

THE EFFECT OF SPATIAL SCALE ON MEASURING
SPATIAL ISOLATION AND PREDICTING THE
INCIDENCE OF A BEETLE PARASITE AND ITS
FUNGAL HOST IN CONTINUOUS AND
FRAGMENTED LANDSCAPES

by

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Abstract

Spatial scale is a central concept in ecology, but is rarely treated explicitly. Here I report on two studies that investigate the effect of scale in a beetle parasite - polypore fungus system. In the first study, the effect of spatial isolation on beetle incidence was measured at three scales in 2 forest types (continuous and fragmented), while controlling for confounding variables. The effect of isolation was investigated using mean nearest-neighbour distances of up to 5 patches. Surprisingly, a negative effect of spatial isolation was evident at all three scales: between fungal carps on a log (mean \pm S.D. of isolation values: 0.20 ± 0.24 metres between carp clusters in a forest (11.19 ± 7.22 meters) and between woodlots (453.5 ± 330 metres). However, the effect of spatial isolation was stronger at the largest scale than at the smallest scale. There was also a small compensatory effect of patch size on isolation, but no effect of forest type or patch density on isolation. I also compared the explanatory power of 10 different isolation measures.

In the second study I built a series of predictive models of beetle and fungus incidence at three scales in two landscapes using logistic regression. These models varied in both the grain of the response and the extents of the predictor variables. The increase in predictive power (as measured by an R^2 -like parameter) with grain size was confounded by the effect of sample size. Large scale models had 1/50 the sample size of small scale models, and I demonstrated how R^2_L is biased for small sample sizes. Therefore, I compared 20 models from subsamples of size 50 from each scale and found that although predictability did differ with scale, there was no consistent increase in predictability with scale, despite a steady decrease in the variance of the response with scale. Variables measured at the same scale as the response were the best predictors of that response. In addition, habitat fragmentation appeared to negatively affect the fungus and in some cases, positively affect the beetle. This result was confirmed by a comparison of patch occupancy rates at two scales within fragmented and continuous forests.

Keywords: prediction, scale, spatial isolation, logistic regression, forest fragmentation, deadwood, conservation, *Bolitotherus*, *Fomes*.

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General Introduction

The concepts of space and spatial scale are central to ecological research as organisms carry out life functions in a spatially heterogeneous world at different scales. Although ecologists have a long history of interest in spatial heterogeneity (see Turner 1989a for a brief review), two recent events have focused attention on the importance of this heterogeneity: the formalization of landscape ecology as a distinct discipline (Forman & Godron 1986, Naveh & Lieberman 1994) and concern over the fragmentation of endemic habitats (Saunders *et al.* 1991). Landscape ecologists are concerned with the generation, maintenance and impact of spatial heterogeneity in biotic and abiotic systems (Turner 1989). Landscape ecologists are interested not only in the effect of processes on spatial patterns, but also in the effect of spatial patterns on processes (Turner 1989). For example, how does the spatial pattern of habitat patches influence the process of migration (Kuussaari *et al.* 1996)? Although landscape ecology was initially concerned with spatial heterogeneity at large, human-perceived scales, it is recognized that spatial heterogeneity is important at all scales (Wiens & Milne 1989, Wiens *et al.* 1993). Landscape ecology also attempts to bridge gaps between different disciplines operating at different scales. For example, how does movement behaviour at the scale of the individual affect the dynamics at the scale of the population (Johnson *et al.* 1992)?

The distribution of resources in space is thought to play an important role in many aspects of ecology (e.g. Huffaker 1958, Addicot *et al.* 1987, Blower and Roughgarden 1989, Kruess & Tschardtke 1994, Kareiva and Wennergren 1995). Theoretical interest in spatial patterning has spawned a number of spatially explicit population models for both

plants and animals (Kareiva 1990, Wallinga 1995). The metapopulation model is the most popular of the spatial models and extends the scale of interest from the local population to a regional population composed of interacting local populations (Hanski and Gilpin 1991). The premise of the metapopulation is that regional population persistence is ensured by a balance in the extinction and recolonization rates of local populations in habitat patches. Although the original formulation was not spatially explicit (Levins 1970), subsequent refinements have included the spatial context (e.g. Hansson 1991, Hanski *et al.* 1994).

The applied interest in spatial dynamics stems from concern over habitat fragmentation at large scales. Habitat fragmentation implies both loss of habitat and increased isolation between remaining fragments, yet, as we have seen, organisms are already adapted to environments that are patchy at all scales (Wiens 1989, Lord & Norton 1990). So why is habitat fragmentation a concern in conservation biology? The answer to this question has 3 components: the scale, the speed and the nature of the disturbance. The scale of the disturbance plays a role, as organisms are confined (either physiologically or behaviourally) by the maximum distances they can travel between patches. The speed of the disturbance is also important, as organisms often do not have enough time to adjust to the new spatial structure. The nature of the disturbance presents a challenge, as the intervening matrix between habitat patches is often changed as well, often resulting in a decline in connectivity between suitable habitat patches (e.g. Fahrig & Merriam 1985). An organism's sensitivity to habitat fragmentation will thus be determined by its response to these three factors.

Spatial Scale

An important aspect in the study of spatial dynamics is the choice of spatial scale. Most ecological patterns and processes are scale-dependent (May 1994, Wiens & Milne 1989); thus spatial scale influences the choice of questions posed, methodologies used and the type of results generated (Dayton and Tegner 1984). Levin (1992) has argued that scale (temporal or spatial) is the “fundamental conceptual problem in ecology, if not in all science”. Explicit recognition of scale can be a useful tool for understanding processes (May 1994) whereas ignoring scale can lead to erroneous conclusions (Wiens 1989, Thomas & Abery 1995, Debouzie *et al.* 1996, Ray & Hastings 1996). In fact, a failure to recognize scale-dependency has led to avoidable debates about the importance of various processes in explaining observed patterns in both applied and theoretical ecology (Murphy 1989, Wiens 1989). For example, the controversy over reserve design, whether several small or a single large reserve is best, is resolved in part by recognizing that larger scale, regional species diversity is best served by both large and small reserves (Murphy 1989). Recognition of scale is also critical to conservation efforts (Lewis *et al.* 1996) since environmental problems require combining information and models from different spatial scales (Turner *et al.* 1989).

Spatial scale has two elements: grain (or resolution size) and extent (Wiens & Milne 1989). A useful analogy is that of a sieve, where the grain represents the mesh size, and the extent represents the surface area of the sieve. However, in referring to spatial scale, authors rarely specify whether they are referring to grain or extent (Wiens 1989). There is general recognition that the behaviour of a system is constrained by

processes and patterns that occur both at smaller and larger scales (see Turner *et al.* 1989, Wiens 1989). For example, the rate of evapotranspiration at the scale of a leaf is bounded at a larger scale by the total amount of radiation energy available, and at a smaller scale by stomatal processes (Turner *et al.* 1989).

In ecological research, the choice of spatial scale studied is dictated by the research questions and by the organism studied (Wiens 1986). But how does one determine the relevant scale for an organism? The relevant grain size and spatial extent is likely to vary with an organism's physiological and behavioural state. Different behaviours are likely to require an organism to perceive different spatial grains. For example, a chipmunk searching for a food patch will likely be perceiving a different grain size than a chipmunk in a food patch foraging for individual food items. Moreover, any stimulus, internal or external, that elicits movement is likely to change the relevant spatial extent. For example, a lizard thermoregulating on a rock is likely to consider a larger spatial extent when a predator is sensed in the distance and the lizard must seek protective cover. Thus, it is difficult to define the exact spatial grain and extent that an organism is perceiving at any given time. Instead, researchers are often forced to adopt a limited set of organism-specific scales, focusing on a set of generalized processes (e.g. feeding, mating, dispersal). In many situations, the set of relevant scales can only be determined by first examining the dynamics of a system at a number of arbitrary scales (Levin 1992). This difficulty highlights the importance of multi-scale studies. Multi-scale studies allow for the elucidation of scale dependent processes and help determine what the relevant

scales are for a particular organism or process. These studies are rare in ecology, despite recognition of their usefulness (Wiens 1989, Doak *et al.* 1992).

Study system: fungivorous beetles living on deadwood-decomposing fungi

The research system used for the following studies provides an excellent opportunity for taking a multi-scale approach. For the forked fungus beetle (*Bolitotherus cornutus* Panzer) and its deadwood-decomposing fungal host (*Fomes fomentarius* (L.:Fr.) Fr.), patches can be defined at several scales. For the beetle, there are three obvious (to humans) ways of defining patches: the individual fungal sporocarp, the clump of carps on a dead log, and the forest fragment. Although deadwood, and hence fungi, exhibits a patchy spatial distribution (Hanski 1986, Harmon & Sexton 1996), neither the beetle nor the fungus can be considered a metapopulation in the strict sense. Unlike classical metapopulations (see Hanski 1995), most local extinctions in this system are deterministic, as they are caused by habitat patch depletion (see Harrison 1991). Depleted patches cannot be recolonized, and thus the total number of available patches changes every year. Nonetheless, spatial structure is likely to be critical to the regional persistence of these species as they must continually disperse to colonize new habitat patches.

In this study, I examined the role of spatial scale in two separate research areas: the effect of patch isolation on beetle incidence and predicting the incidence of the beetle and the fungus in continuous and fragmented forests. Isolation has been extensively investigated in the context of both island biogeography and metapopulation theory (e.g. Lomolino 1986, Hanski & Gilpin 1991). Although the scale-dependency of isolation is

often discussed, no research has attempted to describe the effect of scale on isolation. Predictive models are used extensively, particularly in applied ecology. The scale-dependency of prediction is well known (Turner *et al.* 1989), but scale is rarely treated explicitly. By taking a multi-scale perspective I hope to shed new light on and increase our understanding of both an important ecological process - spatial isolation, and a useful methodology in ecology - predictive modelling.

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CHAPTER 1. A multiscale study of spatial isolation effects on a fungivorous forest beetle in fragmented and continuous forests.

Abstract

The effects of spatial isolation are scale-dependent, but no multi-scale studies of isolation exist. I investigated the effect of spatial isolation on the incidence of a fungivorous forest beetle in continuous and fragmented forests at three spatial scales, while controlling for confounding variables, such as patch size and quality. Isolation was measured using nearest-neighbour distances and I compared the usefulness of measuring multiple patches and considering only occupied patches. I also tested to see if the forest configuration type (fragmented vs. continuous), patch size, or patch density influenced the effect of isolation. An effect of spatial isolation on beetle incidence was evident at all three scales: between fungal carps on a log (mean \pm S.D. of isolation values: 0.20 ± 0.24 metres), between carp clusters in a forest (11.19 ± 7.22 meters) and between woodlots (453.5 ± 330 metres) in an agricultural matrix. The magnitude of the isolation effect was stronger at the largest scale than at the smallest scale. However, isolation was most prevalent at the intermediate scale, but was modeled as a quadratic and could not be directly compared to other scales, where isolation was modeled linearly. The effect of isolation was not influenced by forest configuration type or by patch density, but there was a marginal compensatory effect of patch size on isolation. Isolation measures incorporating only occupied patches were not generally better predictors than isolation measures incorporating all patches. Little information would have been lost by using only the distance to the closest patch to measure isolation effects.

Keywords: scale, logistic regression, isolation, forest fragmentation, deadwood, conservation, *Bolitotherus*, *Fomes*.

Introduction

Increasing spatial isolation of remnant habitat patches is one of the primary consequences of habitat fragmentation (Saunders *et al.* 1991). Isolation can lower the recolonization rate of empty habitat patches and may also increase the probability of local patch extinctions (Brown & Kodric-Brown 1977). An understanding of spatial isolation is thus critical for attempts to mitigate deleterious effects of habitat fragmentation. The effect of isolation has been repeatedly investigated in the context of island biogeography (MacArthur and Wilson 1967) and spatially structured populations (Levins 1970, Hanski 1991) in various organisms, including birds (e.g. Bellamy *et al.* 1996a), small mammals (e.g. van Apeldoorn *et al.* 1994), amphibians (e.g. Vos & Stumpel 1995), plants (e.g. Ouborg 1993), and insects (e.g. Matter 1996).

