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Body size affects the spatial scale of habitat–beetle interactions

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We used abundance data and the program Focus to determine the spatial scale at which 31 species of longhorned beetles (Coleoptera: Cerambycidae) respond to forest habitat amount. We predicted that the spatial scale at which species respond would increase with body size, and that species using ephemeral larval habitat would respond at larger spatial scales than species using more stable larval habitat. We found that forest cover was a better measure of the amount of habitat for polyphagous species than for oligophagous species. Larger species of longhorned beetles responded to forest cover at larger scales. We did not find evidence that species using more ephemeral larval habitat conditions responded at larger scales than species developing in more stable habitat conditions. Our results highlight the importance of accurately describing habitat in studies of species–environment relationships. While scales of response may be species-specific, some generalizations across species are possible.

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Animal species respond to their environment at different spatial scales (Gehring and Swihart 2003). Even within guilds, both parasitoid fly species (Roland and Taylor 1997) and longhorned beetle (Coleoptera: Cerambycidae) species (Holland et al. 2004) respond to habitat variables at different scales. To study the response of animals to their habitat, we must measure habitat variables at a scale that is appropriate for the animal and phenomena being studied (Addicott et al. 1987, Wiens and Milne 1989, Schopf and Ivany 1998, Ludwig et al. 2000). Using an inappropriate spatial scale can cause the researcher to miss an important relationship between the species and its habitat (Lomolino and Creighton 1996, Rukke and Midtgaard 1998), or even to come to the wrong conclusion (Hanski 1987, Schopf and Ivany 1998).

Cale and Hobbs (1994) and Elliott et al. (1998) have suggested that the distance that organisms move is one factor that must be considered in deciding on a spatial scale at which to consider habitat variables. Økland et al. (1996) found that the abundance and richness of flying saproxylic beetles was more strongly related to the amount of decaying wood resources at larger than smaller scales, and that 40×40 m represented much too small a scale to reveal this relationship. They concluded that habitat measures should be made within at least a 1 km^2 area for studying these species. In contrast, Rukke and Midtgaard (1998) found significant effects of habitat isolation on fungus beetles when isolation was measured within less than 50 m from a source habitat. This may be because the beetle species they considered confine their movements to walking over distances less than 50 m (Starzomski and Bondrup-Nielsen 2002).

Several species characteristics have been hypothesized to explain the scale at which different species respond to their environment, some of these by affecting the movement distance of the species. One such characteristic is body size. Larger animals may respond to the environment over a larger scale either because they

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perceive the environment more coarsely (Mech and Zollner 2002) or because they move farther to satisfy their greater energetic requirements (Perry and Garland 2002).

A second characteristic that may affect the movement range of a species, and hence the scale at which it responds to the environment, is the longevity of its habitat. Nicholson (1954) suggested that movement may be influenced by resource complementation and the use of ephemeral habitats. Southwood's habitat templet theory (1977) predicts that species with relatively narrow niches should have good dispersal abilities. Hanski (1987) reiterated this theory, noting that species that use ephemeral habitats are expected to move considerable distances to track these habitats. Observations supporting the link between habitat stability and movement distance has be found in click beetles (Coleoptera: Elateridae; Nilsson and Baranowski 1994) and in longhorned beetles (Hanks 1999). In a study of stream invertebrates, Gjerløv (1997) found that Southwood's templet theory was supported, but only when the correct scale was considered. If movement is related to the scale of response, then longhorned beetle species that develop in ephemeral habitats should respond to habitat at larger spatial scales than species that use longer lasting habitats.

The amount of habitat for forest-dwelling species is often equated to the amount of forest in an area. However, for many species the actual useable habitat may not correspond with the total forest cover. The larva of the longhorned beetle species we are studying develop within dead trees, and have a different range of suitable host wood species depending on the beetle species in question. Total forest then should represent the proportion of habitat for polyphagous species which can utilize a wide range of host tree species. The proportion of habitat for more specialized oligophagous species, which have a narrower host range, will be some subset of the total amount of forest. If overall forest cover is a worse measure of habitat for the oligophagous species then they should show weaker relationships with overall forest cover. For this reason we expected that the proportion of forest would be more strongly related to the abundance of the polyphagous species than to the abundance of the oligophagous species.

