (RANIUS & HEDIN, 2002). The present occupancy pattern could therefore not be directly used when estimating the MVM of these species; in the smaller stands which still harbour a population today, there is a high risk for local extinctions during the next 100 years (RANIUS & HEDIN, 2002).

#### Population ecology of *Osmoderma eremita*

A mark–release–recapture study of *O. eremita* in Bjärka–Säby revealed that the population size was on average 11 adults per tree, per year, but this differed widely (0–85) between trees (RANIUS, 2001). If it is assumed that the abundance is equal in trees not studied and in trees studied, then the number of adult *O. eremita* in 112 hollow oaks with wood mould at Bjärka–Säby would be approximately 1,300 adults per

year. Thus, as the life cycle of the species normally is three years (TAUZIN, 1994), there will be three cohorts present, and the total of individuals which once will emerge as adults would be estimated as 3,900.

Over five years, the population size in each tree varied moderately between years (mean C.V. = 0.51), but more widely than from sampling errors alone ( $p = 0.008$ , Monte Carlo simulation) (RANIUS, 2001). The population size variability in all trees combined, however, was not larger than expected from sampling errors alone in a constant population (C.V. = 0.15,  $p = 0.335$ , Monte Carlo simulation). The constancy in size of the total *O. eremita* population differs considerably from many other insect populations, which display abundance fluctuations of 10–1,000 times between generations (e.g. gyrids: NÜRNBERGER, 1996; aphids: DIXON, 1990; spruce budworm: ROYAMA, 1984; lygaeids: SOLBRECK, 1991). There are also insects with moderate variability (hoverflies: OWEN & GILBERT, 1989; dragonflies: CROWLEY & JOHNSON, 1992; some butterflies: POLLARD & YATES, 1993; carabid beetles: LUFF, 1982), which vary at the same magnitude as for *O. eremita* per tree, but more than for *O. eremita* for all trees combined.

Populations living in more stable habitats are less variable (WOLDA et al., 1992), which could explain the narrow fluctuations of the *O. eremita* populations. The nutrient supply might be constant for *O. eremita* as wood is continuously decomposing inside a trunk hollow. The microclimate inside a trunk is stable and not very sensitive to weather fluctuations. Many insect populations are affected by weather (e.g. KINGSOLVER, 1989; POLLARD & YATES, 1993; SOLBRECK, 1991; WHITTAKER & TRIBE, 1998) or parasitoid abundance (MIKKOLA, 1976) over large areas. On the contrary, the population size of *O. eremita* fluctuated yearly in each tree rather independently of each other, even though the weather conditions varied between years, similarly for all trees studied.

The mark–release–recapture data was also used to study the dispersal rate and range of *O. eremita*. Among those 377 individuals which were captured at least twice, 2.4% moved from one tree to another (RANIUS & HEDIN, 2001). This is a low dispersal rate in comparison to other species, for instance, in a study on *Bolitophagus reticulatus* the corresponding figure was 23–43% (NILSSON, 1997b). However, these figures are underestimates of the dispersal rate, because many individuals disperse to trees without traps or they disperse before the first or after the last time they were captured. A computer simulation program therefore used in this study suggested that 15% of the *O. eremita* individuals moved among trees, while the remaining 85% stayed in the same tree throughout their entire life–time (RANIUS & HEDIN, 2001). This suggests that each hollow tree sustains a local population with limited connection with the populations in surrounding trees. The observed

movements took place between trees situated 30–190 m from each other (RANIUS & HEDIN, 2001). The spatial distribution of the traps made it possible to observe dispersals in a range of 1 km or more in one of the study areas, and a few hundred metres in the other. This means that dispersals between stands are rare events, even though this kind of study can not reveal the maximum dispersal range.