Although the majority of isolation studies have found a negative effect of spatial isolation on incidence, abundance or richness, a number of studies have failed to detect consistent, if any, effects of isolation, including all studies where isolation effects were measured on a species by species basis (e.g. Lynch & Whigham 1984, Opdam *et al.* 1985, Dzwonko & Loster 1988, Peltonen & Hanski 1991, Usher *et al.* 1992, Hinsley *et al.* 1995, Bellamy *et al.* 1996b). A few studies have even demonstrated a positive effect of isolation (Schroeder 1987, Bellamy *et al.* 1996b). Moreover, when an effect of isolation is present, it rarely explains much of the variance in the response variable (Ouborg 1993). The lack of a clear isolation effect is likely a result of ignoring spatial scale, as isolation is strongly dependent on the distance between patches relative to the vagility of a species (Peltonen & Hanski 1991, Celada *et al.* 1994, Dunning *et al.* 1995, Bellamy *et al.* 1996b).

Despite the obvious importance of scale in measuring effects of isolation, no study has explicitly considered the role of scale, or taken a multi-scale perspective. The absence of a thorough treatment of scale when studying isolation may be responsible for the lack of a consistent and strong isolation effect in the literature.

An alternative explanation for the lack of a clear isolation effect in the literature is the diversity of measures used to estimate isolation. Many studies use the distance to the closest “mainland” patch, and ignore the effects of other nearby patches (e.g. Nilsson & Nilsson 1978). There is also variation in whether isolation is based on distances to any patch (e.g. Opdam *et al.* 1985) or only distances to occupied patches (e.g. Vizyova 1986).

It has been hypothesized that patch size may compensate for patch isolation in both island biogeography and metapopulation theory (Lomolino 1986, Hanski 1991). A compensatory effect implies that the effect of isolation is less apparent for larger patches than for smaller patches. Several reports suggest a compensatory effect on species richness (e.g. Lomolino 1984, Crowell 1986), but little empirical evidence exists for such an interaction at the species level (but see Quintana-Ascencio & Menges 1996).

The forked fungus beetle (*Bolitotherus cornutus* Panzer) and its deadwood-decomposing fungal host (*Fomes fomentarius* (L.:Fr.) Fr.) provide an ideal system for the examination of scale-dependent phenomena. For the beetle, patches can be discretely defined at several spatial scales: the individual fungal sporocarp, the cluster of carps on dead wood, and in fragmented landscapes, the forest fragment. Extinction events at the two smaller scales are deterministic and frequent, since habitat patches are depleted.

Spatial structure is thus likely to be important to the regional persistence of this species as it must continually disperse to colonize new habitat patches.

The study objectives were thus: 1) to determine if there is an effect of spatial isolation on the forked fungus beetle at three scales, 2) to see if the effect of isolation is influenced by i) forest configuration type, ii) patch size or iii) the density of patches, and 3) to compare the usefulness and variability among nearest neighbour distance isolation measures that i) incorporate from 1 to 5 patches and ii) consider only occupied patches or all patches.

Study organisms

The forked fungus beetle (Tenebrionidae) carries out its complete life cycle on the fruiting bodies of polypore shelf fungi (Pace 1967). The primary host in Nova Scotia is the hoof fungus but the artist's conk (*Ganoderma applanatum*) is also used. Females lay eggs singly on the surface of fungal carps (fruiting bodies) from late June to August. Adults may emerge in the late summer from eggs laid in the early summer, but most overwinter as larvae inside the fungal carps to emerge as adults the following spring (Liles 1956). Some individuals are known to live and breed over several years (Pace 1967, Bondrup-Nielsen unpublished data.). Adults exhibit limited movement between fungal clusters (Heatwole & Heatwole 1968, Conner 1990). Whitlock (1992) estimated that only 30% of adults move between fungal clusters within a lifetime.

The hoof fungus (Polyporaceae), has a wide distribution across Asia, Europe, Africa and North America (Sinclair *et al.* 1987). These fungi invade decaying deciduous

trees, aiding in the decompositional process (Schwarze 1994) and some carps persists for up to 9 years (Matthewman and Pielou 1971). The primary host trees in Nova Scotia are white birch (*Betula papyrifera*), yellow birch (*Betula lutea*), beech (*Fagus grandifolia*), and large-toothed aspen (*Populus grandidentata*).

Study Area

Sampling took place in isolated woodlots in an agricultural matrix of the northeastern end of the Annapolis Valley, and in continuous forests bordering both sides of the Annapolis Valley in Kings County, Nova Scotia, Canada. Land use in the Annapolis Valley has been predominantly agricultural since the early 18th century. Forest stand species composition ranges from pure softwood to pure hardwood, but most stands are mixedwood (Loucks 1959). Most forests have been logged at least once within the century.

Sampling

Habitat isolation was studied at three spatial scales: 1) between carps on a log, 2) between clusters of carps on deadwood (clusters were defined as deadwood with carps of host fungi, where dead logs were separated by no more than 1 metre) and 3) between woodlots. Forked fungus beetle incidence was measured indirectly by the presence of either beetle eggs or emergence holes on fungal carps. Eggs and emergence holes are species-specific and easily discerned.

At the carp scale, 9 logs from 2 continuous forest sites (315 carps) and 6 logs from 2 fragmented forest sites (165 carps) were selected, for a total of 15 logs and 480

carps. Sites and logs were selected arbitrarily, but only logs with more than 6 carps and variation in the incidence of the beetle eggs or holes on carps were chosen. The distance of each carp from the end of a log was measured, creating a 1-dimensional map, and the incidence of eggs or holes noted for each carp. At the carp cluster scale, 6 continuous forest sites (188 clusters) and 5 fragmented forest sites (209 clusters) were selected, for a total of 11 sites and 397 clusters. Sites were chosen arbitrarily, and clusters were mapped on a Cartesian grid. I stopped mapping if more than 20 clusters had been mapped and no more clusters existed in the immediate vicinity. At the woodlot scale, 79 woodlots were selected and mapped on a Cartesian grid. At each scale, a number of other variables were measured to control for confounding effects on isolation (Table 1).

Table 1. Variables measured at each scale and used to build base models.

VARIABLE		RANGE	MEAN ± SD
Carp Scale			
FRAG	Binary variable (0 = continuous forests, 1 = fragmented forests)		
LOG	blocking variable to control for differences between logs		
DENSITY	Density of carps on a log		
Variables measured for carps from continuous forests only			
CARPSIZE	Size of an individual carp, as indexed by the thickness of the carp	1 - 12	4.25 ± 1.97
DECOMP	Decompositional state (0 = undecayed, 1 = slightly decayed, 2 = well decayed)		
CARPSTATE	Carp state (0 = dead, 1 = live)		
Carp Cluster Scale			
FRAG	Binary variable (0 = continuous forests, 1 = fragmented forests)		
SITE	blocking variable to control for differences between woodlots		
CLUSTSIZE	Number of carps in a cluster	1 - 178	14.2 ± 20.4
CLUSTSTATE	Cluster state (1 = all carps live, 2 = mix of live and dead carps, 3 = all carps dead)		
DENSITY	Density of carp clusters in an area		
SPECIES	Species of fungus (0 = <i>Fomes</i> , 1 = <i>Ganoderma</i> , 2 = both)		
Woodlot Scale			
HWDW	Volume of hardwood deadwood (m ³ / 225 m ²)	0.04 - 8.24	1.03 ± 1.41
MAPLE	Volume of maple deadwood (m ³ / 225 m ²)	0.0 - 0.91	0.098 ± 0.44
ASPEN	Volume of aspen deadwood (m ³ / 225 m ²)	0.0 - 8.15	0.46 ± 1.10
BIRCH	Volume of birch deadwood (m ³ / 225 m ²)	0.0 - 2.67	0.27 ± 0.62
HABDW	Volume of habitat deadwood (m ³ / 225 m ²)	0.02 - 8.24	0.86 ± 1.35
OTHER	Volume of non-habitat hardwood deadwood (m ³ / 225 m ²)	0.0 - 1.72	0.23 ± 0.49
STATE1	Volume of decompositional state1 deadwood (m ³ / 225 m ²)	0.04 - 4.72	0.80 ± 1.22
STATE2	Volume of decompositional state2 deadwood (m ³ / 225 m ²)	0.0 - 3.46	0.29 ± 0.47
STATE3	Volume of decompositional state3 deadwood (m ³ / 225 m ²)	0.0 - 0.50	0.12 ± 0.25
STANDING	Volume of standing deadwood (m ³ / 225 m ²)	0.0 - 5.05	0.54 ± 0.86
FALLEN	Volume of fallen deadwood (m ³ / 225 m ²)	0.0 - 3.18	0.49 ± 0.78
AGE	Age of largest tree (years)	10.5 - 103	63.3 ± 29.6
MEANDBH	Mean diameter at breast height (cm)	8.2 - 46.9	21.9 ± 7.72
TOTDENS	Total tree density	31.2 - 18303.6	2368.8 ± 2619.1
HWDENS	Hardwood tree density	0.0 - 18242.4	1687.6 ± 2436.8
PERCHWDENS	Percent of total density comprising hardwoods	0.0 - 100.0	63.9 ± 36.6
HW10DENS	Density of hardwood trees > 10 cm DBH	0.0 - 2687.8	594.5 ± 539.7
TOTBA	Total basal area	3 - 72	29.3 ± 11.4
HWBA	Hardwood basal area	0 - 54	17.8 ± 11.8
PERCHWBA	Percent of total basal area comprising hardwoods	0 - 100	63.6 ± 34.9
CARPS	Number of carps	0 - 194	6.1 ± 19.0
CLUSTER	Number of fungal clusters. Distinct clusters are > 1 m distant	0 - 11	0.67 ± 1.23
SIZE	In fragmented forests, the size of woodlot and in continuous forests, the equivalent size represented by the number of sampling points along the transect. (ha)	0.08-60.0	

At each scale, 10 isolation variables were calculated: distance to the closest patch (NN1), distance to the closest occupied patch (NNB1), average distance to the 2 closest patches (NN2), average distance to the 2 closest occupied patches (NNB2), and so on, up to the average distance to the 5 closest patches (NN5) and the average distance to the 5 closest occupied patches (NNB5) (Table 2).

Table 2. Isolation variables used at all three scales. The first five variables (NN1-NN5) consider distances to all patches. The second five variables (NNB1-NNB5) consider distances to occupied patches only. All measurements are in metres.