The purpose of this study was to determine whether body size and longevity of larval habitat (i.e. ephemeral or not) are related to the scale at which different species of longhorned beetles respond to forest habitat cover. We predicted that larger species would respond at larger scales. We further expected species whose larvae develop in newly dead wood to respond to forest cover at a larger scale than species whose larvae develop in older, decayed dead wood, because the former represents a more ephemeral habitat than the latter.

Methods

Natural history of Cerambycidae

Most species of longhorned beetles are associated with forest (Gutowski 2002). Most of their life cycle (1–4 years in the Ottawa area) is spent as larvae that feed by excavating galleries in a single piece of living or dead wood (Linsley 1954, Hanks 1999). Some species have larvae that can only develop within a limited number of wood species, while other species can use many wood species, with some being able to develop within both deciduous and coniferous dead wood (Yanega 1996). The mobile adult stage is comparatively short, on the order of 3 to 6 weeks for many species (Safranyik and Moeck 1995).

The condition of the host tree or log differs among species of longhorned beetles. Recently dead wood (within the first few years of tree death) is used by a different set of wood-boring beetle species than wood that has been dead for decades (Blackman and Stage 1924, Graham 1925, Samuelsson et al. 1994). The recently dead wood represents a much more ephemeral resource than the older stage of dead wood (Kletecka 1996).

Longhorned beetle surveys

We surveyed longhorned beetle abundance at 190 sites over the 1999 and 2000 season (April–August) in the Ottawa, Canada area. We used 19 sampling areas that were 1 km^2. Within each sampling area we placed a Lindgren funnel trap baited with ethanol and fresh wood chips at 10 randomly located sampling sites. Most traps were located within forested areas. Traps were checked monthly and abundances within species were summed over the two sampling seasons. Further details on traps and trapping locations can be found in Holland et al. (2004).

During cerambycid surveys carried out during the summers of 1999 and 2000, 11 Lindgren funnel traps were located in non-forest sites. These traps were at least 50 m from the edge of any woodlot or forest. All beetles caught in these traps were considered to be moving outside of forest habitat. During the summer of 2001 we used flight intercept traps to capture longhorned beetles flying from forest into non-forest areas. We put these traps in 7 of the 19 sampling areas from the 1999 and 2000 surveys that had a meadow or old field next to a woodlot edge. The selected woodlot edges all faced roughly northwest, into the prevailing wind direction in this area. We used woodlot edges that faced the same way to control for any possible effects of sunlight or photo-taxiing. As well, adult longhorns often use scent to find suitable larval host trees and mates (Linsley 1954, Schowalter 1985, Hanks et al. 1993). Therefore, our traps caught beetles moving out of woodlots to seek upwind resources by scent.

We designed flight intercept traps that had a very large surface area (5.2 m^2 on a side), but would not require constant maintenance and would alleviate the need for transporting a large volume of killing/preserving fluid to the traps. The resulting trap was a combination of flight intercept and sticky trap. We used wooden posts to support a 4.3 m long by 1.2 m tall piece of black window screen. We stapled clear plastic onto a plywood stage that was 0.3 m wide and was supported at a 45° angle below and in front of the screen. To hold any beetles that hit the trap we applied Rat and Mouse Trapping Adhesive (The Tanglefoot Company, Grand Rapids, Michigan, USA) to the plastic sheet with a caulking gun. Beetles flying into the screen dropped onto the angled plastic sheet and got caught in the adhesive. When the traps were first set up we applied four beads of adhesive along the length of the plastic sheet. As the adhesive became saturated with insects, pollen, or other materials we laid down additional longitudinal beads of adhesive. Further details of trap construction are available from the first author.

