Changing importance of habitat structure across multiple spatial scales for three species of insects

Meg A. Krawchuk and Philip D. Taylor

Considerable scientific effort has gone into examining how the spatial structure of habitat influences organism distribution and abundance in both theoretical and applied contexts. An emerging conclusion from these works is that the overall amount of habitat in the landscape matters most for species persistence and that more local attributes of habitat structure such as the size and arrangement of patches is of secondary importance. In this study, we quantify how and when the effects of habitat configuration (patch size and isolation) influence the density of three species of insects (Order: Diptera; *Wyeomyia smithii*, *Metriocnemus knabi*, *Fletcherimyia fletcheri*) whose larvae are found exclusively in identical habitats (the water-filled leaves of pitcher plants – *Sarracenia purpurea*) in a system that is naturally patchy at multiple spatial scales. We illustrate that relationships with configuration exist regardless of the overall amount of habitat in the broader landscape, and that there are distinct changes in the relationship between insect density and habitat configuration across multiple spatial scales. In general, patch size is more important within the movement range of the individual and isolation is important at larger, aggregation scales. Thus we demonstrate that a) both the amount and configuration of habitat are important attributes of species distribution; b) responses to measures of configuration can be scaled to processes such as movement and c) that hierarchical frameworks extending across very broad scales are essential for understanding how species respond to habitat structure and their role in ecosystem function.

M. A. Krawchuk and P. D. Taylor, Atlantic Co-operative Wildlife Research Network, Biology Dept, Acadia Univ., Wolfville, Nova Scotia, Canada B0P 1X0. Present address for MAK: Dept of Renewable Resources, Univ. of Alberta, 7-51 General Services Building, Edmonton, Alberta, Canada T6G 2H1 (megk@ualberta.ca).

Numerous studies suggest that retaining large amounts of habitat must be the primary concern for conservation (McGarigal and McComb 1995, Fahrig 1997, Bender et al. 1998, Drolet et al. 1999, Trzcinski et al. 1999). Nevertheless, the importance of habitat configuration (e.g. isolation, nearest neighbour distance, patch size, spatial arrangement, level of fragmentation) has been emphasized for other species at some spatial and temporal scales (McGarigal and McComb 1995, Fahrig 1998, Rukke and Midtgaard 1998, Hanski 1999, Villard et al. 1999, Menéndez and Thomas 2000, Flather and Bevers 2002). It is not surprising that configuration is found to have little relevance for organisms in landscapes with abundant habitat; such landscapes contain large or close patches of habitat regardless of their particular arrangement. However, as the amount of habitat decreases patches that remain will become smaller and/or more isolated from one another since amount and configuration are inherently linked (Gustafson and Parker 1992). Thresholds have been demonstrated where the influence of configuration on distribution/abundance of a species appears to increase dramatically as the amount of habitat decreases in the landscape (Andrén 1994, Fahrig 1997, Trzcinski et al. 1999, Villard et al. 1999). This suggests that we should be looking for effects of configuration on the distribution and abundance of organisms over and above the obvious effects of composition, but that we must focus our attention on appropriate scales.

Ecological phenomena occur across a hierarchy of spatial (and temporal) scale and the relative importance of habitat structure likely changes across its continuum. In other words, the distribution of individuals may be influenced differently by habitat structure at local levels compared to broader levels of scale (Wiens 1989). In addition, for a given organism, the influence of amount and configuration of habitat may vary among spatial scales. Furthermore, patch size and isolation are frequently amalgamated to represent configuration, though in general patch size may influence the rate of patch extinction (on a population scale) or selection (on an individual scale) of/by a species, whereas isolation influences the colonization or accessibility of a habitat patch (Matter 1997, Hanski 1999). Thus, the relative influence of patch size and isolation may also change dependent on the amount of habitat in the landscape (Trzcinski et al. 1999), among spatial scales (Rukke and Midtgaard 1998, Menéndez and Thomas 2000, Nielsen and Ims 2000), and among species (Ray and Hastings 1996). When we detect these different responses across scales, we can infer that the underlying ecological processes that give rise to the patterns are also different.