Theoretical studies suggest that the evolution of dispersal propensity should be linked with the heterogeneity of the habitat in space and time (e.g. GADGIL, 1971; COHEN & LEVIN, 1991; TRAVIS & DYTAM, 1999). A large variability in carrying capacity over time in each habitat patch increases the possible benefit of dispersal and would therefore select for a higher degree of mobility. On the contrary, a large variability in carrying capacity in space will select for more resident individuals, because then dispersal would, on the average, cause the individuals to reach an environment worse than the one it was born in (GADGIL, 1971; TRAVIS & DYTAM, 1999). However, if the individuals are able to select favourable targets for their movements, some dispersal is selected for even in a temporally constant and spatially varying habitat (MCPEEK & HOLT, 1992). *O. eremita* is a specialized species, strictly associated with tree hollows. Its population fluctuations are rather narrow in each tree, whereas the variability in population size between trees is much greater (RANIUS, 2001). There is circumstantial evidence suggesting that a tree could be suitable for *O. eremita* for several decades (MARTIN, 1993) and, thus, the species might persist for tens of generations in the same tree. In addition, *O. eremita* has probably evolved in nemoral forests dominated by deciduous trees, which are comparatively stable with a small-scaled disturbance regime (FALINSKI, 1986). Thus, *O. eremita* is specialized to a habitat with a distinct small-scaled patchiness (which increases the cost of dispersal) whereas the variability in carrying capacity is much lower over time (which decreases the possible benefit of dispersal). The low dispersal rate observed is therefore consistent with expectations from the theoretical predictions.

The snapshot study of presence/absence (RANIUS, 2000) and the ecological studies with capture–recapture (RANIUS, 2001; RANIUS & HEDIN, 2001) represent two independent sources of information. By constructing and using a simulation model in RAMAS, tests were performed to determine the consistency of these results (RANIUS & HEDIN, 2002). When the model was parameterised with data from our capture–recapture studies and the stands were assumed to have been isolated over the past 150 year, the presence/absence pattern obtained was consistent with the pattern observed in the field inventory. The model showed that populations inhabiting stands with less than ten oaks face a considerable extinction risk.

#### Evidence for metapopulation dynamics in *Osmoderma eremita*

HANSKI et al. (1995) have established four conditions which, if demonstrated for a population, could reveal that the persistence of the population is due to metapopulation dynamics as opposed to local dynamics. The satisfaction of these conditions was investigated for *O. eremita* with the view that each tree possibly sustains a local population and that the populations in stands together form a metapopulation.

#### Population structure

The dispersal between patches should not be so large that it has a great impact on the population dynamics within each patch. Thus, the population should mainly consist of individuals spending their entire lives in their natal patch.

A study on the dispersal rate with use of mark–release–recapture reveals that most *O. eremita* individuals (85%) remain in the same tree throughout their entire life–time (RANIUS & HEDIN, 2001). This implies that the populations of each tree have a limited connection with each other. The dispersal rate of *O. eremita* seems to be in the same range as for sedentary butterflies, whose populations conform to a metapopulation structure (THOMAS & HANSKI, 1997; THOMAS, 2000). The limited dispersal makes it possible for a suitable tree to remain empty some time after extinction, although there are neighbouring trees with the beetle present.

#### Risk of extinction of the largest local population

If one local population has a much lower extinction risk than all the others, metapopulation dynamics determine the long–term survival to a lower extent, while the demography of one local population becomes more important. Such a system is referred to as a mainland–island metapopulation (HARRISON & TAYLOR, 1997). Metapopulation studies do not usually provide any data on extinction risks for each local population. The conclusions are usually drawn from assessments of the local population size. To conform to a metapopulation model, every local population should be so small that they experience a significant risk of stochastic extinction.

The maximum population size of *O. eremita* in a tree is about 100 adults per year (RANIUS, 2001), and the fluctuations in the population size per tree over time generate an extinction risk in individual trees. The great differences in population size between trees (RANIUS, 2001) imply that the population structure does not perfectly conform to a classical metapopulation model, as the extinction risk would differ considerably between trees. This structure, with large differences in population size between habitat patches, is something that *O. eremita* has in common with many other metapopulations

(e.g. HANSKI, 1994; HARRISON et al., 1988; KINDVALL & AHLÉN, 1992; MOILANEN et al., 1998).

#### Recolonization

If the dispersal rate between patches is absent or extremely low, the extinction rate might exceed the colonization rate. The metapopulation would then be of a non-equilibrium type, which implies that there is no equilibrium between colonizations and extinctions (HARRISON & TAYLOR, 1997).

In *O. eremita*, several movements have been observed in a range of 30–190 m (RANIUS, 2001). This indicates that *O. eremita* is capable of colonizing trees within stands and metapopulation dynamics is thus possible at this scale.

#### Asynchrony

If fluctuations are experienced by all local populations synchronously, the extinction of the metapopulation would take place concurrently with the extinction of the most viable local population. There must be some asynchrony between the local populations, for metapopulation dynamics to be important for long-term persistence.