Variable	Carp Scale		Carp Cluster Scale		Woodlot Scale	
	Range	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD
NN1	0 - 1.20	0.0072 \pm 0.011	1.0 - 27.5	6.84 \pm 4.4	25 - 900	201.4 \pm 185.6
NN2	0 - 1.30	0.011 \pm 0.013	2.02 - 31.4	8.5 \pm 4.96	50 - 950	301.8 \pm 208.3
NN3	0 - 1.33	0.014 \pm 0.015	2.9 - 39.1	9.91 \pm 5.4	83.3 - 966.7	390.8 \pm 229.5
NN4	0 - 1.36	0.018 \pm 0.017	3.48 - 43.9	11.2 \pm 5.8	137.5 - 1050	467.1 \pm 236.2
NN5	1 - 1.43	0.022 \pm 0.020	4.3 - 48.8	12.6 \pm 6.2	170 - 1200	550.6 \pm 270.6
NNB1	0 - 1.54	0.012 \pm 0.018	1.04 - 54.7	9.3 \pm 6.8	50 - 1100	274.3 \pm 252.3
NNB2	0 - 1.60	0.019 \pm 0.024	2.0 - 61.8	11.4 \pm 7.1	75 - 1300	406.4 \pm 287.8
NNB3	0 - 1.70	0.024 \pm 0.028	2.9 - 65.4	13.0 \pm 7.0	83.3 - 1450	514.8 \pm 328.2
NNB4	1.3 - 1.78	0.030 \pm 0.031	4.6 - 68.4	14.7 \pm 8.4	137.5 - 1575	618.1 \pm 368.3
NNB5	3 - 1.91	0.036 \pm 0.035	5.8 - 71.2	16.3 \pm 8.9	190 - 1810	725.4 \pm 407.4

Analysis and Results

Most of the analyses are based on logistic regression models (Hosmer & Lemeshow 1989) performed using the generalized linear model framework in S-PLUS (Mathsoft Inc., 1995). For such models, the equivalent measure to the sums of squares from ordinary least squares (OLS) is the deviance (McCullagh & Nelder 1989). Significance of variables is determined by the likelihood-ratio test, or G test. This tests the reduction in model deviance resulting from the addition of a variable as a X^2 statistic. In logistic regression, an R^2 -like measure (hereafter referred to as R^2_L) can be calculated

by dividing the residual deviance by the null deviance R^2_L (Agresti 1990). This measurement can be used to assess the overall fit of a model, as well as the contribution of individual variables. Regression diagnostics used included the constructed variable plot (Wang 1987), influence and leverage plots (Landwehr *et al.* 1984, McCullagh & Nelder 1989). Given the number of isolation variables, conducting a large number of tests was inevitable. Although p-values were not adjusted, I was conservative in the interpretation of results.

The effect of isolation on beetle incidence

Other variables may covary with patch isolation (e.g. patch size) thus confounding a potential isolation effect. As a consequence, I first built a base model from patch variables using the forward stepwise procedure. Table 1 lists the variables used to build the base models and Table 3 describes the base models used at each scale. Two terms were nested, LOG *in* FRAG and SITE *in* FRAG, as an individual log could only be found in one site and an individual site could only be found in one forest configuration type. At the carp scale, patch measurements were only collected in continuous forests. I therefore analyzed all carps together, and then carps from continuous forests separately.

Table 3. Base models used at each scale. As habitat measurement were not recorded for carps in fragmented forests, two base models are presented; one for all carps and one for carps from continuous forests. $P(\chi^2)$ refers to the p value from a Chi-square table for the G test.

Variables	Deviance	DF	$P(\chi^2)$	Null Deviance	Null DF	Residual Deviance	Residual DF	R^2
Carp Scale (all carps)				542	432	493.6	421	8.9%
LOG <i>in</i> FRAG	48.41	11	<0.00001					
Carp Scale (carps in continuous forests)				361.7	297	265.7	289	26.4%
LOG	40.7	6	<0.00001					
CARPSIZE (+ve)	55.75	1	<0.00001					
CARPSTATE	10.55	1	0.0012					
Carp Cluster Scale				292.4	221	227.2	208	22.2%
SITE <i>in</i> FRAG	28.87	10	0.001					
CLUSTSIZE (+ve)	23.96	1	<0.00001					
SPECIES	10.1	2	0.006					
Woodlot Scale				54.3	52	36.8	51	32.2%
SITEAGE (+ve)	17.33	1	0.00003					

I was unable to measure all ten isolation variables for patches near the edge of the study areas, as the closest patches were occasionally outside the study area. For all analyses, I used only data points which had measurements for all 10 isolation variables. I tested for a significant effect of isolation by adding each isolation variable separately to the appropriate base model at each scale. Isolation was modeled both linearly and as a quadratic, since a threshold effect, whereby isolation only becomes important after a certain distance, seemed plausible. If an isolation variable was better modeled as a quadratic, then results for the linear model were not presented. By adding isolation variables last I took a conservative approach in controlling for confounding variables. This approach is appropriate for the test of an explicit hypothesis.

Prevalence and magnitude of isolation effects

At the carp scale, (for all carps) 5 of 10 isolation variables were significant (Table 4). None of the patch descriptors could be included in the base model, as they were not measured on logs from fragmented sites. I also analyzed the logs from continuous sites separately where 2 of 10 isolation variables were significant, although three of the variables for occupied patches were near significance (Table 4). Since no carp-level variables were included in the base model for the all carps tests, it suggests that some of the isolation effect detected when including all carps was a result of correlations with other independent variables. At the carp cluster scale, all 10 isolation variables were significant (Table 4). At the woodlot scale, 5 of 10 isolation variables were significant and three were near significance ($p < 0.10$)(Table 4). In order to determine the relative magnitude of the isolation effect at each scale, I standardized the isolation variables using a z-transformation and compared parameter estimates. At the carp and woodlot scales, most isolation variables were modeled linearly and there was clearly a larger isolation effect at the woodlot level (Wilcoxon rank sum test $Z = 3.64$, $p = 0.0003$)(Figure 1). At the carp cluster scale, isolation was modeled as a quadratic, making it difficult to compare with other scales. Figure 2 illustrates this problem. For small values, isolation has a positive and hence weaker effect than the other two scales. For larger values, however, isolation appears to have a more dramatic negative effect than at the other two scales.

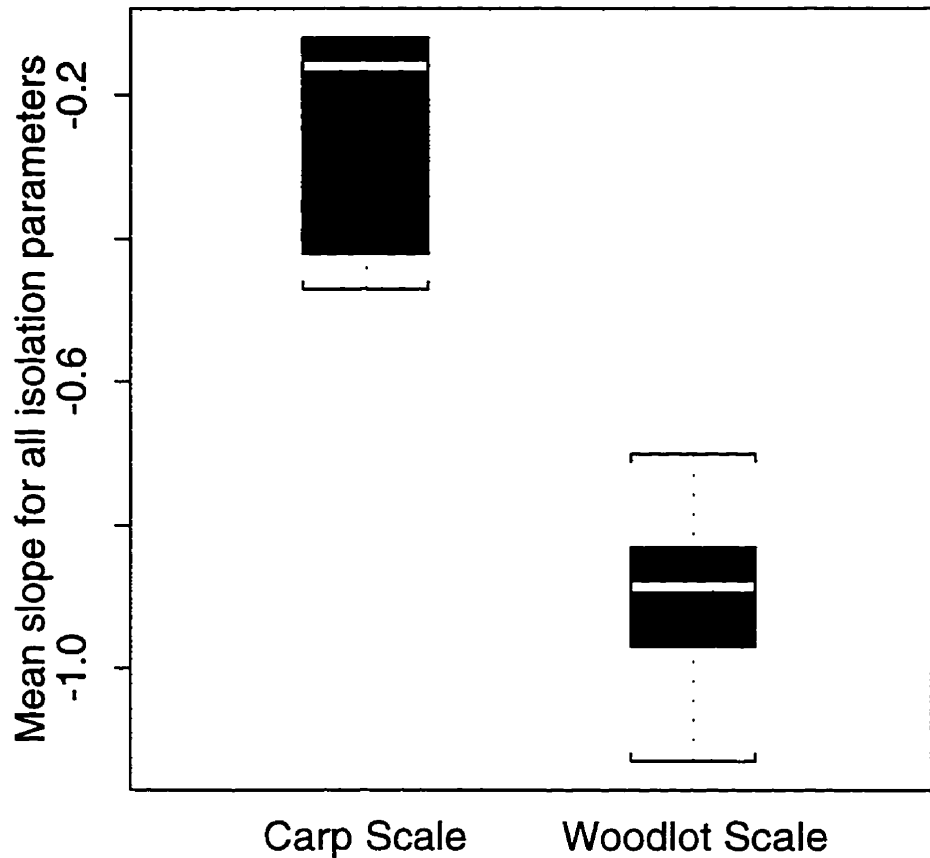


Figure 1. Boxplots comparing the magnitude of isolation effects. At the carp and woodlot scale, all 10 isolation parameter estimates from Z-transformed data are compared. The top and bottom of the box correspond to the 75th and 25th percentile of the data respectively. The white bar is the median for each group, and the upper and lower brackets represent the most extreme data value or 1.5 x the interquartile distance (height of the box) from the median, whichever is less.

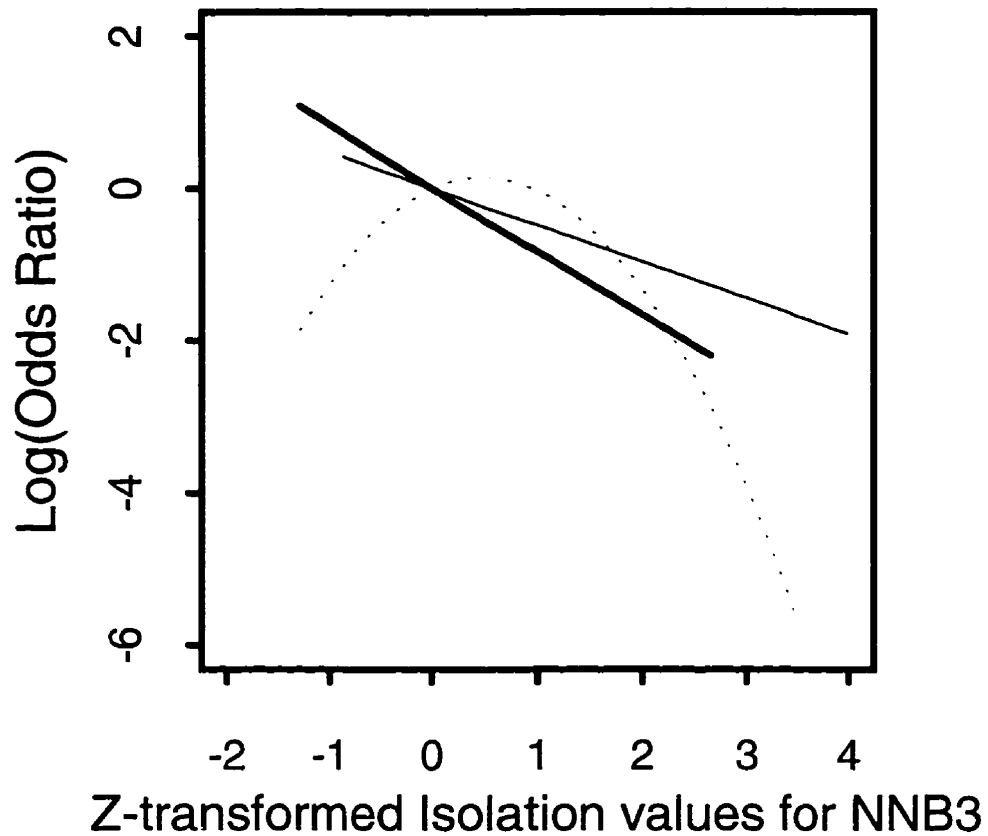


Figure 2. Comparison of slopes. The slope of the isolation variable NNB3 from Z-transformed data is presented for each scale over the range of values observed. the bolded straight line is for the woodlot scale, the dotted curve is for the cluster scale and the lighter straight line is for the carp scale. The Y axis is the log of the odds ratio, which is the unit in which logistic regression parameter estimates are expressed.

Table 4. Results of adding isolation variables individually to base models. Poly refers to whether isolation was modeled linearly (poly=1) or as a quadratic (poly=2). $P(\chi^2)$ refers to the p value from a G test.