Previous studies examining organism response (either landscape- or patch-based) to amount and/or configuration of habitat have had a limited ability to generalize their findings because they: explore a single species' response (Rukke and Midtgaard 1998, Bowers and Dooley 1999); examine relationships at a single spatial scale (McGarigal and McComb 1995, Fahrig 1997, 1998, Drolet et al. 1999, Trzcinski et al. 1999, Villard et al. 1999); have inadequate replication at multiple scales (Nielsen and Ims 2000); and/or lack independent measures of structural attributes at each scale (Rukke and Midtgaard 1998, Bowers and Dooley 1999, Hughes et al. 1999). We suggest that conclusions from both theoretical and empirical studies that examine these questions at single scales, or consider only amount, patch size or isolation of habitat will give rise to limited conclusions and potentially harmful management recommendations.

Here, we present a study that addresses many of these concerns by identifying relationships with two elements of habitat configuration (patch size and isolation) concurrently within a hierarchy of spatial scale for three species of insects living within a naturally patchy environment. We use a framework wherein patch configuration and the amount of habitat in the landscape are defined at each of four spatial scales. For each of three study species at each spatial scale we hypothesize that if configuration metrics (patch size and isolation) are important structural attributes of within-patch dynamics then we will detect a significant relationship between larval density and those metrics independent of relationships with the amount

of habitat in the broader 'landscape' context (i.e. within the next broadest spatial scale). If the influence of patch size and isolation vary with the amount of habitat in the broader context then we will detect a significant interaction between configuration metrics and amount of habitat.

Methods

We examined the relationship between habitat structure and the larval abundance of three species of insects that develop exclusively in the vessel-shaped leaves of the pitcher plant, *Sarracenia purpurea* L. (Sarraceniaceae) (Heard 1994). *Sarracenia purpurea* is a perennial plant abundant in nitrogen-poor areas of peatland. In our study site in western Newfoundland, Canada (UTM: 5514000N 478000E Zone 21U), peatlands containing *S. purpurea* occur as discrete patches within a matrix of boreal scrub and forest (Fig. 1). Within a peatland, these plants can be found clustered together or isolated by tens of meters. Leaf size and the number of leaves per plant are also highly variable (Miner and Taylor 2002). The eggs and/or larvae of the autogenous mosquito, *Wyeomyia smithii* Coq. (Diptera: Culicidae), the midge, *Metriocnemus knabi* Coq. (Diptera: Chironomidae), and the sarcophagid, *Fletcherimyia fletcheri* Aldrich (Diptera: Sarcophagidae) inhabit the fluid-filled leaves of *S. purpurea* during their summer development. All three species of insects are univoltine in this region (Forsyth and Robertson 1975, Heard 1994, Krawchuk, pers. obs.). Multiple females of *W. smithii* and *M. knabi* may deposit eggs in a given leaf, whereas typically, only a single *F. fletcheri* larva is deposited. Though information about these larval stages is abundant, little is known about adult behaviour or life history.

Sampling

We sampled the system at four nested spatial scales: (peatlands, points within peatlands, plants within points, and leaves within plants) replicated across two 64 km² landscapes – one consisting of roughly 7 % peatland, the other consisting of 20 % peatland. We structured the sampling to have balanced, independent effects of amount and configuration (patch size and isolation) of habitat at each spatial scale. Thus, in each landscape, we surveyed 20 smaller (< 5 ha) and larger (> 8 ha) peatlands isolated from their nearest neighbour by short (< 200 m) and long (> 230 m) distances. Within each peatland we selected between two and eight sampling points (more points in larger peatlands) < 20 m from the edge (because plant size is known to decrease with distance from

