# Determining the Spatial Scale of Species' Response to Habitat

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*Species respond to habitat at different spatial scales, yet many studies have considered this response only at relatively small scales. We developed a technique and accompanying software (Focus) that use a focal patch approach to select multiple sets of spatially independent sites. For each independent set, regressions are conducted between the habitat variable and counts of species abundance at different scales to determine the spatial scale at which species respond most strongly to an environmental or habitat variable of interest. We applied the technique to determine the spatial scales at which 12 different species of cerambycid beetles respond to forest cover. The beetles responded at different scales, from 20 to 2000 meters. We expect this technique and the accompanying software to be useful for a wide range of studies, including the analysis of existing data sets to answer questions related to the large-scale response of organisms to their environment.*

*Keywords: spatial scale, habitat interaction, forest cover, Cerambycidae, Focus*

**Ecological attributes such as population abundance** and species richness depend not only on patch characteristics but also on the characteristics of the landscape surrounding the patch, known as patch context (Åberg et al. 1995, Gascon et al. 1999, Saab 1999, Szacki 1999, Fahrig 2001). Focal patch studies are one approach to studying the effects of patch context. In such studies, the data on species abundance or richness are collected in a number of patches or sites. The landscape predictor variables (e.g., habitat amount or fragmentation) are measured in areas that are centered on the patch or site locations (figure 1). Each patch (and its associated landscape) becomes a single data point in the data analysis (Brennan et al. 2002). In this way, researchers can examine the influence of habitat variables, measured at a large scale, on species abundance or richness. In this article, *scale* refers to the area or radius within which habitat predictor variables are measured. Therefore, we are referring only to the extent, and not the grain, of the predictor variable. Focal patch studies have been used to study the effects of road density and the amount of surrounding forest on wetland species richness (Findlay and Houlahan 1997), landscape habitat diversity on alfalfa insect richness (Jonsen and Fahrig 1997), amount of forest on raccoon density (Pedlar et al. 1997), amount of wooded border on alfalfa insect richness and density (Holland and Fahrig 2000), and amount of summer habitat and breeding pond density on leopard frog abundance (Pope et al. 2000).

In addition to these focal patch studies, there are probably hundreds of existing data sets in which researchers have studied the effects of local or patch habitat variables on population abundance or species richness in a number of patches. Can these data sets be reanalyzed to study the effects of landscape context on population abundance or species richness? Given the relative ease of obtaining remotely sensed habitat data, these data sets represent a mine of potential information on the effects of landscape context. The main problem with using these data sets, however, is that in such studies the patches or sites are often rather closely spaced. This can result in data points that are not spatially independent because the landscape areas overlap (figure 1), possibly leading to pseudoreplication. These overlapping sites may constrain the number of data points that can be used for examining the relationship between species abundance or species richness and the measures of landscape context. Nevertheless, because the collection of field data is time-consuming and expensive, it would be beneficial if there were a way to use this data to examine questions related to the larger-scale landscape context. In this article, we present a randomization method and computer program (Focus; www.carleton.ca/lands-ecol/) that permit analysis of effects of landscape context in this situation. Version 2 of this software is available as a free download to researchers and will remain so for the indefinite future.

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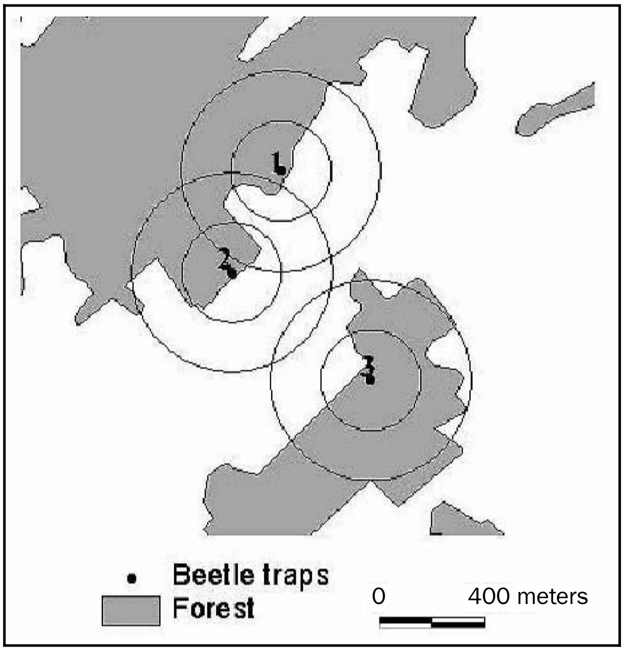