We placed two traps in each of the seven locations. We placed one trap 25 m from the forest edge and the second trap 50 m from the forest edge. We offset the traps by 50 m laterally. Both traps had the "trapping side" of the screen facing the forest, so that they only caught beetles flying from the direction of the woodlot. We visited each trap weekly from the beginning of May until the end of August. During each visit we removed all longhorned beetles and placed them in vials of Histoclear (National Diagnostics, Atlanta, Georgia, USA). We identified the species using Yanega (1996). Species caught by either the Lindgren funnel traps outside forest in 1999 or 2000, or by the flight intercept traps in 2001 were categorized as species that will move in non-forest areas. Species not caught by either method, but caught in a Lindgren funnel trap within forest (Holland et al. 2004) in these same areas were categorized as species that do not move in non-forest areas. While this binary classification is not sufficient to test the idea that there is a relationship between movement and scale of response we use it in a subsequent study of extinction thresholds.

The scale of response to forest habitat

The amount of forest around our 190 trapping sites was measured within 19 different radii (Holland et al. 2004). We determined the spatial scale (focus, sensu Scheiner et al. 2000) at which 31 species of longhorned beetles respond to forest cover using the software program Focus (Holland et al. 2004). The Focus program uses data on the abundance of a species (or any other numerical point data) at sampling locations and the amount of forest habitat (or any other landscape variable) measured at several spatial scales around the sampling locations to determine the scale at which the species abundance responds most strongly to the proportion of forest while avoiding non-independence of landscape measurements (Holland et al. 2004). We refer to this spatial scale as the characteristic scale of response to forest habitat for the species. We use the term 'characteristic scale' because this scale of response may be an inherent trait of different species (Mitchell et al. 2001). Figure 1 shows an example of the output of this program for one species.

In brief, the Focus program conducts linear regressions of the beetle abundance of each species on the proportion of forest. It repeats these regressions at each scale to see where the resulting model best fit the data (Elliott et al. 1998) for each species. At the larger scales the sampling sites were clustered so that the areas within which forest cover was measured were overlapping. This could violate the assumption of independence and artificially inflate the degrees of freedom in the individual regressions. To make use of all points despite the lack of spatial independence Focus uses a randomization procedure (Holland et al. 2004). It conducts the regression between abundance and habitat a number of times at each spatial scale using different sets of randomly selected spatially independent sites. The user sets the number of iterations (regressions) to be done at each spatial scale; the output is then the mean model fit and associated variation at each spatial scale. In this way all or most of the data points are included in the final average measure of model fit, even if only a small proportion are used in individual regression because of spatial non-independence. A sample size of 16 was used in all regressions, because 16 was the number of possible

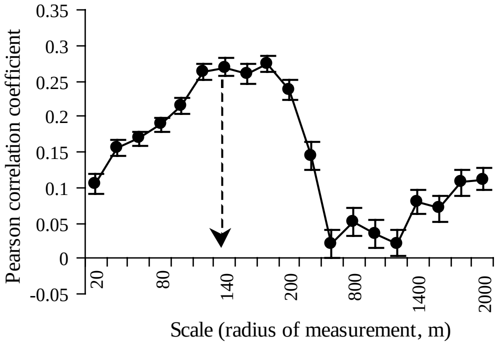

Fig. 1. Example of Focus output showing model fit (Pearson correlation coefficient) between forest cover and beetle abundance for *Urgleptes signatus* (LeC.). Means are from 200 regressions of beetle abundance and forest cover, with each regression done on a randomly chosen set of spatially independent points. Note the change in x-axis scale at 200 m.

spatially independent points at the largest spatial scale (2 km) we considered (Holland et al. 2004).

We considered the scale of response to be the scale at which the Pearson correlation coefficient had a local maximum (peak), and had standard error bars that did not overlap those either at a smaller local maximum or at the smallest scale. It is important to note that we were not conducting a statistical test at this point. We used the standard error bars only as a consistent rule (selected a priori) to select the characteristic scale of response for each species. Using 95% confidence intervals would have been a more conservative method, but the large number of sampling sites with zero abundances combined with the small sample size within each regression caused large variation in the calculated model fit measures. In Holland et al. (2004) we simply took the scale of maximum correlation to be the scale of response. We use a different approach here because we are testing different hypotheses. It is important to refine the selection method (a priori) based on the hypotheses, especially because some species may show several peak scales of response because different species-habitat phenomena operate at different spatial scales (Kinnunen et al. 2001).