A study of *O. eremita* over five years showed that the populations in each tree fluctuate independently of one another (RANIUS, 2001). The strongest evidence for this is that the fluctuations overall were more narrow than the mean fluctuations at the tree level. In a metapopulation consisting of local populations fluctuating independently of each other, the metapopulation variability decreases with spatial scale because local fluctuations tend to cancel each other out when added together (MURDOCH et al., 1985). Another effect, giving the same result, is that sampling error becomes larger when sample size is smaller (LINK & NICHOLS, 1994; MÖNKKÖNEN & ASPI, 1997) which might help to explain smaller fluctuations overall in many cases. In the present study, Monte Carlo simulations also showed that a larger C.V. should be expected at the tree level than for the population combined due to sampling errors. However, this difference was not as large as that in the field data.

#### Implications for conservation

It is known that old, hollow oaks are the habitat for a large number of invertebrate species and there is a general opinion that many of these species are endangered (e.g. EHNSTRÖM & WALDÉN, 1986; MARTIN, 1989; SPEIGHT, 1989). A tree is usually 150 years or more when the trunk hollows begin to develop (SPEIGHT, 1989), and therefore it is very difficult to restore this habitat once it has been destroyed. Thus, to preserve its fauna, conscious and long-term management is required. Knowledge of the habitat requirements is needed to identify the

areas which are most valuable and to decide the most appropriate management. Long-term planning must also be built on an awareness of the size and connectivity of the stands required for metapopulation persistence.

#### Which stands are the most valuable?

As there seem to be more localities with old trees in Sweden than in most other European countries (HULTENGREN & NITARE, 1999), the largest Swedish areas might be essential for long-term persistence even globally, in particular for species sensitive to habitat fragmentation. Because *O. eremita*, *T. opacus*, *E. ferrugineus* and *L. lata* are sensitive to habitat fragmentation, these species might be useful as indicators for areas that are less affected by present or historical habitat fragmentation and thus have a particularly high conservation value. The relation between the occurrence of *O. eremita* and other red-listed saproxylic beetles was also studied and it was observed that trees and stands with *O. eremita* present are more species-rich than similar localities with *O. eremita* absent (RANIUS, 2002). Moreover, survey of fragments of these species in the wood mould is both simple and cheap, another important characteristic when determining species useful as indicators (RANIUS & JANSSON, 2002).

The study in Kättilstad revealed that *O. eremita* was present in all larger assemblages of trees. From this, it could be questioned whether it is necessary to use beetles as indicators at all, as instead the number of hollow trees could be counted and used to evaluate the quality of the stands. However, inventories in other regions of Sweden show that the species richness of saproxylic beetles could be quite low even in comparatively large stands and *O. eremita* is in many cases absent (N. Jansson, pers. com.). This might be because species richness is not only affected by the quality and size of the stands at present, but also the historical stand size, which might differ widely between stands (NILSSON & BARANOWSKI, 1997).

#### Management of pasture woodlands

Most areas with hollow oaks in Sweden have been affected by management for a long time, first as wooded meadows (mainly used for hay-making) and then as pasture woodlands (mainly used for grazing) (ELIASSON & NILSSON, 1999). Plantations and natural regeneration of formerly open pasture woodlands cause existing old trees to die prematurely because of shading and competition for soil moisture and nutrients (KEY & BALL, 1993; ALEXANDER et al., 1996). This study shows that many saproxylic beetle species are harmed by forest regrowth. Thus, to preserve the rarer saproxylic fauna it is important to continue the management of areas with old oaks. Even where management has been abandoned in the

last few decades most saproxylic species are still present, albeit many of them in lower abundance. Such sites should be restored, to delay the deaths of the trees and decrease the risk of extinction of endangered species.

Restoration of regrown sites should include cutting of shrubs and young trees and resumption of grazing. The cutting should be done with care, as dramatic changes of the microclimate could lead to death of the oaks (ALEXANDER et al., 1996). Another problem is that *Formica* spp. often colonize hollow oaks if the surrounding canopy cover suddenly decreases. If grazing has been abandoned for several decades, young trees should be cut in the immediate surrounding of the old trees, but usually not in other parts of the site. On the other hand, in sites where grazing has ceased more recently, a complete restoration including cutting of most shrubs and young trees could be done in one step.