***Figure 1. Example of areas within which forest cover was measured. For clarity, we have only shown two scales around three plots. At the larger scale, the areas within which the predictor variable is measured overlap.***

Multispecies, landscape-scale studies are often conducted at a single spatial scale for all the species studied (e.g., McGarigal and McComb 1995, Trzcinski et al. 1999, Holland and Fahrig 2000). However, it is likely that different species respond to their environments at different scales (e.g., Roland and Taylor 1997) and that these scales are related to the movement ranges of the organisms (Addicott et al. 1987, Wiens and Milne 1989, Wiens et al. 1993, Cale and Hobbs 1994, Vos et al. 2001, Dungan et al. 2002). Often little or nothing is known about the scales at which a species responds to structural characteristics of its environment, and this uncertainty may greatly limit the effectiveness of study designs. One method of estimating the appropriate scale is to model the relationship at a number of scales and determine which scale fits the model best (e.g., Findlay and Houlahan 1997, Elliott et al. 1998, Pope et al. 2000, Savignac et al. 2000). We applied this approach to test the hypothesis that different species of deadwood-boring beetles in the family Cerambycidae (Coleoptera) respond to their habitat at different scales. We refer to the scale at which different species respond most strongly to the amount of habitat as the characteristic scale of response to habitat amount. We use the word *characteristic* to imply that this scale may be an emergent property of a species, determined by the unique relationship between the species and its habitat (Mitchell et al. 2001).

## The Focus program

Three matrices provide the basic inputs to the Focus computer program: a matrix of response variable measure (e.g., species abundance or richness) at each site, a matrix of between-site geometric distances, and a matrix of the predictor variable measurements at various increasing scales around the sites. At each spatial scale, Focus conducts multiple simple linear regressions of the ecological response on the landscape predictor. Each regression at each scale involves a different set of independent and randomly chosen data points.

The program selects spatially independent sites for the regressions in six steps: (1) It randomly selects a site $n_i$ from the entire set of $N$ sites. (2) It selects a second site $n_i$ that satisfies the constraint of spatial independence, $C$. For the case considered here, $C$ is a measure of geometric distance where $C >$ 2 (radius). In other words, areas within which the predictor variable is measured may not overlap (figure 1). (3) It continues to randomly select sites until the constraint $C$ can no longer be met, or until a predetermined number of sites are selected. (4) It fits a regression line to the selected points. In this study, the abundance of each beetle species was regressed separately on the proportion of forest cover around the corresponding sampling location. The following regression statistics are recorded: $R^2$ (coefficient of determination), $r$ (Pearson correlation coefficient), $MSE$ (mean squared error), and $N_p$ (number of points in each regression), among others. (5) It repeats steps 1 through 4 for $X$ different sets of spatially independent sites to develop a distribution of regression model fit, effect size, or both. The sampling is done with replacement between sets. However, the constraint $C$ makes it impossible to sample with replacement within a given set, since it precludes the same point being chosen more than once. The selection of points going into each set is therefore different from that of a bootstrap technique. (6) Finally, steps 1 through 5 are repeated for each spatial scale. The output of the analysis is the mean and standard error (or 95 percent confidence interval) of the regression statistics ($R^2$, $r$, $MSE$, $N_p$) at each scale. The scale of response can then be determined by examining a plot of model fit against increasing spatial scale.

In principle, the constraint $C$ and the pattern of site selection (which in this case is random) could take many different forms. For example, instead of a geometric distance, the constraint $C$ could be defined in such a way that sites must not be significantly spatially autocorrelated to be included in a final set for one of the regressions. The pattern of site selection could also follow a grid-based or stratified random design. We expect that researchers will adapt the program to suit their particular needs and applications.

The procedure has at least three advantages over random selection of a single set of independent sites: (1) Because it includes several regressions, site selection is not affected by the particular site that is selected first; (2) sites at different scales are not nested, because the subsets in any regression at a smaller scale may be quite different from the subsets used at larger scales; and (3) it maximizes the data available. Although the sample size of each individual regression may be much smaller at larger spatial scales, the randomization method allows for multiple estimates of the regression (using different sets of data points), thus increasing the power of the analysis.