Determining body size and whether larvae use ephemeral hosts

We used the median of the range of lengths specified in Yanega (1996) as the body size for each species. Cerambycids whose larvae develop in newly dead wood were considered to be using an ephemeral resource (Kletecka 1996). We searched the literature for information on the condition of larval hosts of the species we caught (Linsley 1962a, b, 1963, 1964, Linsley and Chemsak 1972, 1976, Yanega 1996). Descriptions such as "newly felled," "recently cut," "unseasoned" and "sound deadwood" were considered to indicate recently dead wood. Species whose larvae developed within wood described as "decaying," "soft," or "seasoned," were considered to develop within older dead wood. These larval habitats were considered not to be ephemeral. Of course, such logs do eventually become unavailable to longhorned beetle larvae, but at a rate of decades not one to a few years as for the recently dead wood habitats.

Analyses

To compare the response of oligophagous and polyphagous species to the total amount of forest we used a t-test, assuming unequal variances, to compare the average Pearson correlation coefficients of these two groups at the characteristic scale of response (scale corresponding to the maximum model fit) to habitat amount (Fig. 1). We used the 12 polyphagous species from Holland et al. (2004) plus 15 species determined to be oligophagous. We left out 4 additional species (*Hyperplatys aspersa* (Say), *Molorchus b. bimaculatus* (Say), *Neoclytus a. acuminatus* (F.), *Phymatodes aereus* (Newm.)) that did not respond positively to the proportion of forest habitat at any of the spatial scales considered.

To test the hypothesis that larger beetles responded to habitat at larger scales we conducted a linear regression between the median adult body length of species and the scales at which they responded to habitat amount. The characteristic scales were transformed by taking natural logarithms before analysis because these ranged over three orders of magnitude (Holland et al. 2004). We used analysis of variance (ANOVA) to check the significance of the resulting linear relationship.

To test the hypothesis that species that use ephemeral habitat respond to habitat at a larger characteristic scale than other species we again used a t-test, assuming unequal variances, to compare the natural logarithm of the scale of habitat response.

Results

The t-test did show that the correlation coefficients for the polyphagous species were higher than for the oligophagous species ($df = 23$, $t = 3.56$, $p > 0.002$, Fig. 2a). This indicates that the polyphagous species respond more strongly to the total amount of forest than the oligophagous species. This does not invalidate the scales at which the oligophagous responded to forest, but it does suggest that not all forest is habitat for these species. Therefore, because we do not have a good measure of the amount of habitat for them, the characteristic scales of response may be suspect for the oligophagous species. For this reason, the analyses that follow were done using only the polyphagous species. Table 1 lists all the species and their characteristic scales of response to proportion of forest in the landscape, median body size, as well as whether or not they use an ephemeral larval resource according to our criteria.

There was a marginally significant positive relationship between the median body length for the polyphagous species and the scale at which they responded to forest habitat ($df = 11$, $F = 4.26$, $p = 0.066$, Fig. 3). This relationship explained 30 percent of the variability in the scale of response. Species that used ephemeral habitat did not show a greater scale of response to forest proportion than those not using ephemeral habitats ($df = 3$, $t = 2.19$, $p > 0.1$, Fig. 2b). In fact the general trend was for the species using ephemeral habitats to respond at smaller scales.

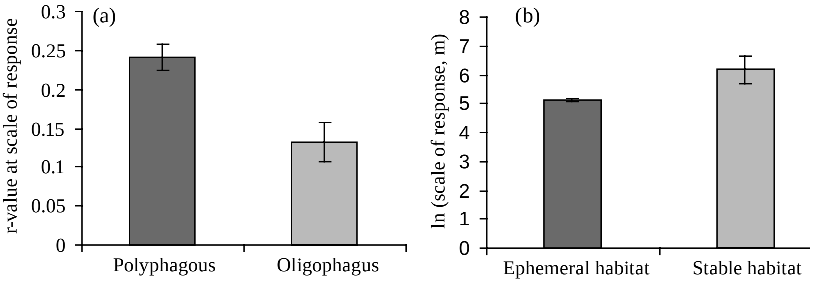

Fig. 2. (a) Comparison of model fit between polyphagous and oligophagous species. The r-values for each species are the mean value at the characteristic scale of response to habitat amount for that species. (b) Comparison of the characteristic scale of response of species with larvae that develop within ephemeral wood conditions and those that develop within longer-lasting wood conditions. Error bars represent one standard error.