Fig. 1. Counts of *Wyeomyia smithii*, *Metriocnemus knabi* and *Fletcherimyia fletcheri* larvae were collected from *Sarracenia purpurea* leaves (a). Three leaves were sampled from each plant (b), three plants were surveyed from each point (c), and between two and eight points were sampled from each peatland (d) surrounded by a boreal forest matrix. Natural groupings of plants are displayed as shaded areas within (white) peatlands. Patch size was measured at four scales as: volume of a leaf, number of leaves per plant, number of plants within a point and both the abundance of plants in a peatland and the area of the peatland. Patch isolation was measured at three scales as: distance to next nearest plant, an index of distance from a point to the next group of plants (e), and the distance to next nearest peatland (f). In addition, peatland-scale context (amount of habitat) was measured as the proportion of peatland in each of two landscapes.
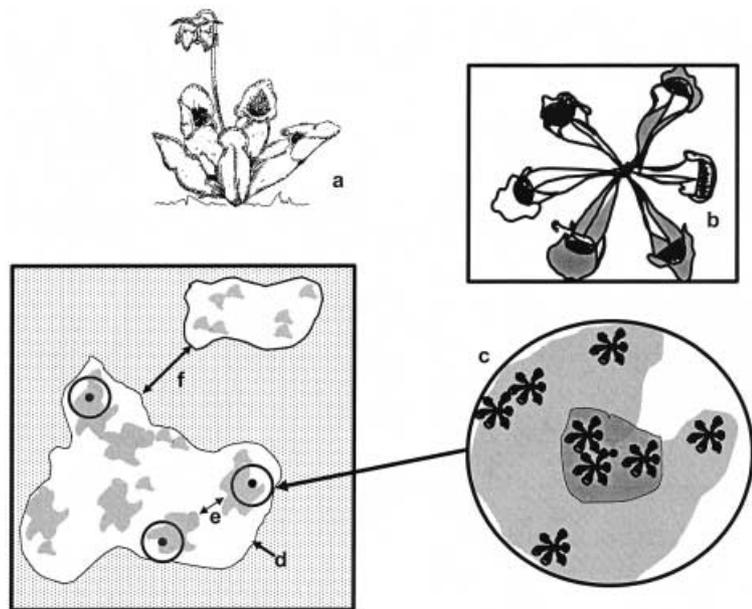
the edge of a peatland; Miner and Taylor 2002). The location of points was selected to have a balanced sampling design of habitat structure. We selected the three closest plants to each point, and from each plant we then sampled the larval community from three randomly selected suitable leaves (Fig. 1). A leaf was considered suitable if it had no rips and was succulent, with a large enough opening for successful navigation by adults of the three study species.

We removed leaves from the plants, and the actual volume of fluid in the leaf was measured by pouring the leaf contents into a 50 ml graduated cylinder. Contents were then dumped into an enamel sorting tray, where the number of larvae of the three target species was counted. The size (potential volume) of the leaf was estimated by filling the leaf to capacity with water then measuring its fluid volume. Leaves were then dissected to completely assess larval abundance and the amount of detritus in each leaf. Detritus was estimated on a simple scale: none, little, abundant. All of these variables are known to be correlated with inquiline abundance (Nastase et al. 1995, Miner and Taylor 2002).

The larvae of *W. smithii* and *M. knabi* overwinter in the leaves of *S. purpurea*, then emerge, mate and oviposit during the spring and summer, so data were collected in two sessions, 6–27 June and 7–25 August 1999 to sample the distribution of both the overwintered and current cohort of larvae (Heard 1994). However, in the fall *F. fletcheri* larvae move into the surrounding sphagnum moss to pupate. They overwinter and emerge in late spring, and so we only encountered them in the second sampling session.

Elements of habitat structure

At each of the four nested spatial scales (leaf, plant, point, peatland) we measured variables that represented the configuration (patch isolation and patch size) and amount (context) of habitat at that particular scale (except the leaf level, for which there was no suitable isolation variable; Fig. 1, Table 1).