The Focus program also allows the user to test two assumptions that apply to the overall process of resampling the data to find the scale at which the model has the best fit: (1) functional stability at different scales and (2) representative sampling. A test for functional stability is necessary because Focus uses linear regression at all scales, whereas the relationship between the organism and the habitat variable may be nonlinear at some scales. Nonlinear relationships would cause the measures of model fit to decrease at these scales simply because a linear model is less able to represent the data at these scales, not because the actual relationship is weaker. The Focus program tests for such a nonlinear trend by using forward, stepwise multiple regression to attempt to fit second- and third-order polynomial terms (of the landscape predictor) to the model. The models are considered to be significantly improved by the addition of these higher-order terms if the fit is improved at the $\alpha = 0.05$ level. A test to ensure representative sampling is necessary because, if the number of regressions chosen is too small, the resulting distribution of regression statistics may not adequately represent the entire data set. If the variability in the data is not adequately represented by the sets of independent points that have been selected, then repeating the analysis could lead to very different measures of model fit reported at different scales. The representative sampling test verifies that the number of iterations used is sufficient by rerunning the analysis (including the data-point selection process) 10 times at the smallest scale and determining the mean and variance of the resulting *MSE* distribution as well as the mean and standard error of the regression coefficient. If these values are relatively constant across the 10 analyses, then the number of iterations used is sufficient and the results are representative of the data set. This assumption is tested at the smallest scale because, for many data sets, it is at this scale that the number of possible ways to sample the data is greatest. For the hypothetical set of points in figure 2, for example, at the smaller scale shown (figure 2h), there are 56 ways that five of the points could be chosen. At the larger scale, there are only 6 possible independent sets of points (figure 2b through 2g).

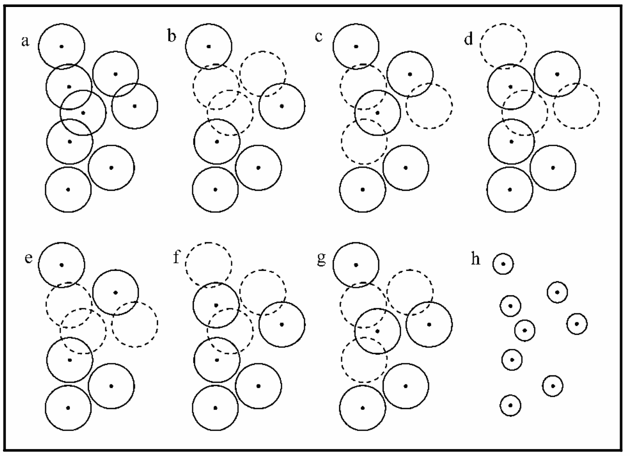


***Figure 2. Possible sets of spatially independent points. (a) Spatial locations of eight hypothetical points. (b through g) All possible ways to select five spatially independent points to include in a regression. Dashed circles indicate overlapping areas that are not included because of a lack of spatial independence. (h) At a smaller scale, the areas where the predictor variable is measured are independent. At this scale there are $_8C_5$ (combinations, "eight choose five") or 56 ways to select five independent points.***

## Characteristic scales of wood-boring beetle response to habitat amount

Most long-horned beetles have larvae that develop within the wood of living or dead trees or shrubs. Species with larvae that develop within dead woody material are much less host-specific than species whose larvae develop within living or very recently dead trees (Linsley 1954), probably because the trees' defensive chemicals are not as important in deadwood (Kletecka 1996). In a study that considered three different scales, Økland and colleagues (1996) found that long-horned beetles responded to environmental habitat variables within 1 square kilometer ($km^2$) of trapping sites. Schiegg (2000) found that saproxylic beetles (those that are dependent on deadwood) responded to the spatial connectedness of deadwood pieces within 150 meters (m) in a study that considered spatial scales ranging from 50 to 200 m in 50-m increments.

We used the Focus program to determine the scales at which different species of deadwood-boring beetles respond to the amount of forest cover in the landscape. The beetles were sampled as part of a study on the response of wood-boring beetles to ice storm damage in the area surrounding Ottawa, Canada. Beetles were trapped across an area measuring approximately 80 km by 40 km, with the trapping locations clustered in 19 1-$km^2$ areas with 10 sampling points each (figure 3). This means that the number of spatially independent points decreased as the radius of the area under consideration increased up to about 0.5 km (figure 4). At each trapping location, a Lindgren multiple-funnel trap was baited with ethanol and chipped wood. Traps were checked monthly, and all long-horned beetles were identified to species in the lab using Yanega's field guide to Cerambycidae (1996). We used only species whose larvae develop in deadwood. We also used only species that do not appear to show a preference for any particular tree species (Linsley 1962, 1963, 1964, Linsley and Chemsak 1972, 1976, Yanega 1996) to ensure that the proportion of forest would be a fair approximation of the proportion of breeding habitat in the landscape. We refer to these species as *polyphagous.* The response variable for each species was the number of individuals caught at each site, summed over 2 years. We only used species that were caught in at least five of the sampling locations during the 2 years.