Discussion

Different species of longhorned beetles responded to habitat amount at different spatial scales, with the characteristic scales of response varying over 3 orders of magnitude. This was shown in a previous study for the polyphagous species in this study (Holland et al. 2004). The different scales of response suggest that it may not be appropriate to use a single spatial scale in studies of multiple species, at least in cases where the species respond at very different spatial scales. Using a single scale for all species in such cases may cause the trends being examined to be weakened for many species. Single-scale studies can lead to some species showing a stronger response to habitat variables because they happen to be measured closer to the characteristic scale of response of those species. The response of other species will appear to be weaker simply because the species–habitat relationship is strongest at a different scale.

It is not surprising that the polyphagous species showed a stronger relationship with overall forest cover than the more specialized oligophagous species. If these latter species are responding to only a subset of the overall forest this response will be weaker than for species that are responding to all forest. However, despite the intuitive nature of this result, it suggests a cautionary message to ecological researchers, namely that if habitat is not carefully defined from the organism's point of view the detected relationships between the organism and it's habitat will be weakened. Some species will appear to respond more strongly to some measured variable not because the actual relationship is stronger, but only because the habitat is better defined for those species.

Table 1. Species of cerambycid beetles that feed on dead wood and were caught at at least five trapping sites. Poly./Olig. refers to whether the species is polyphagous or oligophagous in the larval stage according to our criteria (methods). Ephem? refers to whether the larvae develop within an ephemeral stage of log decay. A blank in the Ephem? column indicates that we were unable to assign the larval habitat to either condition.

Species	Poly./Olig.	Scale (m)	Size (mm)	Ephem?
Bellamira scalaris (Say)	Poly.	1000	21.5	n
Evodinus m. monticola (Rand.)	Poly.	160	10.5	
Gaurotes cyanipennis (Say)	Poly.	160	11.0	y
Liopinus alpha (Say)	Poly.	20	6.5	
Microgoes oculatus (LeC.)	Poly.	60	11.5	
Stictoleptura c. canadensis (Oliv.)	Poly.	1600	12.5	
Strangalepta abbreviata (Germ.)	Poly.	120	12.0	n
Strangalia luteicornis (F.)	Poly.	800	11.5	n
Trachysida mutabilis (Newm.)	Poly.	1200	11.5	n
Trigonarthris minnesotana (Csy.)	Poly.	200	15.5	
Urgleptes signatus (LeC.)	Poly.	140	6.5	
Urographis fasciatus (DeG.)	Poly.	180	12.0	y
Analeptura lineola (Say)	Olig.	200	9.0	
Anthophylax attenuatus (Hald.)	Olig.	400	14.5	n
Astylopsis macula (Say)	Olig.	20	8.5	
Astylopsis sexguttata (Say)	Olig.	600	8.5	
Clytus ruricola (Oliv.)	Olig.	100	12.5	n
Cyrtophorus verrucosus (Oliv.)	Olig.	20	9.0	y
Hyperplatys maculata Hald.	Olig.	100	6.0	
Lepturges symmetricus (Hald.)	Olig.	800	7.5	
Oplosia nubila (LeC.)	Olig.	1000	11.5	n
Saperda imitans Felt & Joutel	Olig.	20	13.0	n
Sarosesthes fulminans (F.)	Olig.	180	17.0	y
Stenocorus schaumii (LeC.)	Olig.	40	23.5	
Trigonarthris proxima (Say)	Olig.	40	16.5	n
Urgleptes querci (Fitch)	Olig.	40	5.0	
Xylotrechus colonus (F.)	Olig.	40	11.5	y

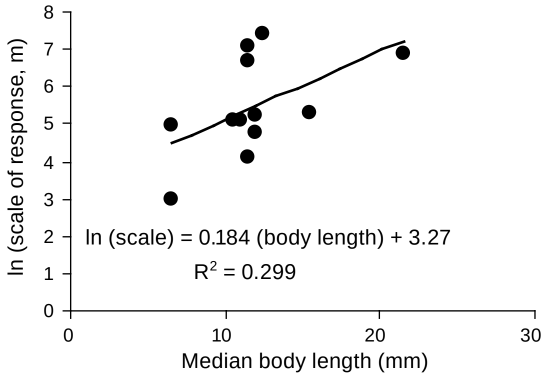

Fig. 3. Relationship between median body length and the characteristic scale of response at which dead wood polyphagous species responded to proportion of forest.