Isolation Variable	Carp Scale (All Carps)			Carp Scale (Carps from continuous forests)			Carp Cluster Scale			Woodlot Scale		
	poly	Deviance	$P(\chi^2)$	poly	Deviance	$P(\chi^2)$	poly	Deviance	$P(\chi^2)$	poly	Deviance	$P(\chi^2)$
NN1	2	10.22	0.006	2	8.4	0.015	2	16.35	0.00028	1	5.33	0.021
NN2	1	1.15	0.28	1	0.84	0.36	2	9.07	0.011	1	4.22	0.04
NN3	1	1.83	0.18	1	0.44	0.51	2	10.72	0.0047	1	4.07	0.044
NN4	1	1.64	0.2	1	0.26	0.61	2	9.62	0.0081	1	3.58	0.058
NN5	1	1.82	0.17	1	0.19	0.66	2	10.18	0.0062	1	3.62	0.057
NNB1	1	1.33	0.25	1	0.35	0.56	2	10.44	0.0054	2	11.36	0.0034
NNB2	1	9.15	0.0025	1	3.2	0.074	2	7.6	0.022	1	4.19	0.041
NNB3	1	13.02	0.00031	1	4.37	0.037	2	10.61	0.005	1	3.06	0.08
NNB4	1	11.87	0.00057	1	3.56	0.059	2	12.51	0.0019	1	2.38	0.12
NNB5	1	10.69	0.001	1	3.25	0.071	2	12.48	0.002	1	2.16	0.14
BASE MODEL	LOG <i>in</i> FRAG			LOG + CARPSIZE + CARPSTATE			SITE <i>in</i> FRAG + CLUSTSIZE + SPECIES			SITEAGE		

Explanatory power of the of the isolation variables

For the isolation variables that described distances to patches regardless of the presence of the beetle (NN1-NN5), the first variable was the best predictor of incidence at all scales (Table 4). For the isolation variables that described distances to occupied patches (NNB1-NNB5), there was no clear trend. At the carp scale, the variables that measured distances to an intermediate number of patches (NNB2-NNB4) were the best predictors. At the carp cluster scale, the variables incorporating more patches (NNB4 - NNB5) tended to be better predictors, whereas at the woodlot scale, the variables incorporating fewer patches (NNB1 - NNB2) were better predictors. There was no clear superiority of one group of isolation variables (NN1-NN5 vs. NNB1-NNB5) over the other.

The effect of forest configuration type (continuous vs. fragmented) on isolation.

In order to see if beetles responded similarly to the spatial structure of fungal carps and carp clusters in continuous and fragmented forests, I tested for an interaction between all significant isolation variables in Table 4 and the forest configuration type variable (FRAG). Analyses could only be conducted at the carp and carp cluster scales, as woodlots were only measured in one forest configuration type. At the carp scale, since I needed to use logs from both forest configuration types, and only carps the base model could not include any patch descriptors. Only one interaction proved significant (carp cluster scale: interaction between NNB1 (modeled as a quadratic) and FRAG, $X^2 = 9.1$, $p = 0.011$). Hence, forest configuration type does not appear to influence the way the beetle responds to spatial structures at finer scales.

Compensatory effect of patch size on isolation

Using the models from Table 4, I tested for an interaction between the patch size variable and each isolation term in the same way they were modeled in Table 4 (i.e. linearly or as a quadratic). There were five significant interactions between isolation variables and measurements of patch size (CARPSIZE, or CLUSTSIZE) (Table 5).

Table 5. Compensatory effect of patch size on patch isolation. Patch size at the carp scale was measured as the thickness of a carp (CARPSIZE). Patch size at the carp cluster scale was measured as the number of carps (CLUSTSIZE). At the carp scale, only logs from continuous sites could be included. Poly refers to whether isolation was modeled linearly (poly=1) or as a quadratic (poly=2).

Carp Scale (Carps from continuous forests)				Carp Cluster Scale			
Interaction with:	Poly	Deviance	P(χ^2)	Interaction with:	Poly	Deviance	P(χ^2)
NN3	1	4.16	0.041	NNB1	2	9.16	0.010
NN4	1	4.77	0.029	NNB2	2	8.31	0.016
NN5	1	5.15	0.023				

An interaction could not be tested for at the woodlot level, as all resulting models were unstable. In all 5 interactions, increasing patch size depressed the effect of increasing isolation (e.g. Figure 3). Thus, patch size appears to compensate for patch isolation in certain circumstances.

Interaction between patch density and spatial isolation.

It is likely that the importance of patch isolation is greater in areas where patches are more isolated. To determine if the degree of patch isolation (measured as patch density) within a scale influenced the isolation effect, I tested for an interaction between the patch density term and each isolation variable. Patch density was measured for both carps and carp clusters. The appropriate base model could not contain the blocking variables LOG or SITE, as they preclude the addition of other variables measured at those scales. Hence, new base models were built for this analysis, and had to include DENSITY. Again, isolation variables were modeled linearly or as quadratics.

Of 20 interactions tested, two were significant (NN4 x DENSITY, $G(X^2) = 4.22$, $p = 0.04$, NN5 x DENSITY, $G(X^2) = 4.54$, $p = 0.03$). Both significant interactions were at the carp scale (all carps), and positive, indicating that as density increased, the effect of isolation also increased. As these interactions were absent from the continuous forest carp scale models, where other independent variables were included, it is possible that these interactions are simply artifacts of confounding variables.

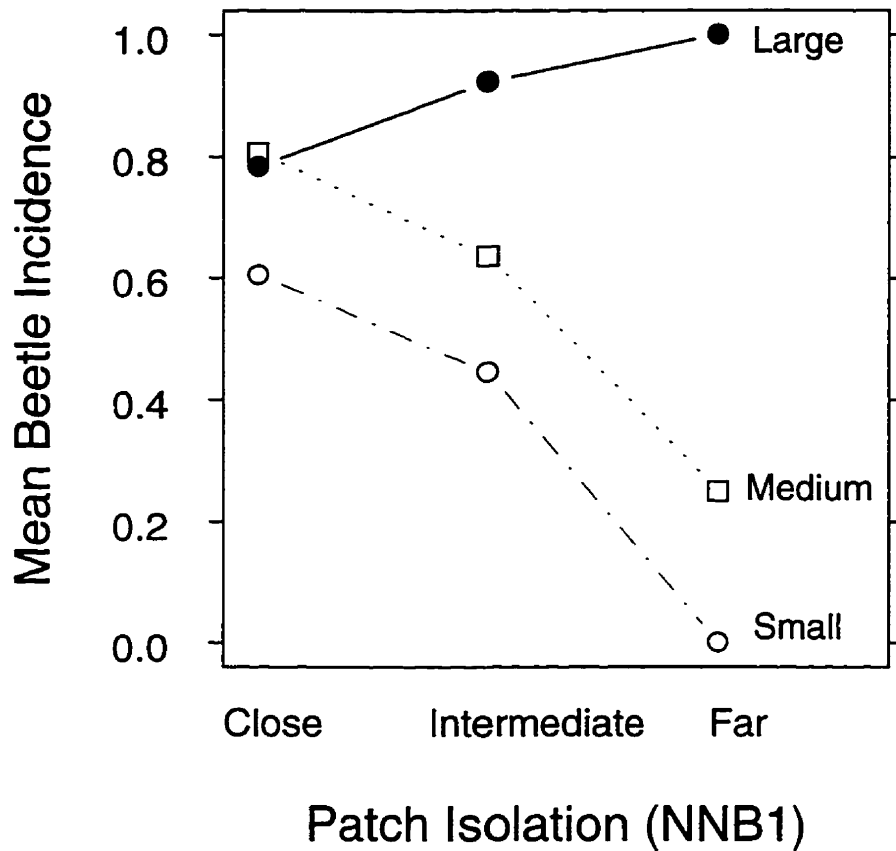


Figure 3. Interaction plot. This plot illustrates a compensatory effect of patch size on patch isolation for NNB1 at the carp cluster scale. For the purpose of clarity, the two continuous variables: patch size and patch isolation were divided into 3 categories. Isolation: category 1 = 0 - 5 m, category 2= 6 - 10 m, category 3 =11+ m . Size: category 1 = 0-10 carps, category 2= 11-20 carps, category 3 = 21+ carps. For the two smaller patch sizes, isolation exerts a negative effect on mean beetle incidence, but not for large patches.

Discussion

As isolation effects are scale-dependent, I expected to find the strongest isolation effect at the largest (woodlot) scale and weakest effect at the smallest (carp) scale. Although I did find a stronger effect at the largest than at the smallest scale, what was surprising was that isolation was important at all three scales studied here. In addition, differences in the density of patches at the two smaller scales did not seem to have an effect on isolation. I found evidence for a limited compensatory effect of patch size on patch isolation, but no effect of forest configuration type on isolation. Lastly, although there was variation in the explanatory power of the different isolation variables, the only clear pattern to emerge was for the variables that measured distances to any patch, where the distance to the closest single patch was the best predictor at all scales.

The effect of isolation was also surprising given two factors that would dampen my ability to detect an effect of isolation. First, beetle incidence was measured indirectly, by searching for beetle eggs or emergence holes. As eggs and emergence holes can persist for several years, the measure of incidence is cumulative and does not imply current use. This multi-year incidence measure would tend to make any effect of isolation more difficult to detect. Secondly, I used a conservative approach in testing for any effect of isolation, by adding isolation variables last to a base model. Therefore, actual isolation effects for this beetle are likely to be stronger than reported in this study.

The magnitude of the spatial isolation effect was smaller (in terms of the parameter estimate) at the carp scale than at the woodlot scale, but isolation was most prevalent at the carp cluster scale. As isolation at the carp cluster scale was best modeled

as a quadratic function, I could not compare the magnitude of the effect with other scales. The quadratic relationship suggests that isolation becomes important only beyond some minimum or threshold isolation distance (Figure 2). It is possible that the isolation distances at the carp and woodlot scale were not sufficiently large, in relative terms, to exceed this threshold. This could explain why isolation effects were not as prevalent at these scales. At the carp scale, the fact that logs with less than 10 carps were excluded may have biased the parameter estimates, however, it is not clear in what direction the bias may have occurred. The direction of the bias would depend upon the costs and benefits of using smaller patches versus finding a larger patch. If it is more advantageous to remain and fully utilize a small patch, then even remote carps would be used, and effects of isolation would be weak. However, if it is more advantageous to leave a small patch and search for a larger patch, then isolation may have been even stronger on small patches, as remote carps would rarely be used..

Another element that may influence the effect of scale on isolation is that beetles have two different movement mechanisms, which may be operating at different scales. To move between carps, beetles may elect to walk, where distances in the range of 1 to 2 meters may be relatively far. To move between carp clusters or between woodlots, however, beetles are likely flying. Beetles may also be using spatially relative movement rules, where the decision to travel to a carp 1 metre or 2 metres distant is analogous to deciding whether to travel to a woodlot 1000 or 2000 metres distant. If beetles are in fact using two different movement mechanisms at the carp and carp cluster scales, these two scales might be considered domains, as proposed by Wiens (1989). Processes within

domains are either scale-insensitive or vary monotonically with scale which would explain the lack of significance of patch density at both of these scales.

Although habitat fragmentation has the potential to affect complex interactions among insects (e.g. Kareiva 1987, Kruess & Tschamtkke 1994, Didham *et al.* 1996), the lack of a forest configuration type effect indicates that beetles are reacting to the spatial configuration of their habitat in the same way in continuous and fragmented forests.

Patch size was important at the carp and cluster scale, and appears to compensate, in part, for the effect of isolation. Of the 5 significant interactions discovered between patch size and isolation, three were from models in which patch size and isolation were already significant. Thus, patch size may alleviate the effect of isolation, but does not necessarily subsume it. Compensatory effects have been discussed both for species richness (e.g. Lomolino 1986) and individual species abundance or incidence (e.g. Hanski 1991). An interaction between isolation and patch size on species richness is a corollary of island biogeography theory (MacArthur & Wilson 1967:23). Although evidence for a compensatory effect on species richness exists (MacArthur & Wilson 1967, Lomolino 1984, Crowell 1987), earlier claims of evidence for a compensatory effect at the species level have been misleading, as an interaction between patch size and patch isolation was not explicitly tested (e.g. Hanski 1986, Lomolino 1986, Lomolino *et al.* 1989, Peltonen & Hanski 1989). The only documented interaction between isolation and size for an individual species I could find was a recent study by Quintana-Ascencio & Menges (1996) where a significant compensatory effect existed for 9 of 62 Florida scrub plant species.