#### Size and density of assemblages of hollow trees

Hollow trees are a habitat with a limited persistence. Therefore it is impossible to maintain exactly the same spatial distribution of hollow trees in the future as today. There is a slow, although continuous, shifting of the habitat which the saproxylic fauna tracks by going extinct where a tree is no longer suitable and colonizing where a suitable tree arises. In dense assemblages of hollow trees, the fauna is able to track the shifting habitat mosaic. However, if the trees are too scarce and isolated, some species fail to keep up with the habitat shift. Because extinctions may occur stochastically, and the recolonization rate may be limited (as for *O. eremita*), populations may go extinct also in stands with a continuous occurrence of suitable trees, if the number of trees is low (RANIUS & HEDIN, in press). In all the areas of the present study (Bjärka-Säby, Kättilstad and Sankt Anna), there is a great supply of mature oaks which might become hollow within a few decades if the stands are properly managed. Where there are problems with age gaps, decay could be initiated prematurely, by injuring younger trees and inoculating saproxylic fungi (KEY & BALL, 1993; ALEXANDER et al., 1996). The spatial structure of the hollow trees could thus be governed for the next two centuries.

The larger the stand, the greater the number of species able to persist therein and for a longer time. If the number of hollow oaks decreases and is lower for a period, the extinction rate rises sharply. Therefore, in conservation work the highest priority should be given to the maintenance of the quality and size of the largest localities in order to avoid bottle-necks in the population sizes. In many regions, hollow oaks occur in assemblages with only 5–10 trees, although the trees were much denser previously (for example in Kättilstad: RANIUS, 2000). In such

regions, many saproxylic species probably have relict distributions and will finally go extinct unless the density of old trees is increased. The present bottle-neck should therefore be reduced as much as possible by increasing the number of oaks to at least some tens of trees. It would also be desirable to connect smaller stands, so that they together form a denser network of hollow tree assemblages. However, in many landscapes that would require such extensive efforts that this may be unrealistic. If resources are available, density of hollow trees should also be increased in the largest sites, as this is probably necessary for the preservation of most endangered species. Even in those stands which are presently the largest in Sweden, the amount and connectivity of habitats with old oaks was greater 100–300 years ago (e.g. Bjärka-Säby, JOHANSSON, 1997). Therefore, they might harbour extremely sensitive species presently at high risk of extinction.

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#### References

- ALEXANDER, K. N. A., 1998. The links between forest history and biodiversity: the invertebrate fauna of ancient pasture-woodlands in Britain and its conservation. In: *The ecological history of European forests: 73–80* (K. J. Kirby & C. Watkins, Eds.). CAB International, Oxon.
- ALEXANDER, K. N. A., GREEN, E. E. & KEY, R., 1996. The management of over mature tree populations for nature conservation—the basic guidelines. In: *Pollard and veteran tree management II: 122–135* (H. J. Read, Ed.). Corporation of London, Burnham Beeches.
- ANONYMOUS, 1749. Östergötlands landskanslis arkiv. EIII: 1 Förteckning över tillgången av ekar i Östergötland [Handwriting in Swedish. Available at Landsarkivet i Vadstena].
- ANTONSSON, K. & WADSTEIN, M., 1991. *Ekländskapet. En naturinventering av hagar och lövskogar i ekländskapet S. om Linköping*. Länsstyrelsen i Östergötlands län, Linköping [in Swedish].
- ARAYA, K., 1993. Relationship between the decay types of dead wood and occurrence of lucanid beetles (Coleoptera: Lucanidae). *Appl. Entomol. Zool.*, 28: 27–33.
- COHEN, D. & LEVIN, S. A., 1991. Dispersal in patchy environments: the effects of temporal and spatial structure. *Theor. Popul. Biol.*, 39: 63–99.
- CROWLEY, P. H. & JOHNSON, D. M., 1992. Variability and stability of a dragonfly assemblage. *Oecologia*, 90: 260–269.
- DAJOZ, R., 1980. *Écologie des insectes forestiers*. Gauthier-Villars, Paris.