We suspect that stronger correlations would be found between species numbers or occurrence and habitat measures with a better classification of habitat. Although we have distinguished forest habitat from forest non-habitat, we are still essentially using a binary view of the environment. A classification within forest habitat based on habitat quality would be still more biologically meaningful (Thomas and Kunin 1999). This may be difficult to achieve in a way that can applied to several different species at once (Clarke et al. 1997), but this is a logical next step in our efforts to tune into environment-species signals with spatial scaling.

The hypothesis that larger beetles should respond to amount of forest habitat at larger scales was supported. The relationship between median body length and scale of response to forest was quite strong, explaining 30% of the variation in scale of response (Fig. 3). As far as we know, this is one of the first empirical tests of this specific hypothesis, although Roland and Taylor (1997) made a similar discovery in that the scale of response of four parasitoid fly species to forest structure was positively related to body mass. Steffan-Dewenter et al. (2002) found that the different bee (Hymenoptera) guilds responded to landscape context at different spatial scales. Researchers have found that larger animals tend to move farther and this may lead to larger animals responding to their surroundings at larger scales. Bowman et al. (2002) controlled for the relationship between mammalian body mass and movement distance in their study. Although this was not the main focus of their work, they found that body mass explained 50% of the variance in dispersal distance, and 67% of the variance in maximum successful return distance following relocation. Sutherland et al. (2000) and Peters (1983) have found a positive relationship between body mass and maximum dispersal distance for both mammals and birds. It is possible that greater movement of larger species is behind the relationship between body length and characteristic scale of response. Regardless, the larger species are responding to forest cover at larger scales.

We did not find any evidence that species that develop in more ephemeral habitats responded to forest at greater scales than those developing in longer-lasting habitat. This prediction was based on the idea that species that move greater distances will respond to the amount of habitat at larger spatial scales. It is possible that species of saproxylic longhorned beetles that must disperse between ephemeral habitats do not necessarily move farther than those species that utilize longer-lasting larval hosts. While some longhorned beetle species do not need to move from the larval host log to feed as adults, mate and oviposit (examples described in Craighead 1950), other species require adult food resources that are potentially far from the larval host. These latter species tend to disperse farther than those whose larval and adult resources are in close proximity (Shibata 1987, Barbalat 1995, Hanks et al. 1998, Hanks, 1999). Therefore, movement may be determined as much by the food requirements of the adults as it is by whether or not the larval host conditions are stable.

It is also possible that the relationship between the size of the species and the scale of response obscured the effects of ephemeral larval habitats. Kletecka (1996) noted that species using the more ephemeral early dead wood tended to develop faster and be smaller. The very small number of polyphagous species for which we have data on whether the larval habitat is ephemeral or stable precluded the separation of these effects. More data on the movement and life history of more longhorned beetle species would allow the relationships between these traits and the characteristic scale of response to be further examined.

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References

Addicott, J. F., Aho, J. M., Antolin, M. F. et al. 1987. Ecological neighborhoods: scaling environmental patterns. – Oikos 49: 340–346.

Barbalat, S. 1995. Efficacité comparée de quelques méthodes de piégage sur certains coléopteres et influence de l'anthophilie sur le résultat des captures. – Bull. Soc. Neuchâteloise Sci. Nat. 118: 39–52.

Blackman, M. W. and Stage, H. H. 1924. On the succession of insects living in the bark and wood of dying, dead and decaying hickory. – New York State College of Forestry at Syracuse University, Tech. Publ. No. 17.

Bowman, J., Jaeger, J. A. G. and Fahrig, L. 2002. Dispersal distance of mammals is proportional to home range size. – Ecology 83: 2049–2055.