To detect the characteristic scale at which individual beetle species respond to forest habitat, we used Focus to estimate the fit of simple linear regressions of beetle abundance on the proportion of forest in the landscapes around the beetle sampling sites. The proportion of forest was measured at multiple scales: radii of 20 to 200 m in 20-m increments, 400 to 2000 m in 200-m increments, and 3000 to 7000 m in 1000-m increments. We used digital topographical maps (National Capital Commission 1999) in ArcView to extract forest cover measures within the 24 different-sized circular areas near each site. At each scale, the regressions were repeated 200 times to generate the mean and standard error of the regression statistics. The choice of characteristic scale was made by examining a plot of a measure of model fit against the various scales at which forest proportion was measured.

We chose to conduct our analyses using the same number of data points for each regression at each scale, because the purpose of our analysis was to compare the results at different scales. This causes a tradeoff between the maximum scale considered and the number of data points used in each regression. Including all scales up to 7 km would have limited the number of points in each regression to five. We found no indication in the literature that saproxylic beetles would respond to habitat at scales much larger than 1 km. However, none of the literature focused on the exact species we used in this study, so we decided to include scales up to 2 km. Using a maximum spatial scale of 2 km allowed us to increase the number of points in each regression to 16 (figure 4).

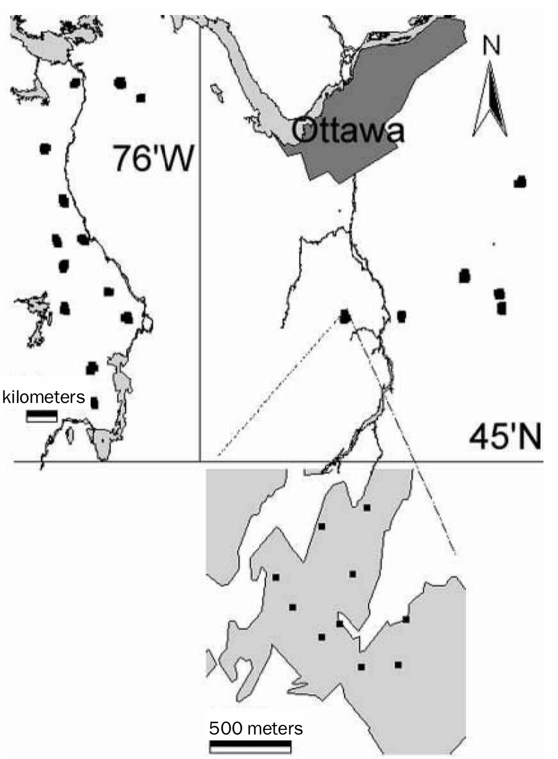


***Figure 3. Locations of beetle sampling sites in the Ottawa, Ontario, region of Canada. Each of the 19 sampling areas (top panel) was 1 square kilometer and had 10 randomly located trapping sites (bottom panel).***

To evaluate the relationship between beetle abundance and proportion of forest cover, we used the correlation coefficient (*r*) as our measure of model fit, because for some species there was a range of scales over which this relationship was negative. The other possible measures of model fit ($R^2$, *MSE*) do not differentiate between positive and negative relationships. Using $R^2$ or *MSE* is also problematic as a measure of the strength of the regression, because we are averaging over many regressions. If the regressions at a given scale show both positive and negative relationships, as is likely in the case of a very weak relationship, the mean of measures such as $R^2$ and *MSE* will be artificially high. This occurs because the values of these statistics from individual regressions are always positive, even if some of the regressions result in negative relationships.

For each species, we examined the plot of *r* against spatial scale to determine the characteristic scale of response to forest cover. The scale corresponding to the best model fit was the characteristic scale of response to habitat amount.

### Results of spatial scale analysis

We caught 13 species of polyphagous long-horned beetles associated with deadwood in at least five of the traps. Voucher specimens of all species were placed in the Carleton University entomological collection. The scales at which different species respond to forest cover varied from 20 to 2000 m (table 1). Figure 5 shows an example of the distribution of correlation coefficients from the regressions at different scales for one species, *Urgleptes signatus*. This figure shows that the distributions of the *r* values extended over both positive and negative values within a scale, justifying the use of *r*, rather than $R^2$, as a measure of model fit for these species.