Of the 10 isolation variables used in this study, none was clearly superior at all scales, nor was one group of predictors superior in predicting an effect of isolation than the other group (i.e. NN1-5 vs. NNB1-5). Vos and Stumpel (1995), studying tree frogs, also compared a series of isolation variables for both occupied ponds and all ponds. They found that the linear distance to the occupied pond was as good a predictor as a “circular isolation measure”, which incorporates the area of occupied ponds within a certain radius. Conversely, they found that circular isolation measures of all ponds (occupied or not) were better predictors than the linear distance to the closest pond. Overall, however, variables associated with occupied ponds were better predictors than variables associated with all ponds.

In conclusion, little information would have been missed by only measuring the distance to the closest patch (NN1), regardless of occupancy. Results from this study suggest that there may be two causes for the lack of a consistent isolation effect in the literature: 1) variability in the explanatory power of the different isolation variables and 2) the importance of spatial scale on the effect of isolation. In addition, a multi-scale approach yielded a surprising result: isolation was important at all scales. Finally, I found a limited compensatory effect of patch size, but no effect of patch density or forest configuration type on isolation.

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CHAPTER 2. The effect of scale and sample size on predictive models and patch occupancy rates for a beetle parasite and its fungal host in continuous and fragmented forests.

Abstract

Predictive models have been widely used in conservation biology, but the scale-dependency of prediction is seldom treated explicitly. For the forked fungus beetle (*Bolitotherus cornutus* Panzer) and its wood-decay fungal host (*Fomes fomentarius* (Fr.:L.) Fr.), habitat patches can be discretely described at different hierarchical spatial scales. In this study I built a series of predictive models of incidence for the beetle and the fungus using multiple logistic regression at three scales and in 2 forest configuration types (continuous and fragmented). These models varied in both the spatial grain of the response variable and the spatial extent of the predictor variables so as to assess the relative usefulness of variables measured at the same scale as the response and to test for a relationship between predictability and scale.

Although model predictive power (R^2_L) increased with grain size, this was likely a result of a decrease in model sample size with increasing scale. To test for an effect of sample size on R^2 , I built a series of models (150) from subsamples of data ranging in sample size from 50 to 1500. These models showed that the mean and variance of R^2_L is sensitive to small sample sizes (< 300). Thus, researchers must be careful in comparing the predictive power of models based on very different sample sizes. To control for the effect of sample size, I took 20 random samples of size 50 from each scale and built new models. Mean R^2_L did differ between scales, but did not do so in a consistent fashion. The variance in the response variable, however, decreased linearly with scale for both species. These results suggest that a critical reexamination of the predictability-scale relationship would be useful. Variables measured at the same scale as the response proved to be better predictors than variables measured at larger scales. There was a small effect of forest configuration type on the predictive models at the smallest scale for both the fungi and beetle models. Analysis of patch occupancy rates indicated that hoof fungi had a reduced ability to find and/or use their deadwood hosts in fragmented forests at two scales within forest stands. Conversely, beetles had a higher patch occupancy rate in fragmented forests at one of two scales within forest stands.

Keywords: prediction, scale, logistic regression, forest fragmentation, deadwood, conservation, *Bolitotherus*, *Fomes*.

Introduction

Spatial scale plays an important role in ecological research as the choice of scale influences the questions posed, the methodologies used and the type of results generated (Dayton and Tegner 1984). The scale-dependency of ecological processes and patterns is particularly evident when trying to develop an understanding of the distribution or abundance of organisms. Several studies have shown how different factors explain the distribution or abundance of organisms at different scales (e.g. Wiens *et al.* 1986, Galzin 1987, Wiens 1989, Smogor *et al.* 1996). For example, in studying shrubsteppe birds, Wiens *et al.* (1986) found that for the sage thrasher, increasing shrub coverage had a positive effect at a large scale, but a negative effect at a smaller scale, indicating that once the general habitat is chosen (shrubsteppe) thrashers preferred areas with less dense cover. Knowing how ecological variables change with scale can be useful as it may allow us to extrapolate to larger, unstudied scales (Turner *et al.* 1989), as well as to use small-scale mechanistic understandings to explain large-scale patterns (Wiens *et al.* 1993, With & Crist 1996).

Spatial scale is also important in predictive modelling. Predictive models are common and useful tools in applied ecology (e.g. Gribko *et al.* 1995, Lavers & Haines-Young 1996, Wahlberg *et al.* 1996). For example Wahlberg *et al.* (1996) successfully predicted the distribution of an endangered butterfly using a spatially explicit metapopulation model. Although the scale-dependency of predictive models is well-known in other disciplines, such as geography (Wiens 1989), it has only recently been recognized in ecology (Meetenmeyer & Box 1987, Wiens 1989, Turner *et al.* 1989). It is

useful to think of spatial scale as having two elements: spatial grain, or resolution size, and spatial extent. In predictive modelling, the information that generates a prediction may be derived from variables measured at different spatial grains or extents, but the prediction is only relevant at one grain size. It has also been hypothesized that predictability of patterns and processes in nature increases with the scale of observation (Wiens 1989, Galzin 1991)

The appropriate choice of scale (grain and extent) depends on both the study organism and the research questions posed (Wiens 1989, Levin 1992). In applied research, these two factors can conflict, if the scale appropriate to the organism is not the scale (grain or extent) at which a disturbance is occurring. For example, small-scale selective forest harvesting is not conducted at a scale appropriate for studying the effects of anthropogenic disturbance on a species whose individuals range daily over tens of square kilometres. The importance of scale to prediction, and in particular the difficulty in choosing the appropriate scale in applied research led to the first objective of this study: to determine the effect of varying the spatial grain and extent of both response and predictor variables on predictive models for the forked fungus beetle, *Bolitotherus cornutus* Panzer, and its fungal host, the hoof fungus, *Fomes fomentarius* (Fr.:L.) Fr.

The hoof fungus inhabits dead wood, and the beetle parasitizes the fruiting bodies (basidiocarps) of the fungus. For these forest-dwelling organisms, large-scale habitat fragmentation implies conversion of previously continuous forest into a series of forest fragments. The effects of habitat fragmentation on insects are poorly understood, especially how higher order interactions such as predator-prey or parasite-host

relationships are impacted (Didham *et al.* 1996). Fragmentation may affect the beetle or fungus due to smaller-sized, increasingly isolated patches or changes in the microsite conditions of fragments (Saunders *et al.* 1991). The second objective of this study was thus to determine the effect of anthropogenic habitat fragmentation on the fungus and beetle and on the interaction between these two species.

Study organisms

The hoof fungus (Polyporaceae) has a wide distribution across Asia, Europe, Africa and North America (Sinclair *et al.* 1987). These fungi invade decaying deciduous trees, aiding in the decompositional process (Schwarze 1994) and some fungal carps (fruiting bodies) persist for up to 9 years (Matthewman and Pielou 1971). The primary host trees in Nova Scotia are white birch (*Betula papyrifera*), yellow birch (*Betula lutea*), beech (*Fagus grandifolia*), and large-toothed aspen (*Populus grandidentata*).

The forked fungus beetle (Tenebrionidae) carries out its complete life cycle on the fruiting bodies of polypore shelf fungi (Pace 1967). The primary host in Nova Scotia is the hoof fungus, but the artist's conk (*Ganoderma applanatum*) is also used. Females lay eggs singly on the surface of the fungi from late June to August. Adults may emerge in the late summer from eggs laid in the early summer, but most overwinter as larvae inside the fungus, to emerge as adults the following spring (Liles 1956). Some individuals are known to live and breed over several years (Pace 1967, Bondrup-Nielsen, unpublished data). Adults exhibit limited movement between fungi-infested logs (Heatwole & Heatwole 1968, Conner 1990). Whitlock (1992) estimated that only 30% of adults move between logs within a lifetime.

Study Area

Sampling took place in isolated woodlots of the northeastern end of the Annapolis Valley, and in continuous forests bordering both sides of the Annapolis Valley in Kings County, Nova Scotia, Canada. Land use in the Annapolis Valley has been predominantly agricultural since the early 18th century. Forest stand species composition ranges from pure softwood to pure hardwood but most stands are mixedwood (Loucks 1959). Most forests have been logged at least once within the century.

Sampling

Seventy-nine woodlots (forest fragments) and 17 areas of adjacent continuous forests were sampled. Woodlots were considered distinct if separated by at least 10 m of non-forested area. To measure habitat characteristics in these sites, I used sampling points situated along transects. Information from sampling points was used to devise habitat variables at three scales: 1) the deadwood log scale, 2) the sampling point scale) and 3) the site scale. In fragmented forests, the woodlot constituted a site (79), whereas in continuous forests, each area sampled by a transect constituted a site (17). Most habitat values at the site scale were obtained by averaging variables measured from the points within a site.

At each sampling point, I used a 15m² quadrat to quantify deadwood by position, state, size, and species (Table 1). Only deadwood greater than 9 cm diameter at the largest end was measured. Results from a prism sweep were used to quantify tree species

composition, density, and basal area. The prism sweep is a method of proportionate sampling used extensively in forest inventories (Avery 1967). The largest tree in each prism sweep was bored to determine its age. Hoof fungus incidence was based on the presence of carps. A fungal cluster was defined as all carps on logs separated by less than 1 meter (Table 1). Forked fungus beetle incidence was measured indirectly by the presence of either beetle eggs or emergence holes on fungal carps. Eggs and emergence holes are species-specific and easily discerned. Table 1 lists all variables measured or amalgamated at each scale.

Table 1. Environmental variables used for building predictive models.

Variables measured at the log scale		Range	Mean +/- SD
VOL	Volume of log (m ³)	0.0006 - 4.81	0.05 ± 0.14
LEN	Length of log (m)	0.1 - 25.0	3.81 ± 3.43
BIGD	Largest log diameter (cm)	2 - 145	14.63 ± 7.65
LOGSP	Log species		
STATE	Log state (1 = undecayed, 2 = slightly decayed, 3 = well decayed)		
POS	Log position (0 = fallen, 1 = standing)		
FRAG	Binary variable coding for forest landscape (0 = continuous, 1 = fragmented)		
YEAR	Binary variable coding for year of sampling		
Variables measured at the point and site scale			
HWDW	Volume of hardwood deadwood (m ³ / 225 m ²)	0.04 - 24.2	1.03 ± 1.41
MAPLE	Volume of maple deadwood (m ³ / 225 m ²)	0.0 - 1.78	0.098 ± 0.44
ASPEN	Volume of aspen deadwood (m ³ / 225 m ²)	0.0 - 17.25	0.46 ± 1.10
BIRCH	Volume of birch deadwood (m ³ / 225 m ²)	0.0 - 2.67	0.27 ± 0.62
HABDW	Volume of habitat deadwood (m ³ / 225 m ²)	0.0 2 - 19.8	0.86 ± 1.35
OTHER	Volume of non-habitat hardwood deadwood (m ³ / 225 m ²)	0.0 - 4.41	0.23 ± 0.49
STATE1	Volume of decompositional state1 deadwood (m ³ / 225 m ²)	0.0 4 - 17.5	0.80 ± 1.22
STATE2	Volume of decompositional state2 deadwood (m ³ / 225 m ²)	0.0 - 5.60	0.29 ± 0.47
STATE3	Volume of decompositional state2 deadwood (m ³ / 225 m ²)	0.0 - 1.12	0.12 ± 0.25
STANDING	Volume of standing deadwood (m ³ / 225 m ²)	0.0 - 15.29	0.54 ± 0.86
FALLEN	Volume of fallen deadwood (m ³ / 225 m ²)	0.0 - 8.94	0.49 ± 0.78
AGE	Age of largest tree (years)	10.5 - 113.5	63.3 ± 29.6
MEANDBH	Mean diameter at breast height (cm)	8.2 - 46.9	21.9 ± 7.72
TODENS	Total tree density	31.2 - 18304	2369 ± 2619
HWDENS	Hardwood tree density	0.0 - 18242	1688 ± 2437
PERCHWDENS	Percent of total density comprising hardwoods	0.0 - 100.0	63.9 ± 36.6
HW10DENS	Density of hardwood trees > 10 cm DBH	0.0 - 2688	594.5 ± 539.7
TOTBA	Total basal area	3 - 72	29.3 ± 11.4
HWBA	Hardwood basal area	0 - 54	17.8 ± 11.8
PERCHWBA	Percent of total basal area comprising hardwoods	0 - 100	63.6 ± 34.9
CARPS	Number of carps	0 - 194	6.1 ± 19.0
CLUSTER	Number of fungal clusters. Distinct clusters are > 1 m distant	0 - 11	0.67 ± 1.23
DIST	Signs of disturbance from logging or cattle grazing		
FUNGSP	Species of fungi (0 = <i>Fomes</i> , 1 = <i>Ganoderma</i> , 2 = both)		
Variables measured only at the site scale			
SIZE	In fragmented forests: the size of woodlot. In continuous forests: the equivalent size represented by the number of sampling points along the transect. (ha)	FRAG: 0.045-49.2 CONT: 1.0 - 45.0	4.3 ± 6.76 26.8 ± 20.5