Cale, P. G. and Hobbs, R. J. 1994. Landscape heterogeneity indices: problems of scale and applicability, with particular reference to animal habitat description. – Pac. Conserv. Biol. 1: 183–193.

Clarke, R. T., Thomas, J. A., Elmes, G. W. et al. 1997. The effects of spatial patterns in habitat quality on community dynamics within a site. – Proc. R. Soc. Lond Ser. B. 1380: 347–354.

Craighead, F. C. 1950. Insect enemies of eastern forests. Misc. Publication No. 657. – US Government Printing Office. Washington.

Elliott, N. C., Kieckhefer, R. W., Lee, J.-H. et al. 1998. Influence of within-field and landscape factors on aphid predator populations in wheat. – Landscape Ecol. 14: 239–252.

Gehring, T. M. and Swihart, R. K. 2003. Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. – Biol. Conserv. 109: 283–295.

Gjerløv, C. 1997. Disturbance and refugia in the ecology of stream benthic communities. PhD thesis. – School of Biological Sciences, Queen Mary and Westfield College, Univ. of London.

Graham, J. A. 1925. The felled tree trunk as an ecological unit. – Ecology 6: 397–411.

Gutowski, J. M. 2002. The role of Cerambycidae and Buprestidae (Coleoptera) in forest ecosystems and some remarks on their economic significance. – In: 4th Symp. Protection of Forest Ecosystems, Warsaw Agric. Univ., pp. 165–175.

Hanks, L. M. 1999. Influence of the larval host plant on reproductive strategies of cerambycid beetles. – Annu. Rev. Entomol. 44: 483–505.

Hanks, L. M., Paine, T. D. and Millar, J. G. 1993. Host species preference and larval performance in the wood-boring beetle *Phoracantha semipunctata* F. – Oecologia 95: 22–29.

Hanks, L. M., Millar, J. G. and Paine, T. D. 1998. Dispersal of the eucalyptus longhorned borer (Coleoptera: Cerambycidae) in urban landscapes. – Environ. Entomol. 27: 1418–1424.

Hanski, I. 1987. Colonization of ephemeral habitats. – In: Gray, A. J., Crawley, M. J. and Edwards, P. J. (eds), Colonization, succession and stability. Blackwell, pp. 155–185.

Holland, J. D., Bert, D. G. and Fahrig, L. 2004. Determining the spatial scale of species' response to habitat. – Bioscience 54: 229–235.

Kinnunen, H., Tiainen, J. and Tukia, H. 2001. Farmland carabid beetle communities at multiple levels of spatial scale. – Ecography 24: 189–197.

Kletecka, Z. 1996. The xylophagous beetles (Insecta, Coleoptera) community and its succession on scotch elm (*Ulmus glabra*) branches. – Biologia 51: 143–152.

Linsley, E. G. 1954. Ecology of Cerambycidae. – Annu. Rev. Entomol. 4: 99–138.

Linsley, E. G. 1962a. The Cerambycidae of North America, Part II Taxonomy and classification of the Parandrinae, Prioninae, Spondylinae and Aseminae. – Univ. of California Press.

Linsley, E. G. 1962b. The Cerambycidae of North America, Part III Taxonomy and classification of the subfamily Cerambycinae, tribes Opsimini through Megaderini. – Univ. of California Press.

Linsley, E. G. 1963. The Cerambycidae of North America, Part IV Taxonomy and classification of the subfamily Cerambycinae, Elaphidionini through Rhinotragini. – Univ. of California Press.

Linsley, E. G. 1964. The Cerambycidae of North America, Part V. Taxonomy and classification of the subfamily Cerambycinae, tribes Callichromini through Ancylocerini. – Univ. of California Press.

Linsley, E. G. and Chemsak, J. A. 1972. The Cerambycidae of North America, Part VI No. 1 Taxonomy and classification of the subfamily Lepturinae. – Univ. of California Press.

Linsley, E. G. and Chemsak, J. A. 1976. The Cerambycidae of North America, Part VI No. 2 Taxonomy and classification of the subfamily Lepturinae. – Univ. of California Press.