- DIXON, A. F. G., 1990. Population dynamics and abundance of deciduous tree-dwelling aphids. In: *Population dynamics of forest insects*: 11–23 (A. D. Watt, S. R. Leather, M. D. Hunter & N. A. C. Kidd, Eds.). Intercept, Andover.
- DOAK, D. F. & MILLS, L. S., 1994. A useful role for theory in conservation. *Ecology*, 75: 615–626.
- EHNSTRÖM, B., GÄRDENFORS, U. & LINDELÖW, Å., 1993. *Rödlistade evertetrater i Sverige 1993* [Swedish Red List of Invertebrates 1993]. Databanken för hotade arter, Uppsala [In Swedish, English abstract].
- EHNSTRÖM, B. & WALDÉN, H. W., 1986. *Faunavård i skogsbruket. Del 2—Den lägre faunan*. Skogsstyrelsen, Jönköping [In Swedish].
- ELIASSON, P. & NILSSON, S. G., 1999. Rättat efter Skogarnes aftagande —en miljöhistorisk undersökning av den svenska eken under 1700–och 1800-talen [The Swedish oak-tree during the 18th and 19th centuries —quantities, qualities and biodiversity]. *Bebyggelsehistorisk tidskrift*, 37: 33–64 [In Swedish, English summary].
- FALINSKI, J. B., 1986. Vegetation dynamics in temperate lowland primeval forests. *Geobotany*, 8: 1–537.
- GADGIL, M., 1971. Dispersal: Population consequences and evolution. *Ecology*, 52: 253–261.
- GÄRDENFORS, U. & BARANOWSKI, R., 1992. Skalbaggar anpassade till öppna respektive slutna ädellövskogar föredrar olika trädslag [Beetles living in open forests prefer different tree species than those living in dense forests]. *Entomol. Tidskr.*, 113: 1–11 [in Swedish, English abstract].
- HANNAH, L., CARR, J. L. & LANKERANI, A., 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. *Biodivers. Conserv.*, 4: 128–155.
- HANSKI, I., 1994. A practical model of metapopulation dynamics. *J. Anim. Ecol.*, 63: 151–162.
- HANSKI, I. & GILPIN, M. E., 1997. *Metapopulation biology. Ecology, genetics and evolution*. Academic Press, San Diego.
- HANSKI, I., MOILANEN, A. & GYLLENBERG, M., 1996. Minimum viable metapopulation size. *Am. Nat.*, 147: 527–541.
- HANSKI, I., PAKKALA, T., KUUSSAARI, M. & LEI, G., 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos*, 72: 21–28.
- HANSKI, I. & SIMBERLOFF, D., 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. In: *Metapopulation biology. Ecology, genetics and evolution*: 5–26 (I. Hanski & M. E. Gilpin, Eds.). Academic Press, San Diego.
- HARDING, P. T. & ROSE, F., 1986. *Pasture-woodlands in lowland Britain. A review of their importance for wildlife conservation*. Institute of Terrestrial Ecology, Huntingdon.
- HARRISON, S., MURPHY, D. D. & EHRLICH, P. R., 1988. Distribution of the bay checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. *Am. Nat.*, 132: 360–382.