The arrangement of sampling points along a transect differed between years and between continuous and fragmented forests. In 1994, only continuous forests were sampled, and sampling points were clustered in groups of three. The central point, positioned along the transect, was located wherever a host fungus was encountered. Two additional points were located 100 metres away in a random direction. The number of sampling points per transect ranged from 9 to 27 points, for a total of 159 points. In 1996, both continuous and fragmented forests were sampled, where sampling points were located every 75 meters, provided that hardwood deadwood was present. Transects in continuous forests ranged from 16 to 18 points, for a total of 142 points. The number of points per transect in woodlots was determined by the formula: $\text{no. of points} = 2 * \text{SQRT}(1.5 * \text{WOODLOT AREA}(\text{ha}) + 1)$. This formula was used in order to adequately sample small woodlots, and to avoid spending too much time sampling larger woodlots. For woodlots that were not long enough to encompass the transect or were irregularly shaped, transects were divided into multiple linear segments. I surveyed at least 50 % of each woodlot to determine the presence/absence of the fungi and beetle. To determine the size of sites in continuous forests, I used the above formula, and calculated an area based on the number of points in the transect.

Statistical Analysis and Results

Most of the analyses are based on logistic regression models performed using the generalized linear model framework in S-PLUS (Mathsoft Inc.1990). For such models, the equivalent measure for the sum of squares from ordinary least squares (OLS) is the deviance (McCullagh & Nelder 1989). Significance of variables was determined by the

likelihood-ratio test, or G test. This tests the reduction in model deviance, resulting from the addition of a variable, as a χ^2 statistic. In logistic regression, an R^2 -like measure can be calculated (hereafter referred to as R^2_L) by taking: $1 - \text{residual deviance}/\text{null deviance}$ (Agresti 1990). This measurement can be used to assess the overall fit of a model, as well as the contribution of individual variables. As in OLS, R^2_L can be adjusted to take into account the number of variables in the model by taking: $1 - (\text{residual deviance}/\text{residual df}) / (\text{null deviance}/\text{null df})$. Regression diagnostics used included the constructed variable plot (Wang 1987), influence and leverage plots (Landwehr *et al.* 1984, McCullagh & Nelder 1989).

I used the forward stepwise procedure to build multiple logistic regression models. Separate models were built for each species at each grain size of the response variable: log, point and woodlot. For each model, independent variables measured at the same scale as the response were added as well as independent variables measured at, or amalgamated from, larger scales. To control for any effect of having used different sampling schemes between years, I included a binary YEAR term among the list of variables for possible inclusion in the models. For each model, the sample size was based on the number of habitable sampling units. For the fungi, at the log scale, only host logs were used. At the point and woodlot scales, only points and woodlots with HABDW > 0 were used. For the beetle models, habitable sampling units at all scales were defined simply by the presence of fungal carps. The predictive models of fungal and beetle incidence are presented in Table 2.

Table 2. Predictive models of fungal and beetle incidence at each of three scales. For each predictor variable, the degrees of freedom, deviance, significance and direction of the effect (Sign) are given. Null (intercept only) and residual (unexplained) deviances are also given. Variables that are squared were modelled both linearly and as a quadratic. Interactions with these terms include interaction with both the linear and quadratic term. $P(\chi^2)$ refers to the p value the G test.

FUNGUS INCIDENCE MODELS					BEETLE INCIDENCE MODELS				
	DF	Deviance	$P(\chi^2)$	Sign		DF	Deviance	$P(\chi^2)$	Sign
LOG SCALE									
Null	3481	2966.9			Null	528	726.3		
<i>BIGD</i> ²	2	15.2	0.0005	+ve	<i>LOGCARPS</i> ²	1	51.2	<0.00001	+ve
<i>LOGSP</i>	6	123.2	< 0.00001	*	<i>POS</i>	1	14.4	0.00015	-ve
<i>VOL</i>	1	12.17	0.0005	+ve	<i>LOGSP</i>	5	34.9	<0.00001	*
<i>POINTAGE</i>	1	17.29	0.00003	+ve	<i>POINTCLUSTER</i>	1	11.2	0.00083	+ve
<i>POINTASPEN</i>	1	17.33	0.00003	-ve	<i>POINTMAPLE</i>	1	3.92	0.048	+ve
<i>POINTBIRCH</i> ²	2	17.05	0.002	-ve	<i>SITESIZE</i>	1	7.13	0.0076	-ve
<i>POINTDIST</i>	1	6.4	0.011	-ve	Residual	517	604.2		
<i>POINTPERCHWDENS</i>	1	7.03	0.0008	+ve					
<i>POINTSTANDING</i>	1	14.78	0.0001	+ve					
<i>SITEPERCHWDENS</i>	1	11.6	0.00066	-ve					
<i>FRAG</i>	1	3.4	0.06	-ve					
<i>FRAG:BIGD</i> ²	2	10.52	0.005	+ve					
Residual	3461	2394.8							
POINT SCALE									
Null	451	589.9			Null	219	302.4		
<i>POINTBIRCH</i> ²	2	28.3	< 0.00001	+ve	<i>POINTCARPS</i>	1	13.6	0.00022	+ve
<i>POINTHABDW</i>	1	22.2	< 0.00001	-ve	<i>POINTOTHER</i> ²	2	13.03	0.00033	+ve
<i>POINTHWDW</i>	1	31.5	< 0.00001	+ve	<i>POINTCLUSTER</i>	1	7.2	0.0075	+ve
<i>POINTMAPLE</i>	1	6.44	0.011	+ve	<i>POINTASPEN</i>	1	8.4	0.0038	+ve
<i>POINTOTHER</i>	1	35.7	< 0.00001	-ve	<i>SITEPERCHWDENS</i>	1	4.06	0.044	+ve
<i>FRAG</i>	1	22.7	< 0.00001	-ve	Residual	213	223.3		
<i>SITEMAPLE</i>	1	13.9	0.00019	-ve					
<i>SITESTATE3</i>	1	8.34	0.0039	+ve					
Residual	442	485.2	169.08						
WOODLOT SCALE									
Null	73	54.8			Null	64	30.05		
<i>SITEAGE</i>	1	10.4	0.001	+ve	<i>SITEHWDW</i>	1	7.48	0.0062	+ve
<i>SITEHWDENS</i>	1	3.84	0.05	+ve	<i>SITESIZE</i>	1	4.24	0.039	+ve
Residual	71	42.5			Residual	62	20.79		

(* - a unique sign cannot be assigned for factor variables)

The deviance explained by predictor variables presented in Table 1 represents the deviance that could be uniquely assigned to that variable. When the deviance explained by all variables in a model is summed and added to the residual deviance, the total does

not equal the null deviance. This is because a portion of the deviance could not be uniquely allotted, due to correlations between variables.

Of note for the fungal models was a negative effect of the forest configuration term (FRAG) on incidence at both the log and point scales. Thus, forest fragmentation decreases the likelihood of finding fungi on deadwood (log scale) and clumps of deadwood (point scale). At the log scale there was only one significant interaction between the forest configuration term and the log diameter (BIGD). Also of note was a negative effect of disturbance (DIST) on log fungal incidence. A confusing result was that the volume of birch deadwood exerted a negative effect at the log scale but a positive effect at the point scale.

For the beetle model at the log scale, there was an effect of log species (LOGSP), indicating that beetles chose logs not based solely on the number of carps, but on the species of dead tree the carps were found on. Fungi on both aspen and yellow birch logs tended to have higher beetle occupancy rates than other logs. At the log and point scale, the number of carps were predictors of incidence, but not at the woodlot scale. At the woodlot scale, only the volume of hardwood deadwood and the woodlot size had an effect on incidence.

For the beetle models, predictive power increased with grain size (Table 3).

Table 3. Percent of total deviance explained by models at different grain sizes. R^2_L was calculated by dividing the model deviance by the null deviance and were adjusted for the number of variables in the model. The coefficient of variation (CV) of the response variable is also presented for each scale and species.

Grain size	Beetle			Fungus		
	R^2_L	n	CV	R^2_L	n	CV
LOG	0.17	529	372.6	0.19	3482	236.3
POINT	0.26	220	201.2	0.17	452	134.1
WOODLOT	0.31	65	46.5	0.22	74	37.5

The fungus models differed less in predictive power, although the woodlot scale had the highest R^2_L value. The coefficient of variation of the response variable decreased with increasing scale for both beetle and fungus models (Table 3). However, sample size also decreased dramatically with increasing scale and was potentially a confounding factor. In OLS, the expected value of the coefficient of determination (R^2) is a function of $1/n$. (Seber 1977: 115). To test if a similar relationship existed for the logistic regression equivalent of R^2_L , I took 150 random samples of different sample sizes, ranging from 50 to 1500, from the log scale data set. For each sample, I built a model using an automated stepwise procedure, and calculated an R^2_L value. Both the mean and the variance in R^2_L appear to decrease with increasing sample size (Figure 1). Thus, the observed increase in predictive power with increasing scale may be largely due to differences in sample sizes between models.

To control for the effect of sample size on prediction, I took 20 samples of size 50 from each scale for each species. Cramer (1986) reported that both the bias and the high variability of R^2 in OLS were substantially diminished with a sample size of 50. For each sample, I built a model in the same way as before for each species at each scale and then

calculated the mean R^2 for all 20 models, again for each scale and each species (Figure 2). There was a difference in R^2_L between scales for both the beetle and the fungus (Table 4). However, this difference was not consistent across scales or between species. For the fungus, R^2_L at the carp scale was smaller than at the other two scales (Table 4). For the beetle, R^2_L at the cluster scale was larger than at the other two scales. The coefficient of variance, however, decreased consistently with scale for both species (Figure 3, Table 4), as seen earlier.