*Hyperplatys aspersa* had *r* values that were negative throughout the range of scales considered, with the value at 180 m

***Table 1. Characteristic scales of response to forest cover for long-horned beetles, as determined by maximum linear model fit using Focus software. These values reflect the spatial scale at which the species abundance responded most strongly to the proportion of forest cover as determined by the maximum value of* r.**

| Species | Characteristic scale of response (radius in meters) |
|---|---|
| *Bellamira scalaris* (Say) | 1000 |
| *Evodinus m. monticola* (Rand.) | 2000 |
| *Gaurotes cyanipennis* (Say) | 160 |
| *Liopinus alpha* (Say) | 20 |
| *Microgoes oculatus* (LeC.) | 60 |
| *Stictoleptura c. canadensis* (Oliv.) | 1600 |
| *Strangalepta abbreviata* (Germ.) | 400 |
| *Strangalia luteicornis* (F.) | 1800 |
| *Trachysida mutabilis* (Newm.) | 1200 |
| *Trigonarthris minnesotana* (Csy.) | 200 |
| *Urgleptes signatus* (LeC.) | 180 |
| *Urographis fasciatus* (DeG.) | 180 |

approaching a zero correlation. This species did not appear to respond to forest cover in the same way as the other species and so was not included in figure 6 and table 1. Several other species had negative mean *r* values across some range of scales, but the mean *r* value at the scale of maximum model fit was positive for all species other than *H. aspersa*.

### Getting the spatial scale right

It is important to use an appropriate spatial scale when considering how species respond to environmental variables. Figure 6 shows that the strength of the relationship between species abundance and proportion of forest cover varies at different spatial scales. Both the likelihood of researchers detecting this relationship and the importance ascribed to it will vary with the relationship's strength. Therefore, it is important to get the scale right when conducting such studies. In our study, different species of beetles from the family Cerambycidae responded to forest habitat at different spatial scales, showing that the scale appropriate for such research may vary even within a single family of beetles.

One interesting result is that some species showed more than one positive peak in model fit. It is possible that habitat variables are important at more than one scale for different reasons (Kotliar and Wiens 1990, Jonsen and Taylor 2000, Nathan 2001). For example, Kinnunen and colleagues (2001) and Rukke and Midtgaard (1998) suggest that some habitat variable may cause beetles to select habitat at a fine scale, while larger-scale habitat availability may limit the areas within which a beetle species can occur.

The maximum correlation coefficient for *H. aspersa* was very close to zero, and the correlation coefficient values were negative across all scales. The abundance of this species may depend more on resources found outside the forest than on the forest cover itself. If this is the case, then the scale with the most negative peak may be characteristic of this relationship. The reason this species does not appear to respond positively to forest cover at all may be that it requires relatively open habitat. Many species of long-horned beetles are thermophilic, even in the larval stage (Barbalat 1998).

It is possible for the *r* values of individual regressions to range over both positive and negative values within a scale (figure 5). This shows the importance of using all the data to determine the nature of the relationship between species abundance and the predictor variable, as the Focus program does. The constraint of spatial independence results in relatively few points being included in each regression. Relying on a single regression, using a single set of independent points, would not result in reproducible results. Using only a single regression could also result in incorrect conclusions about the direction of the relationship between abundance and forest cover. The repeated regressions on sets of inde-

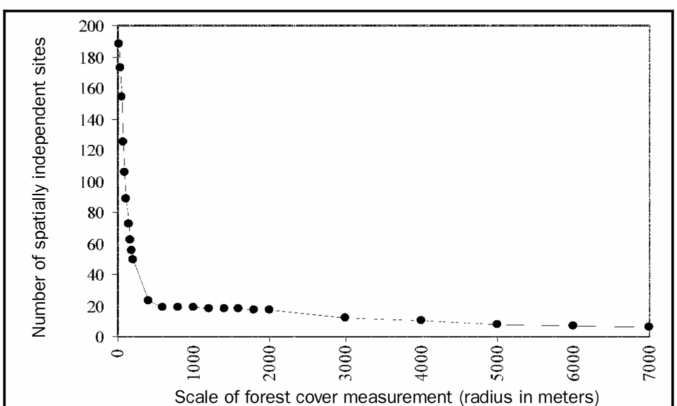


***Figure 4. Relationship between the spatial scale (radius within which forest cover was measured, in meters) and the average number of points that could be included in the individual regressions while maintaining nonoverlapping predictor variable areas (spatial independence).***