- HARRISON, S. & TAYLOR, A. D., 1997. Empirical evidence for metapopulation dynamics. In: *Metapopulation biology. Ecology, genetics and evolution*: 27–42 (I. Hanski & M. E. Gilpin, Eds.). Academic Press, San Diego.
- HOSMER, D. W. & LEMESHOW, S., 1989. *Applied logistic regression*. John Wiley and Sons, New York.
- HULTENGREN, S. & NITARE, J., 1999. Inventering av jätteträd. Skogsstyrelsen, Jönköping [In Swedish].
- HYMAN, P. S., 1992. *UK Nature Conservation No. 3: A Review of the Scarce and Threatened Coleoptera of Great Britain*. The UK Joint Nature Conservation Committee, Peterborough.
- JANSSON, N., 1998. *Miljöövervakning av biotoper med gamla ekar i Östergötland*. Länsstyrelsen i Östergötlands län, Linköping [In Swedish].
- JOHANSSON, T., 1997. Förändringar av markanvändning i Eklandskapet i Bjärka-Säby under 300 år [Changes of land use during 300 years in the oak-dominated landscape near Bjärka-Säby, SE Sweden]. *Svensk Bot. Tidskr.*, 91: 193–208.
- JONSELL, M. & NORDLANDER, G., 2002. Insects in polypore fungi as indicator species: a comparison between forest sites differing in amounts and continuity of dead wood. *Forest Ecol. Manage.*, 157: 101–118.
- JONSELL, M., NORDLANDER, G. & EHNSTRÖM, B., 2001. Substrate associations of insects breeding in fruiting bodies of wood-decaying fungi. *Ecol. Bull.*, 49: 173–194.
- JONSELL, M., WESLIEN, J. & EHNSTRÖM, B., 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodivers. Conserv.*, 7: 749–764.
- JONSSON, M., JONSELL, M. & NORDLANDER, G., 2001. Priorities in conservation biology: a comparison between two polypore-inhabiting beetles. *Ecol. Bull.*, 49: 195–204.
- KAILA, L., MARTIKAINEN, P. & PUNTTILA, P., 1997. Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. *Biodivers. Conserv.*, 6: 1–18.
- KEHLER, D. & BONDRUP-NIELSEN, S., 1999. Effects of isolation on the occurrence of a fungivorous forest beetle, *Bolitotherus cornutus*, at different spatial scales in fragmented and continuous forests. *Oikos* 84: 35–43.
- KELNER-PILLAULT, S., 1974. Étude écologique du peuplement entomologique des terraux d'arbres creux (châtaigniers et saules). *Bull. Ecol.*, 5: 123–156.
- KEY, R. S. & BALL, S. G., 1993. Positive management for saproxylic invertebrates. In: *Dead wood matters: the ecology and conservation of saproxylic invertebrates in Britain*: 89–105 (K. J. Kirby, C. M. Drake, Eds.). English Nature Science No. 7. English Nature, Peterborough.
- KINDVALL, O. & AHLÉN, I., 1992. Geometrical factors and metapopulation dynamics of the bush cricket *Metriopetra bicolor* in Sweden.