Lomolino, M. V. and Creighton, J. C. 1996. Habitat selection, breeding success and conservation of the endangered American burying beetle *Nicrophorus americanus*. – Biol. Conserv. 77: 235–241.

Ludwig, J. A., Wiens, J. A. and Tongway, D. J. 2000. A scaling rule for landscape patches and how it applies to conserving soil resources in savannas. – Ecosystems 3: 84–97.

Mech, S. G. and Zollner, P. A. 2002. Using body size to predict perceptual range. – Oikos 98: 47–52.

Mitchell, M. S., Lancia, R. A. and Gerwin, J. A. 2001. Using landscape–level data to predict the distribution of birds on a managed forest: effects of scale. – Ecol. Appl. 11: 1692–1708.

Nicholson, A. J. 1954. An outline of the dynamics of animal populations. – Aust. J. Zool. 2: 9–65.

Nilsson, S. G. and Baranowski, R. 1994. Indikatorer på jätteträdskontinuitet – svenska förekomster av knäppare som är beroende av grova, levande träd. – Entomol. Tidskrift 115: 81–97.

Økland, B., Bakke, A., Hågvar, S. et al. 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. – Biodiv. Conserv. 5: 75–100.

Perry, G. and Garland, T. 2002. Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny. – Ecology 83: 1870–1885.

Peters, R. H. 1983. The ecological implications of body size. – Cambridge Univ. Press.

Roland, J. and Taylor, P. D. 1997. Insect parasitoid species respond to forest structure at different spatial scales. – Nature 386: 710–713.

Rukke, B. A. and 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.

Safranyik, L. and Moeck, H. A. 1995. Wood borers. – In: Armstrong, J. A. and Ives, W. G. H. (eds), Forest insect pests in Canada. Nat. Resour. Can. Can. For. Serv, pp. 171–177.

Samuelsson, J., Gustafsson, L. and Ingelög, T. 1994. Dying and dead trees – a review of their importance in nature conservation. – SLU Info/Repro, Uppsala, Sweden.

Scheiner, S. M., Cox, S. B., Willig, M. et al. 2000. Species richness, species-area curves and Simpson's paradox. – Evol. Ecol. Res. 2: 791–802.

Schopf, K. M. and Ivany, L. C. 1998. Scaling the ecosystem: a hierarchical view of stasis and change. – In: McKinney, M. L. and Drake, J. A. (eds), Biodiversity dynamics: turnover of populations, taxa, and communities. Columbia Univ. Press.

Schowalter, T. D. 1985. Adaptations of insects to disturbance. – In: Pickett, S. T. A. and White, P. S. (eds), The ecology of natural disturbance and patch dynamics. Academic Press, pp. 235–252.

Shibata, E. 1987. Oviposition schedules, survivorship curves, and mortality factors within trees of two cerambycid beetles (Coleoptera: Cerambycidae), the Japanese pine sawyer, *Monochamus alternatus* Hope, and Sugi bark borer, *Semanotus japonicus* Lacordaire. – Res. Popul. Ecol. 29: 347–367.

Southwood, T. R. E. 1977. Habitat, templet for ecological strategies – presidential address to British Ecological Society, 5 January 1977. – J. Anim. Ecol. 46: 337–365.

Starzomski, B. M. and Bondrup-Nielsen, S. 2002. Analysis of movement and the consequence for metapopulation structure of the forked fungus beetle, *Bolitotherus cornutus* Panzer (Tenebrionidae). – Ecoscience 9: 20–27.

Steffan-Dewenter, I., Munzenberg, U., Burger, C. et al. 2002. Scale-dependent effects of landscape context on three pollinator guilds. – Ecology 83: 1421–1432.

Sutherland, G. D., Harestad, A. S., Price, K. et al. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. – Conserv. Ecol. 4: 16. [online] URL: http://www.consecol.org/vol4/iss1/art16.

Thomas, C. D. and Kunin, W. E. 1999. The spatial structure of populations. – J. Anim. Ecol. 67: 647–657.

Wiens, J. A. and Milne, B. T. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. – Landscape Ecol. 3: 87–96.

Yanega, D. 1996. Field guide to northeastern longhorned beetles (Coleoptera: Cerambycidae). – Illinois Nat. Hist. Surv.

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