Configuration

Patch size
We considered the following as measures of habitat patch size: leaf scale – the volume of the leaf; plant scale – the number of leaves per plant, point scale – the number of plants within a two m radius of the point; and peatland scale – both the area of each peatland and the abundance of mature, healthy plants (i.e. peatland area and quality). We estimated peatland plant abundance from the multiplication of plant density and peatland area. Plant density was based on counts of healthy plants in two randomly chosen one m-wide transects across each peatland.

Patch isolation
We considered the following as measures of habitat patch isolation: leaf scale – no suitable measure; plant scale – the distance to the nearest neighbouring plant; point scale – plant density in the peatland (an index calculated from transects described above); peatland scale – the distance to the nearest neighbouring peatland. Since point isolation was derived from the density

Table 1. Data summary of dependent and independent variables used in generalized linear mixed models.

Description	Structural variable	June sample (Mean ± SD)	August sample (Mean ± SD)
Metriocnemus knabi (larval count per leaf)		0–90 (9 ± 9)	0–65 (6 ± 7)
Wyeomyia smithii (larval count per leaf)		0–24 (1 ± 2)	0–37 (2 ± 3)
Fletcherimyia fletcheri (larval count per leaf)		na	0 or 1 (0.05 ± 0.2)
potential volume (mL)	leaf: patch size	1–49 (12 ± 7)	0.5–48 (10 ± 6)
actual volume (mL)	leaf: patch size	0–27 (2 ± 3)	0–40 (6 ± 5)
detritus (categorical)		0–2	0–2
number of leaves	leaf: amount of habitat plant: patch size	3–47 (7 ± 6)	3–32 (7 ± 4)
distance to nearest neighbour (m)	plant: patch isolation	0.02–3.5 (0.5 ± 0.5)	0.03–2.7 (0.4 ± 0.4)
plants within 2 m radius of centre	plant: amount of habitat point: patch size	2–62 (14 ± 11)	2–62 (14 ± 11)
point neighbour index (m²)	point: patch isolation	0.1–0.5 (0.7 ± 0.6)	0.1–0.5 (0.7 ± 0.6)
peatland area (km²)	point: amount of habitat peatland: patch size	0.002–0.2 (0.04 ± 0.04)	0.002–0.2 (0.04 ± 0.04)
abundance of plants/peatland	point: amount of habitat	1700–77535 (19357 ± 18110)	1700–77535 (19357 ± 18110)
	peatland: patch size (quality)		
peatland nearest neighbour (km)	peatland: patch isolation	0.02–0.7 (0.2 ± 0.1)	0.02–0.7 (0.2 ± 0.1)
proportion of peatland in landscape	peatland: amount of habitat	landscape A: 7% landscape B: 21%	landscape A: 7% landscape B: 21%

of plants within a peatland we consider it a relative index of isolation. This point measure is acquired in a different dimension than isolation at the plant or peatland scale, the index is measured in m² (see Results for further concerns). All peatland isolation and area calculations were made using SPANS GIS software (Intera Tydac Technologies, Nepean, Ontario, Canada) on scanned 1:50 000 aerial photographs taken in 1985. The structure of peatlands and the surrounding matrix of coniferous-dominated boreal forest have changed very little from 1985 to 1999 (McCarthy 2001).

Amount

For each spatial scale where the two elements of configuration were estimated, we also estimated the amount of habitat available in the surrounding context (in other words, at the next broadest spatial scale). It is extremely important to recognize that with this study design, habitat patch size and isolation are measures of patch configuration within the landscape and that amount is a measure of overall habitat available in the landscape wherein these patches are located. With the exception of landscape and leaf volume, habitat patch size at one scale also represented amount of habitat at the adjacent scale. We considered the following as measures of amount of habitat: leaf scale – the number of leaves on a plant; plant scale – the number of plants within a 2 m radius circle; point scale – the area and quality of the peatland; peatland scale – the total amount of peatland in the landscape.