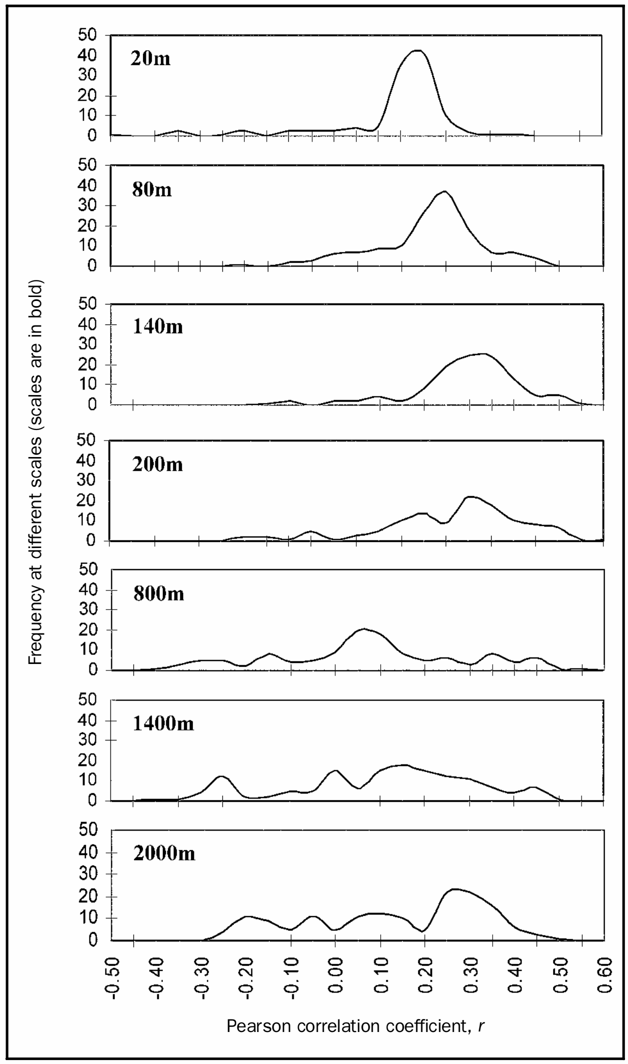


***Figure 5. Example of the distribution of Pearson correlation coefficients from regressions between abundance of a species and proportion of forest cover at different scales. Plots show that both positive and negative relationships occur at the same scale for this species,* Urgleptes signatus *(LeC.). For clarity, only every third scale (radius in meters) considered is shown. The characteristic scale of response was 180 meters (see table 1).***

pendent points ensure that more information contained in the data is used to determine the relationship between abundance and forest cover.

Some of the beetle species were absent from the samples taken at many sites. This resulted in some regressions being left out of the analyses because all the data points selected for those regressions had no individuals. Therefore, the estimates of mean model fit for the less commonly caught species often had large standard errors, because the number of regressions used to estimate the fit was small. It would be possible to use Focus to resample the pool of data points for regressions that have this problem, so that the number of regressions would be constant at all scales, but this could lead to another problem: If there were relatively few points where individuals were found, it is likely that the same set of points would be regressed repeatedly using this alternative. This would result in a deceptively low standard error being reported. Both of these problems will be addressed in future versions of the software.

The sampling points in our example came from a large area, but because our study included the effects of habitat at scales of several kilometers, the number of spatially independent data points was small. However, with 190 sampling locations, we were able to use 200 regressions per scale and adequately represent the data without oversampling. With very small data sets, especially if the sampling points are close together, the issue of oversampling can be much more restrictive. When using the Focus program, researchers will have to decide on the number of regressions to use at each spatial scale. The actual number of iterations that can be used has lower and upper limits determined, respectively, by the assumption of representative sampling and by the criterion that no exact duplicate sets of points be used within a given scale.

The program we describe here should increase the use of existing data sets to answer larger-scale questions, as long as the locations where the response variables were measured are known. We did a survey of the literature to see how many studies had data appropriate for this application, using *Cambridge Scientific Abstracts* to search within the "Ecology Abstracts" subfile of "Biological Sciences." Our search criteria were that the listings not contain the term *model* anywhere, but that they contain the term *landscape* or *patch*. This search yielded 6985 studies. We picked a random sample of 40 abstracts from these studies to check for the proportion of studies producing data sets that would lend themselves to larger-scale questions using the Focus program. To be considered appropriate, the studies had to produce numerical response data measured at multiple locations, and these locations had to be spread over an extent large enough that multiple independent data points would exist when the predictor variables were measured beyond the patch level. In other words, the sampling locations had to extend over more than one patch. Twenty of these 40 studies created data sets that met our criteria. This leads us to estimate that there are about 3500 data sets in the ecological literature that would lend themselves to answering large-scale questions of characteristic scale of response of organisms to their environment using the Focus program.