- Biological Conservation*, 73: 51–58.
- KINGSOLVER, J. G., 1989. Weather and the population dynamics of insects: integrating physiological and population ecology. *Physiol. Zool.*, 62: 314–334.
- KIRBY, K. J. & WATKINS, C. (Eds.), 1998. *The ecological history of European forests*. CAB International, Oxon.
- KOMONEN, A. & PENTTILÄ, R., LINDGREN, M. & HANSKI, I., 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus.
- LEVINS, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.*, 15: 237–240.
- 1970. Extinction. In: *Some Mathematical Problems in Biology*: 75–107 (M. Gerstenhaber, Ed.). American Mathematical Society, Providence, RI.
- LINK, W. A. & NICHOLS, J. D., 1994. On the importance of sampling variance to investigations of temporal variation in animal population size. *Oikos*, 69: 539–544.
- LOMOLINO, M. V., BROWN, J. H. & DAVIS, R., 1989. Island biogeography of montane forest mammals in the American southwest. *Ecology*, 70: 180–194.
- LOTT, D., 1999. A comparison of saproxylic beetle assemblages occurring under two different management regimes in Sherwood Forest. *Naturalist*, 124: 67–74.
- LUCE, J.-M., 1996. *Osmoderma eremita* (Scopoli, 1763). In: *Background information on invertebrates of the Habitats Directive and the Bern Convention. Part I: Crustacea, Coleoptera and Lepidoptera*: 64–69 (P. J. van Helsdingen, L. Willemse, & M. C. D. Speight, Eds.). Council of Europe, Strasbourg.
- LUFF, M. L., 1982. Population dynamics of Carabidae. *Ann. Appl. Biol.*, 101: 164–170.
- MACARTHUR, R. H. & WILSON, E. O., 1967. *The theory of island biogeography*. Princeton University Press, Princeton.
- MARTIN, O., 1989. Smældere (Coleoptera, Elateridae) fra gammel løvskov i Danmark. *Ent. Meddr.*, 57: 1–107 [In Danish, English abstract].
- 1993. Fredede insekter i Danmark. Del 2: Biller knyttet til skov. *Ent. Meddr.*, 57: 63–76 [In Danish, English abstract].
- MCPEEK, M. A. & HOLT, R. D., 1992. The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.*, 140: 1,010–1,027.
- MIDTGAARD, F., 1996. The significance of fragmentation of boreal forest for the occurrence of selected Cloeoptera. PhD Thesis, University of Oslo, Oslo.
- MIKKOLA, K., 1976. Alternate-year flight of northern *Xestia* species (Lep., Noctuidae) and its adaptive significance. *Ann. Entomol. Fenn.*, 42: 191–199.
- MOILANEN, A., SMITH, A.T. & HANSKI, I., 1998. Long-term dynamics in a metapopulation of the American pika. *Am. Nat.*, 152: 530–542.
- MÖNKKÖNEN, M. & ASPI, J., 1997. Sampling error in measuring temporal density variability in animal populations and communities. *Ann. Zool. Fenn.*, 34: 47–57.
- MURDOCH, W. W., CHESSON, J. & CHESSON, P. L., 1985. Biological control in theory and practice. *Am. Nat.*, 125: 344–366.
- NILSSON, S. G., 1997. Forests in the temperate-boreal transition: natural and man-made features. *Ecol. Bull.*, 46: 61–71.
- 2001. Sydsveriges viktigaste områden för bevarandet av hotade arter —vedskalbaggasom vägvisare till kärnområdena (The most valuable areas for preservation of biodiversity in southern Sweden —woodliving beetles as guides to hot-spots). *Fauna och Flora*, 96: 59–70 [in Swedish, English summary].
- NILSSON, S. G. & BARANOWSKI, R., 1997. Habitat predictability and the occurrence of wood beetles in old-growth beech forests. *Ecography*, 20: 491–498.
- NILSSON, T., 1997a. Survival and habitat preferences of adult *Bolitophagus reticulatus*. *Ecol. Entomol.*, 22: 82–89.
- 1997b. *Spatial population dynamics of the black tinder fungus beetle Bolitophagus reticulatus (Coleoptera: Tenebrionidae)*. Acta Universitatis Upsaliensis. Uppsala University, Uppsala.
- NORDÉN, B. & APPELQVIST, T., 2001. Conceptual problems of ecological continuity and its bioindicators. *Biodivers. Conserv.*, 10: 779–791.
- NÜRNBERGER, B., 1996. Local dynamics and dispersal in a structured population of the whirlyig beetle *Dineutus assimilis*. *Oecologia*, 106: 325–336.
- ØKLAND, B., 1996. Unlogged forests: important sites for preserving the diversity of Mycetophilids (Diptera: Sciaroidea). *Biological Conservation*, 76: 297–310.
- 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. *Biodivers. Conserv.*, 5: 75–100.
- OWEN, J. & GILBERT, F. S., 1989. On the abundance of hoverflies (Syrphidae). *Oikos*, 55: 183–193.
- PALM, T., 1959. Die Holz- und Rindenkäfer der Süd- und Mittelschwedischen Laubbäume [The wood and bark coleoptera of deciduous trees in southern and central Sweden]. *Opusc. Entomol. Suppl.* XVI [in German, English summary].
- POLLARD, E. & YATES, T. J., 1993. *Monitoring butterflies for ecology and conservation*. Chapman & Hall, London.
- PULLIN, A. S. (Ed.), 1995. *Ecology and conservation of butterflies*. Chapman & Hall, London.
- RANIUS, T., 2000. Minimum viable metapopulation size of a beetle, *Osmoderma eremita*, living in tree hollows. *Anim. Conserv.*, 3: 37–43.
- 2001. Constancy and asynchrony of populations of a beetle, *Osmoderma eremita* living in tree hollows. *Oecologia*, 126: 208–215.
- 2002a. Influence of stand size and quality of