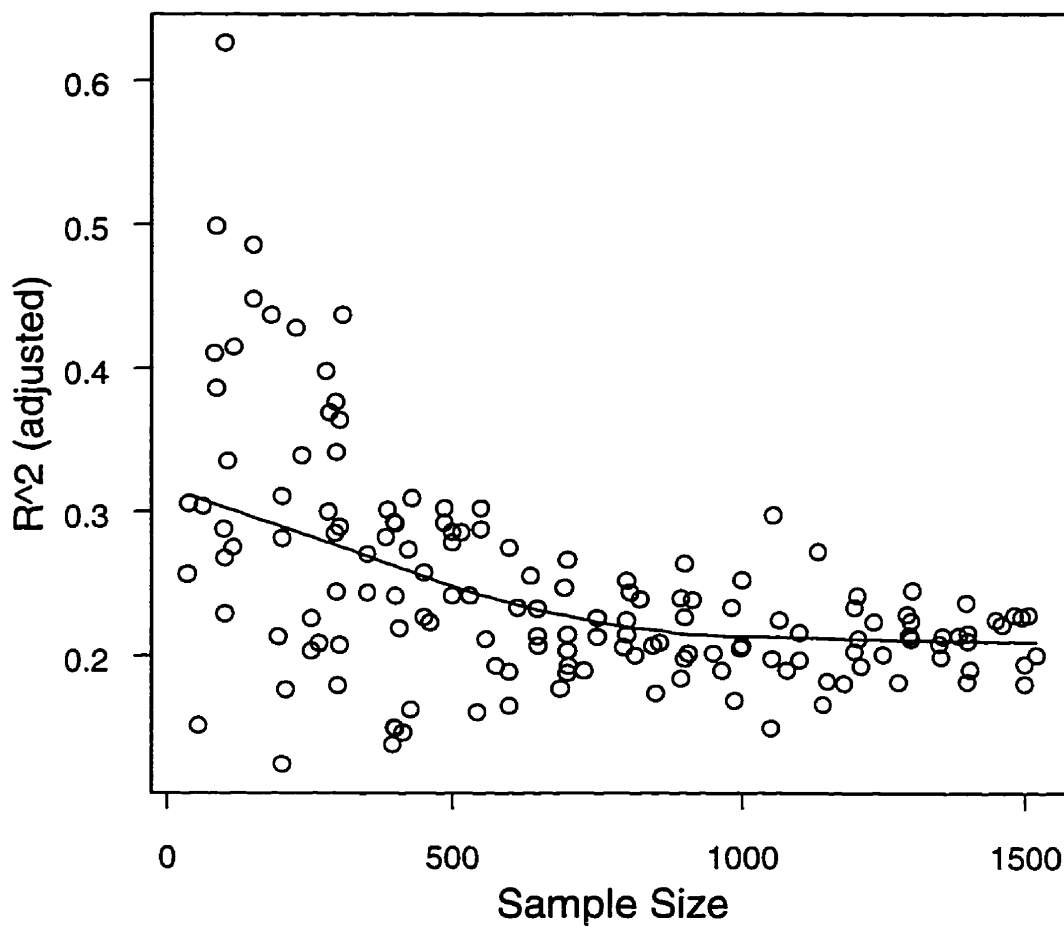


Figure 1. Predictive power and sample size at the log scale. The adjusted R^2 measure from each of 150 logistic regression models are plotted against the sample size of the model. Models are based on random samples of size 50 to 1500 taken from the log scale data with fungal incidence as a response.

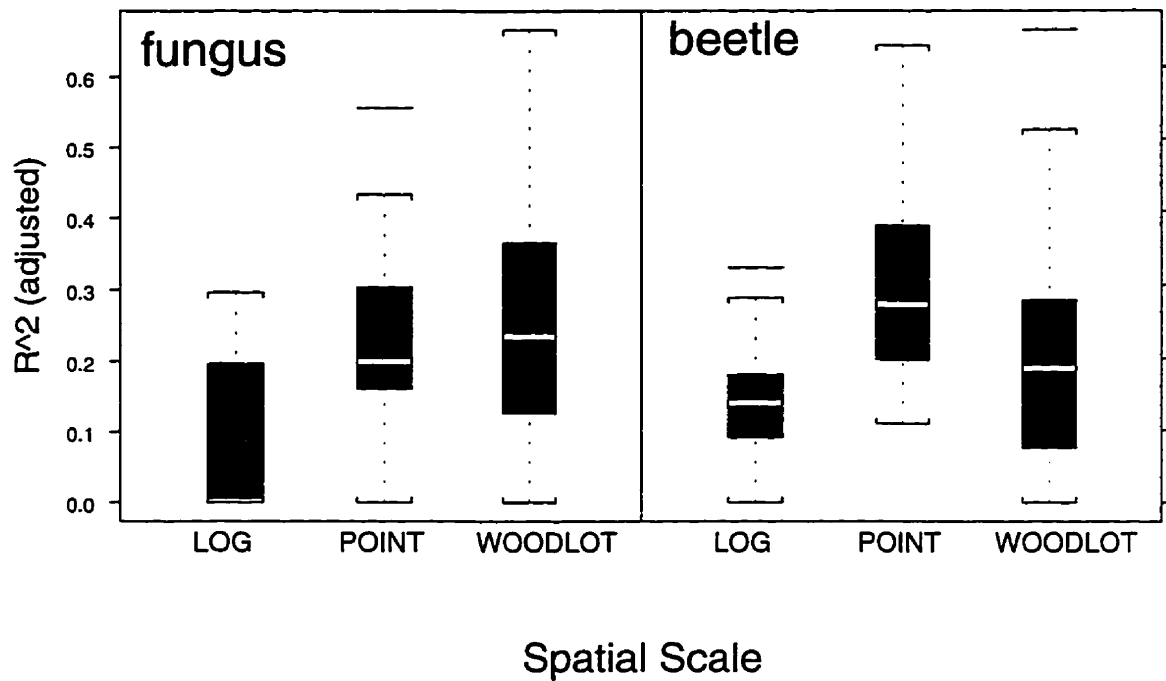


Figure 2. Predictive power and scale. These boxplots present the mean adjusted R^2 from 20 models at each scale. Models are based on data from random samples of 50 points. The top and bottom of the box correspond to the 75th and 25th percentile of the data respectively. The white bar is the median for each group, and the upper and lower brackets represent the most extreme data value or 1.5 x the interquartile distance (height of the box) from the median, whichever is less. Lines beyond the upper and lower brackets represent outliers.

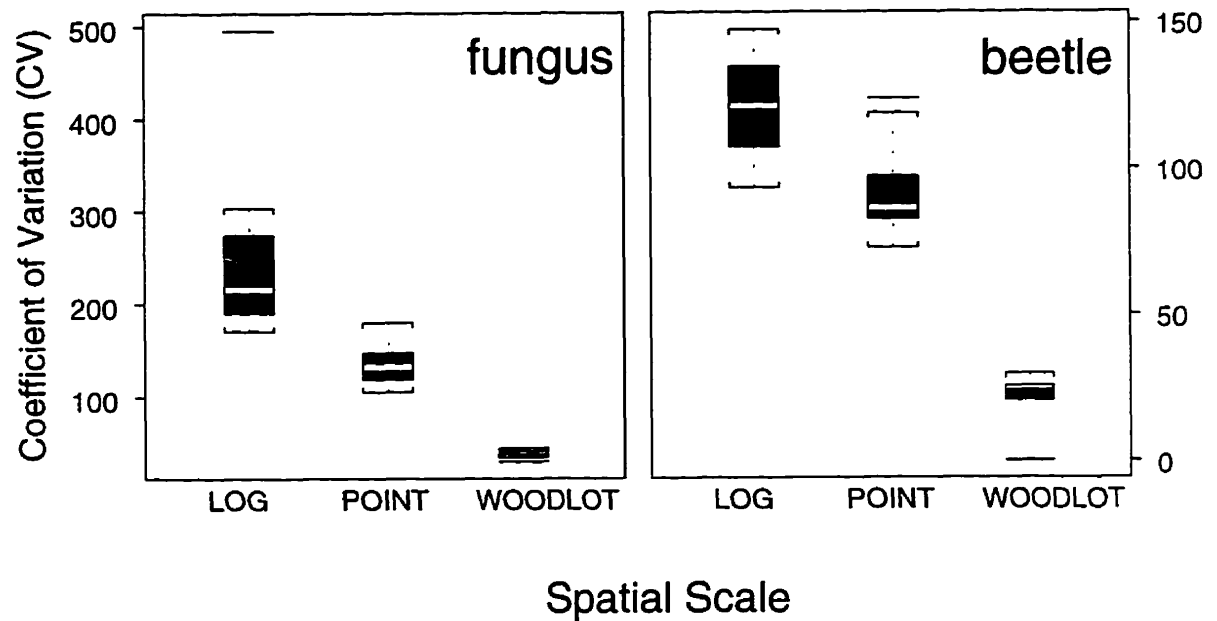


Figure 3. Variability and scale. These boxplots illustrate the change in the coefficient of variance with scale for a) beetle and b) fungal models. The coefficient of variation is a mean from 20 models based on random samples of 50 points. The Y axis of the two plots are on different scales. The white bar is the median for each group, and the upper and lower brackets represent the most extreme data value or 1.5 x the interquartile distance (height of the box) from the median, whichever is less. Lines beyond the upper and lower brackets represent outliers.

Table 4. A comparison of R^2_L and coefficient of variation values across scales for beetle and fungus models. Results from Kruskal Wallis tests and non-parametric Niemenyi multiple comparisons (Zar 1996) are given. Median values for each R^2_L and CV at each scale are given in Figures 2 and 3.

	Fungus	Beetle
R^2_L (adjusted)		
Kruskal Wallis		
χ^2	13.6	15.52
p-value	0.001	0.004
Niemenyi Multiple Comparisons		
LOG vs. POINT	<0.005	<0.001
LOG vs. WOODLOT	<0.005	>0.2
POINT vs. WOODLOT	>0.5	<0.05
Coefficient of Variation		
Kruskal Wallis		
χ^2	52.4	48.5
p-value	<0.00001	<0.00001
Niemenyi Multiple Comparisons		
LOG vs. POINT	<0.0001	<0.0001
LOG vs. WOODLOT	<0.00001	<0.00001
POINT vs. WOODLOT	<0.0001	<0.0001

To calculate the contribution of variables measured at different spatial extents for each model reported in Table 2, I used the following procedure. The reduction in deviance resulting from the addition of all variables of a particular scale was summed and divided by the degrees of freedom used by variables at that scale, in order to standardize the information contributed by each scale. I then expressed the (deviance/degrees of freedom) explained by each scale as a percentage of the total (deviance/degrees of freedom) that could be uniquely assigned to variables at all scales (see above). In all four

models, variables measured at the same scale as the response variable explained the greatest proportion of the total uniquely attributable deviance (Table 5).

Table 5. Percent of total deviance explained by variables measured at different spatial extents. Values are for deviance that can be uniquely assigned to one variable.

	Fungal models			Beetle models		
	LOG	POINT	SITE	LOG	POINT	SITE
LOG	46.4	33.4	19.8	49.4	26.0	24.5
POINT		58.0	42.0		67.5	32.5

To test for an effect of forest configuration, I added the forest configuration term (FRAG) to the models at the log and point scales that did not already include it (Table 2) and tested for significant interactions between the forest configuration term and all the covariates in the model. At the log scale, there was one significant interaction for both the beetle and fungus model (Table 6). The fungus model already included the forest configuration term (FRAG). At the point scale, there were no significant interactions, although again, the forest configuration term was already included in the fungus model. The scarcity of interactions with the forest configuration term implies that fungi and beetles are responding in a similar way to their habitat in both continuous and fragmented forests.

Table 6. Significant interactions between the forest configuration term (FRAG) and covariates at the log scale. No significant interactions existed at the point scale. Sign refers to the direction of the interaction. $P(\chi^2)$ refers to the p value from the G test.

Model	Interaction	Deviance	$P(\chi^2)$	Sign
Beetle incidence	FRAG:POS	6.73	0.0095	(+ve)
Fungus incidence	FRAG:BIGD + FRAG:BIGD^2	10.53	0.0052	(+ve)

Patch Occupancy

Patch occupancy was measured at all three scales for both the beetle and the fungus on the basis of habitable patches. Habitable patches were easily defined for fungi at the log (habitable logs included white birch, yellow birch, grey birch, large-toothed aspen and beech), point and site scales (habitable points or sites were those with HABDW values > 0). For the beetle, habitable patches were simply those containing fungal carps. Patch occupancy rates were calculated at the log and point scale separately for continuous and fragmented forests. The results are presented in Table 7, although these patterns are largely the ones indicated by the results of the predictive models (Table 2).