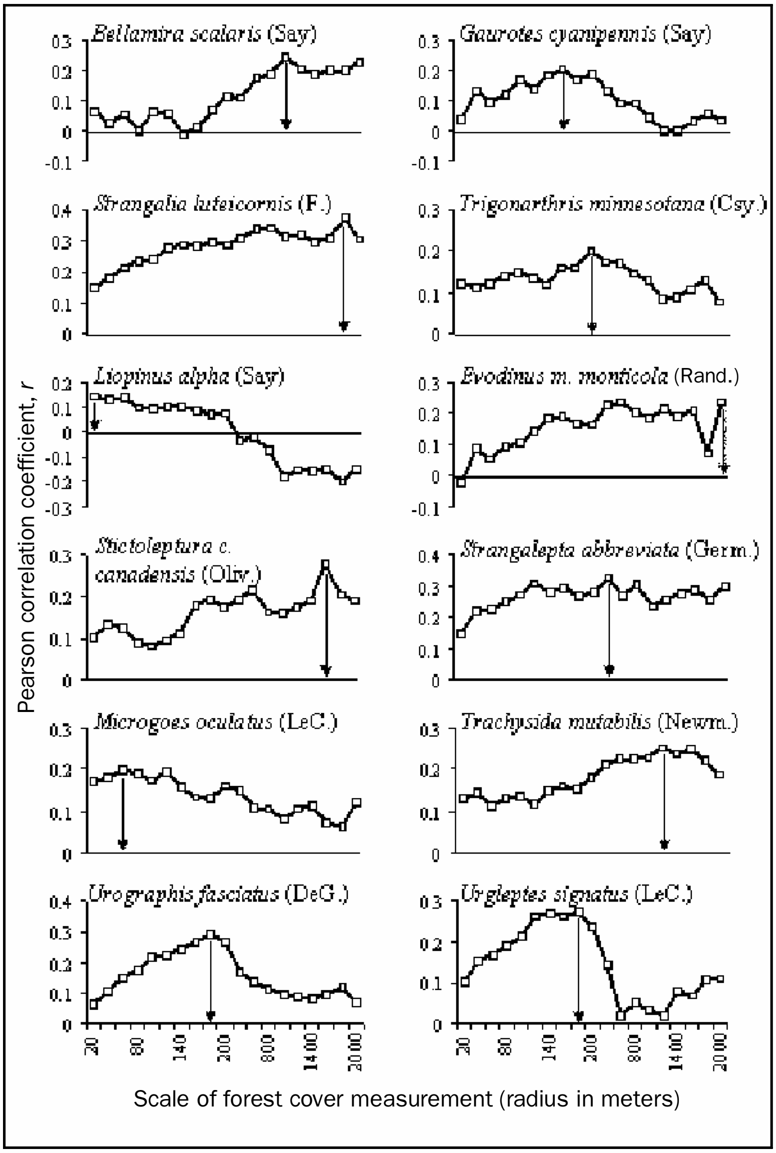


***Figure 6. Focus program output showing model fit (Pearson correlation coefficient) between forest cover and beetle abundance for the 12 polyphagous species. Characteristic scale of response to forest habitat (maximum model fit) is indicated (drop-down arrow). Note change in scale interval at 200 meters from 20- to 200-meter increments.***

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## References cited

Åberg J, Jansson G, Swenson JE, Angelstam P. 1995. The effect of matrix on the occurrence of hazel grouse *(Bonasa bonasia)* in isolated habitat fragments. Oecologia 103: 235–269.

Addicott JF, Aho JM, Antolin MF, Padilla DK, Richardson JS, Soluk DA. 1987. Ecological neighborhoods: Scaling environmental patterns. Oikos 49: 340–346.

Barbalat S. 1998. Importance of forest structures on four beetle families (Col.: Buprestidae, Cerambycidae, Lucanidae and phytophagous Scarabaeidae) in the Areuse Gorges (Neuchâtel, Switzerland). Revue Suisse de Zoologie 105: 569–580.

Brennan J, Bender DJ, Conteras TA, Fahrig L. 2002. Focal patch landscape studies for wildlife management: Optimizing sampling effort across scales. Pages 68–91 in Liu J, Taylor WW, eds. Integrating Landscape Ecology into Natural Resource Management. Cambridge (United Kingdom): Cambridge University Press.

Cale PG, Hobbs RJ. 1994. Landscape heterogeneity indices: Problems of scale and applicability, with particular reference to animal habitat description. Pacific Conservation Biology 1: 183–193.

Dungan JL, Perry JN, Dale MRT, Legendre P, Citron-Pousty S, Fortin M-J, Jakomulska A, Miriti M, Rosenberg MS. 2002. A balanced view of scale in spatial statistical analysis. Ecography 25: 626–640.