- tree hollows on saproxylic beetles in Sweden. *Biol. Conserv.*, 103: 85–91.
- 2002b. *Osmoderma eremita* as an indicator of species richness of beetles in tree hollows. *Biodivers. Conserv.*, 11: 931–941.
- RANIUS, T., ANTONSSON, K., JANSSON, N. & JOHANNESSON, J., 2001. Inventering och skötsel av gamla ekar i Eklandskapet söder om Linköping (Inventories and management of old oaks in an area south of Linköping, Sweden). *Fauna och Flora*, 96: 97–107 [In Swedish, English summary].
- RANIUS, T. & HEDIN, J., 2001. The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. *Oecologia*, 126: 363–370.
- In press. The occupancy pattern of a saproxylic beetle, *Osmoderma eremita*, in a fragmented landscape predicted from a RAMAS meta-population model. In: *Species conservation and management: case studies* (H. R. Akcakaya, M. Burgman, O. Kindvall, P. Sjögren-Gulve, J. Hatfield & M. McCarthy, Eds.). Oxford University Press, Oxford.
- RANIUS, T. & JANSSON, N., 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biol. Conserv.*, 95: 85–94.
- In press. A comparison of three methods to survey saproxylic beetles in hollow oaks. *Biodivers. Conserv.*
- RANIUS, T. & NILSSON, S. G., 1997. Habitat of *Osmoderma eremita* Scop. (Coleoptera: Scarabaeidae), a beetle living in hollow trees. *J. Insect Conserv.*, 1: 193–204.
- RANIUS, T. & WILANDER, P., 2000. Occurrence of *Larca lata* H. J. Hansen (Pseudoscorpionida: Garypidae) and *Allochernes wideri* C. L. Koch (Pseudoscorpionida: Chernetidae) in tree hollows in relation to habitat quality and density. *J. Insect Conserv.*, 4: 23–31.
- ROSENZWEIG, M. L., 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge.
- ROYAMA, T., 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecol. Monogr.*, 54: 429–462.
- RUKKE, B. A. & MIDTGAARD, F., 1998. The importance of scale and spatial variables for the fungivorous beetle *Bolitophagus reticulatus* (Coleoptera, Tenebrionidae) in a fragmented forest landscape. *Ecography*, 21: 561–572.
- SANDELL, A., 1999. *Landskapskartering av gamla träd och alléer i Östergötland*. Länsstyrelsen i Östergötlands län, Linköping [In Swedish].
- SIITONEN, J. & SAARISTO, L., 2000. Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biol. Conserv.*, 94: 211–220.
- SOLBRECK, C., 1991. Unusual weather and insect population dynamics: *Lygaeus equestris* during an extinction and recovery period. *Oikos*, 60: 343–350.
- SPEIGHT, M. C. D., 1989. *Saproxylic invertebrates and their conservation*. Council of Europe, Strasbourg.
- SVENNING, J.-C., 2002. A review of natural vegetation openness in north-western Europe. *Biol. Conserv.*, 104: 133–148.
- SVERDRUP-THYGESON, A. & IMS, R. A., 2002. The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. *Biol. Conserv.*, 106: 347–357.
- TAUZIN, P., 1994. Le genre *Osmoderma* Le Peletier et Audinet-Serville 1828 (Coleopt., Cetoniidae, Trichiinae, Osmodermatini). Systématique, biologie et distribution (Deuxième Partie). *Entomologiste*, 50: 217–242.
- THAM, W., 1855. *Beskrifning öfver Linköpings län. Sednare delen*. L. J. Hjertas förlag, Stockholm [In Swedish].
- THOMAS, C. D., 2000. Dispersal and extinction in fragmented landscapes. *Proc. R. Soc. Lond. B Biol. Sci.*, 267: 139–145.
- THOMAS, C. D. & HANSKI, I., 1997. Butterfly metapopulations. In: *Metapopulation biology. Ecology, genetics and evolution*: 359–386 (I. Hanski & M. E. Gilpin, Eds.). Academic Press, San Diego.
- THOMAS, J. A., 1991. Rare species conservation: Case studies of European butterflies. In: *The scientific management of temperate communities for conservation*: 149–197 (I. F. Spellerberg, F. B. Goldsmith, M. G. Morris, Eds.). Blackwell Scientific Press, Oxford.
- 1993. Holocene climate changed and warm man-made refugia may explain why a sixth of British butterflies possess unnatural early-successional habitats. *Ecography*, 16: 278–284.
- TRAVIS, J. M. J. & DYTAM, C., 1999. Habitat persistence, habitat availability and the evolution of dispersal. *Proc. R. Soc. Lond. B Biol. Sci.*, 266: 723–728.
- VERA, F. V. M., 2000. *Grazing ecology and forest history*. CABI, Wallingford.
- VERNON, P., VANNIER, G. & LUCE, J.-M., 1996. Découverte de larves tolérantes et intolérantes a la congélation dans une même guildes de détoines (Coléoptères) en forêt de Fontainebleau. *Écologie*, 27: 131–142.
- 1997. Diminution de la capacité de surfusion au cours de l'embryogenèse et du développement larvaire chez un coléoptère. *C. R. Acad. Sci. Paris, Sciences de la vie*, 320: 359–366.
- WARREN, M. S. & KEY, R. S., 1991. Woodlands: past, present and potential for insects. In: *The conservation of insects and their habitats*: 155–211 (N. M. Collins & J. A. Thomas, Eds.). London, Academic Press.
- WHITTAKER, J. B. & TRIBE, N. P., 1998. Predicting numbers of an insect (*Neophilaenus lineatus*: Homoptera) in a changing climate. *J. Anim. Ecol.*, 67: 987–991.
- WOLDA, H., SPITZER, K. & LEPS, J., 1992. Stability of environment and of insect populations. *Res. Popul. Ecol.*, 34: 213–225.