Table 7. Patch occupancy rates for habitable patches at different scales. Rates are also given for fragmented and continuous forests separately. χ^2 and p values are for goodness of fit tests comparing occupancy rates between fragmented and continuous forests. At all three scales, fungus occupancy rates were lower in fragmented forests. Beetle occupancy rates did not differ between forest configurations.

	All Observations		Fragmented forests		Continuous forests		χ^2	p-value
	n	% Occupied	n	% Occupied	n	% Occupied		
Fungus								
LOG	2899	11.80%	1621	8.10%	1278	16.50%	48	<0.00001
POINT	452	35.80%	235	31.60%	217	41.50%	4.44	0.035
SITE	90	90%	74	67.70%	16	100%	5.51	0.019
Beetle								
LOG	343	36.70%	132	41%	211	34.10%	1.33	0.25
POINT	167	46.70%	73	47.90%	94	45.70%	0.016	0.9
SITE	81	92.60%	65	93.80%	16	87.50%	0.11	0.74

Although the fungi showed lower patch occupancy rates at all scales, the patterns observed at smaller scales are constrained by the patterns at larger scales. For example, the number of logs that can be occupied is limited by number of occupied sites. To control for the effect of larger scale patterns, I conducted a second analysis for patches that were occupied at a larger scale. I compared point occupancy patterns only in occupied sites and log occupancy patterns only within occupied points (Table 8).

Table 8. Patch occupancy rates once the effect of differences in patch occupancy rates at a larger scale was removed. χ^2 and p values are for goodness of fit tests

Scale	Fragmented Forests		Continuous Forests		χ^2	p-value
	n	% occupied	n	% occupied		
FUNGUS						
POINTS WITHIN OCCUPIED SITES	226	31.8	217	41.0	4.0085	0.045
LOGS WITHIN OCCUPIED POINTS	634	18.0	593	34.1	41.4	<0.0001
BEETLE						
POINTS WITHIN OCCUPIED SITES	69	49.3	89	47.2	0.0099	0.92
LOGS WITHIN OCCUPIED POINTS	80	67.5	142	50.7	5.2	0.022

Fungi had lower occupancy rates in fragmented forests for both points in occupied sites, and for logs in occupied points. However, the age of points differed significantly between forest configurations (mean SITEAGE in fragmented: 43.7 ± 18.3 , in continuous: 77.4 ± 20.5 , $t_{(88)} = 6.5$, $p < 0.0001$). Beetles on the other hand, had higher parasitism (occupancy) rates for logs within occupied points in fragmented forests.

Lastly, I tested to see if there was an effect of woodlot isolation on log occupancy rates for both the fungus and the beetle. For both species, I built a base model using woodlot (site) variables (Table 9), and then tested for a significant effect using 10 isolation variables. Isolation variables included distance to nearest woodlot, up to mean distance to nearest 5 woodlots, as well as distance to nearest occupied (potential source) woodlot, up to the mean distance to the nearest 5 occupied woodlots. There were no significant isolation variables for either the fungus or the beetle. For the fungi, the base model revealed a positive effect of fungal abundance on log occupancy rates.

Table 9. Base models used to test for an isolation effect on log scale occupancy rates for both the beetle and the fungus in woodlots. The fungus model is generalized linear model with a poisson error distribution. The beetle model is a linear regression. Sign refers to the direction of the effect. The p value is from a G-test for the fungus model and an F-test for the beetle model.

Model	n	Variable	Sign	p-value	R ²
Fungus	74	log(SITECARPS)	(+ve)	< 0.0000	0.48
Beetle	34	SITEHWBA	(+ve)	0.0063	0.20

Discussion

A positive relationship between predictability and spatial scale is thought to be a common occurrence in natural systems (Wiens 1989, Jackson 1991). However, most of the evidence for this relationship has been inferred from studies not specifically addressing the issue of scale and predictability, and direct empirical evidence for this relationship is scarce (e.g. Wiens 1989, Jackson 1991). In this study, I found only limited evidence for an increase in predictability with scale once the effect of sample size was removed. The effect of sample size on predictive power, as measured by R^2 , is important as it compromises our ability to draw inferences from studies conducted at different sample sizes. Although this phenomenon is known in other fields (e.g. Seber 1977, Cramer 1987, Ohtani & Hasegawa 1993, Kromrey & Hines 1996) it has not been previously described in the ecological literature.

The theoretical premise for the relationship between scale and predictability is discussed by Wiens (1989). As the spatial grain of the response variable increases, a greater proportion of the total heterogeneity is contained within the grain. Thus variation within the grain gets averaged out and between grain variability decreases. A decrease in variability of the response for both studies with scale was observed in this study, for both the original models and for the subsets of sample size 50. Although Wiens' (1989) argument about decreasing variability is supported, there is little evidence to suggest that less variance in the response leads to increased predictability, as measured by R^2_L , since neither the beetle or fungus models showed a consistent increase in predictability with scale, as variation in the response decreased. If the variability of the response is

decreasing with scale, variability in the predictor variables is also likely to decrease, rendering them less useful as predictors. The decrease in variability with scale may help explain why variables measured at the same scale as the response contributed the most to the model, since variables measured at larger scales were generally averages of smaller scale data. My results question the generality of the scale-predictability relationship and suggest that a critical reevaluation of both the logic of and evidence for this relationship would be useful.

The significant predictor variables varied with the grain size of the response. This suggests that the relevant mechanisms or processes influencing beetle and fungus incidence are also changing with scale and highlights the scale-dependency of ecological processes and patterns. For example, in the beetle models, the amount of fungus present was important at the point and site scales, but not at the woodlot scale. Some variables exerted opposite effects at different scales. For example, in the fungus models, POINTBIRCH had a negative effect at the log scale but a positive effect at the point scale. Similar results were found by Wiens *et al.* (1986) who studied habitat associations of shrubsteppe birds at several spatial scales and the authors concluded that “the scale at which a system is viewed has major effects on the patterns that are detected and how they are interpreted...”.

It is puzzling that several variables had opposite effects of what would have been predicted knowing the habitat requirements of the fungus and beetle. For example, why would POINTASPEN and POINTBIRCH have a negative effect on the incidence of the fungus at the log scale? This relationship may be the result of a dilution effect, whereby

having numerous dead logs at the point level reduces the probability of any one log having fungi present. This explanation does not conflict with the generally positive effect of deadwood on incidence seen at the point scale. Alternatively, opposite signs and unstable parameter estimates can occasionally result from multicollinearity between independent variables (Neter *et al.* 1990), although multicollinearity does not affect the overall significance of the variables (Myers 1990, Neter *et al.* 1990). Hence, care must be taken before inferring causal relationships.

Large scale habitat fragmentation had a positive effect on beetle parasitism rates at one of two scales within forest stands. This result is in contrast with most studies of the effect of large-scale fragmentation on insects, which report negative impacts (Didham *et al.* 1996, Kruess & Tscharntke 1993, but see Aizen & Feinsinger 1994). In other systems, however, there is evidence that fragmentation can increase parasitism rates, as in the case of nest parasitism of songbirds by brown-headed cowbirds (Paton 1994). For the cowbird, fragmentation serves to increase the exposure of forest dwelling hosts to the open/edge dwelling nest parasite (Loye & Carroll 1995). This rationale does not explain the pattern observed in this study, as both the beetle and the fungus are forest-dwelling species. Higher parasitism rates of fungi in occupied points from fragmented forests may result from 1) beetles in fragmented sites having a higher tendency of staying within a point than in continuous sites, which would tend to increase habitat use within a point or 2) beetles in fragmented sites showing a greater aggregative response than in continuous sites. At present, insufficient evidence exists to discern between these two possibilities.

Results from both the predictive models and the patch occupancy comparisons indicated that large scale habitat fragmentation had a pervasive negative impact on the fungi. It is possible that the difference in occupancy rates (but not the results of the predictive models) resulted from differences in forest ages between forest configurations. It seems unlikely, however, that, at least at the smallest scale, time would be an important factor in the colonization of other logs within a point, when mature sporocarps produce upwards of 1×10^{11} spores per year. This reasoning, combined with evidence of a negative impact of fragmentation from predictive models, suggests that difference in occupancy rates are not solely due to differences in age. I could find no published studies that examined the effect of habitat fragmentation on fungi, although Dyer (1995) suggests that species that disperse passively (as does the hoof fungus) are more sensitive to habitat fragmentation than species with an active dispersal mechanism.

In conclusion, this study reported 4 important results: 1) contrary to current theory and despite a decrease in the variance of the response variable, predictive power did not increase consistently with scale. 2) It is critical to consider the effect of small sample sizes on measuring R^2 in both linear and logistic models when trying to compare models. 3) The importance of predictor variables changes with scale, but variables measured at the same scale as the response are generally better predictors than variables measured at larger scales. 4) Habitat fragmentation has a negative effect on the hoof fungus at all three scales, but a positive effect on the forked fungus beetle at one scale. The use of a multi-scale perspective allowed for a greater appreciation of the magnitude of the negative effect of habitat fragmentation on the fungus, and detected a positive

effect on the beetle that would otherwise have been missed. This study highlights how forest fragmentation can affect species dynamics not simply at the scale of the forest fragment but also within fragments.

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General Conclusions

Consideration of spatial scale brought a greater understanding both to the effects of spatial isolation and to predicting the incidence of the beetle and the fungus. In the case of spatial isolation, a multiscale approach revealed that patch isolation was important at all three scales. This is surprising, as each scale encompassed a very different range of values (mean \pm S.D. of isolation values - carp scale: 0.20 ± 0.24 metres, cluster scale: 11.19 ± 7.22 metres, woodlot scale: 453.5 ± 330 metres). However, as predicted, isolation was weaker at the smallest scale than at the largest scale. These results led to speculation about the use of different movement mechanisms, walking vs. flying, at different scales and the possibility of spatially relative movement rules. In addition, the density of patches at the two smaller scales did not influence the isolation effect. Thus, although the effect of isolation appears to be scale-dependent, isolation can i) be important at different scales due to different processes occurring at different scales and ii) be scale-independent over small changes in scale.

In the study of prediction, scale was informative as it revealed that the importance of variables differed with scale. Some variables were important at several scales, whereas some variables were only important at one scale. However, I did not find the expected relationship between increasing predictability and scale, despite a decrease in the variance of the response variable with scale. These results suggest that a review of the logical underpinning and empirical evidence for a scale-predictability relationship would be useful. I also found that similar to the OLS R^2 , the mean and variance of the R^2 equivalent for logistic regression varied with sample size. This observation has

implications for researchers comparing predictive power of models with differing sample size.

A multiscale approach revealed interesting differences in patch occupancy rates between fragmented and continuous forests. Patch occupancy rates for fungi were not only lower at the point scale in fragmented forests, but once this difference in occupancy rates was removed (by considering only occupied patches), patch occupancy at the log scale was also lower in fragmented than in continuous forests. This may be the first documented evidence for an effect of habitat fragmentation on a fungus.

The effect of habitat fragmentation on the beetle would likely have been missed without a multiscale approach. Only within colonized points did we see a difference between log scale occupancy rates. Unlike the fungi, the beetle had higher occupancy rates in fragmented than in continuous forests. This result is interesting, given that the isolation study revealed that isolated woodlots have a lower probability of being occupied by beetles. This result is also contrary to published findings of the effect of habitat fragmentation on insects, which have generally been negative for parasites (Didham *et al.* 1996, Kruess & Tschamtkke 1993).

In conclusion, these two studies clearly showed both the scale-dependency of ecological patterns and processes and the importance of adopting a multi-scale perspective in ecological research.

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