Elliott NC, Kieckhefer RW, Lee J-H, French BW. 1998. Influence of within-field and landscape factors on aphid predator populations in wheat. Landscape Ecology 14: 239–252.

Fahrig L. 2001. How much habitat is enough? Biological Conservation 100: 65–74.

Findlay CS, Houlahan J. 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. Conservation Biology 11: 1000–1009.

Gascon C, Lovejoy TE, Bierregaard RO, Malcolm JR, Stouffer PC, Vasconcelos HL, Laurance WF, Zimmerman B, Tocher M, Borges S. 1999. Matrix habitat and species richness in tropical forest remnants. Biological Conservation 91: 223–229.

Holland JD, Fahrig L. 2000. Effect of woody borders on insect density and diversity in crop fields: A landscape-scale analysis. Agriculture, Ecosystems and Environment 78: 115–122.

Jonsen I, Fahrig L. 1997. Response of generalist and specialist insect herbivores to landscape spatial structure. Landscape Ecology 12: 185–197.

Jonsen I, Taylor PD. 2000. Calopteryx damselfly dispersions arising from multiscale responses to landscape structure. Conservation Ecology 4: 57–76.

Kinnunen H, Tiainen J, 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.

Kotliar NB, Wiens JA. 1990. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. Oikos 59: 253–260.

Linsley EG. 1954. Ecology of Cerambycidae. Annual Review of Entomology 4: 99–138.

———. 1962. Taxonomy and Classification of the Subfamily Cerambycinae, Tribes Opsimini through Megaderini. Part III of The Cerambycidae of North America. Berkeley: University of California Press.

———. 1963. Taxonomy and Classification of the Subfamily Cerambycinae, Elaphidionini through Rhinotragini. Part IV of The Cerambycidae of North America. Berkeley: University of California Press.

———. 1964. Taxonomy and Classification of the Subfamily Cerambycinae, Tribes Callichromini through Ancylocerini. Part V of The Cerambycidae of North America. Berkeley: University of California Press.

Linsley EG, Chemsak JA. 1972. Taxonomy and Classification of the Subfamily Lepturinae. Part VI, no. 1, of The Cerambycidae of North America. Berkeley: University of California Press.

———. 1976. Taxonomy and Classification of the Subfamily Lepturinae. Part VI, no. 2, of The Cerambycidae of North America. Los Angeles: University of California Press.

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

Mitchell MS, Lancia RA, Gerwin JA. 2001. Using landscape-level data to predict the distribution of birds on a managed forest: Effects of scale. Ecological Applications 11: 1692–1708.

Nathan R. 2001. The challenges of studying dispersal. Trends in Ecology and Evolution 16: 481–483.

National Capital Commission. 1999. 1:25,000 scale topographic mapping [computer file]. Ottawa (Canada): National Capital Commission.

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

Pedlar JH, Fahrig L, Merriam HG. 1997. Raccoon habitat use at two spatial scales. Journal of Wildlife Management 61: 102–112.

Pope SE, Fahrig L, Merriam HG. 2000. Landscape complementation and metapopulation effects on leopard frog populations. Ecology 81: 2498–2508.

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

Rukke BA, 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.

Saab V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: A hierarchical analysis. Ecological Applications 9: 135–151.

Savignac C, Desrochers A, Huot J. 2000. Habitat use by pileated woodpeckers at two spatial scales in eastern Canada. Canadian Journal of Zoology 78: 219–225.

Schiegg K. 2000. Effects of dead wood volume and connectivity on saproxylic insect species diversity. Ecoscience 7: 290–298.

Szacki J. 1999. Spatially structured populations: How much do they match the classic metapopulation concept? Landscape Ecology 14: 369–379.

Trzcinski MK, Fahrig L, Merriam HG. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecological Applications 9: 586–593.

Vos CC, Verboom J, Opdam PFM, Ter Braak CJF. 2001. Toward ecologically scaled landscape indices. American Naturalist 157: 24–41.

Wiens JA, Milne BT. 1989. Scaling of "landscapes" in landscape ecology, or, landscape ecology from a beetle's perspective. Landscape Ecology 3: 87–96.

Wiens JA, Crist TO, Milne BT. 1993. On quantifying insect movements. Environmental Entomology 22: 709–715.

Yanega D. 1996. Field Guide to Northeastern Longhorned Beetles (Coleoptera: Cerambycidae). Illinois Natural History Survey Manual 6. Champaign (IL): Illinois Natural History Survey.