Statistical models

The relationship between larval distribution and habitat structure was assessed by fitting separate generalized linear mixed models (GLMMs) for each species. Data are summarized in Table 1. The study design made it necessary to account for the nested structure of the data when assessing the significance of the fixed effects representing amount and configuration. In the GLMM, the fixed effects were the terms for patch size, isolation, and amount of habitat, and the random (i.e. grouping, cluster) effects were factors for each level of the spatial hierarchy (leaf nested within plant nested within point nested within peatland within landscape). Models were fit in the R 1.4.1 (The R Design Team 2002) statistical program under the glmmPQL routine using a Poisson family argument for *W. smithii* and *M. knabi* models and using a binomial family argument for *F. fletcheri* (Pinheiro and Bates 2000).

In all models we first accounted for variation in larval abundance (or incidence, for *F. fletcheri*) due to leaf-level effects by fitting terms for leaf size (potential volume), actual volume of water in the leaf, amount of detritus, and the presence or absence of other target species (which are known to influence community composition; Heard 1994, Miner and Taylor 2002). We then tested for additional relationships with habitat configuration (patch size and isolation) at the plant, point and peatland scales. Since the leaf-level effects are treated as a priori co-variates, the relationships at these broader spatial scales can be considered to relate to the larval density per leaf. For each species we fit a series of models beginning with the fine scales, and moving

towards broader scales. The main configuration terms from finer scales were retained in the models fit at each of the broader spatial scales.

We assessed the independence of patch size and isolation metrics at each scale by comparing models where the two terms were fit in opposite order. Further, we verified the independent significance of configuration above and beyond the influence of amount of habitat by including amount of habitat at each scale prior to the two configuration terms (patch size and isolation). After this verification, the terms for amount of habitat were removed before testing for the effects of configuration at the next spatial scale, since as mentioned above, patch size is equivalent to amount of habitat at finer spatial scales.

We determined whether any configuration effects were dependent on the broader-scale amount of habitat. For example, isolation of habitat at one scale may only be important when, at a broader scale, there is limited habitat (Jonsen and Taylor 2000). We did this by including an interaction term between the habitat amount and configuration terms at each scale. In all cases, interaction terms were removed before testing configuration effects at the next broadest scale.

We interpreted the results of all models by assessing: the estimated p-value of the likelihood ratio statistic associated with the reduction in deviance in the model obtained by the addition of that term, the significance of the t-value of the Wald statistic, and relative size of the standard error of the estimated coefficient for each term (Harlow et al. 1997, Pinheiro and Bates 2000). Where a significant relationship was detected with point isolation, we also fit a quadratic term to the model to assess if a simple non-linear trend existed; this was done to account for the disparity in measurement units of isolation among spatial scales (see Configuration: *Patch isolation*). Residual plots were used to visually assess model fit. A value of $\alpha = 0.05$ was used to assess significance. No post-hoc power analysis was performed (Hoenig and Heisey 2001).

Spatial scales of aggregation

Variance components are estimates of the random effects in the GLMM and are provided in association with the fitting of each model. Variance components analysis (VCA) can be used to reveal differences in the variance of data grouped at various scales (Greig-Smith 1979, Hughes et al. 1999). These differences describe natural aggregation or patchiness of organisms and thus can be used to infer spatial scales of movement (Harvey and Miller 1996, Miner and Taylor 2002).

Results

The proportion of leaves occupied by *W. smithii* larvae in the samples was 0.3 (503/1817) and 0.4 (702/1817)

for the first and second surveys respectively; 0.9 (1703/1817) and 0.8 (1528/1817) for *M. knabi*; and 0.05 (98/1817) in the second sample for *F. fletcheri* (Table 1). There was minimal correlation between configuration and amount of habitat (it never exceeded 0.3) indicating that at each spatial scale, we successfully surveyed a range in patch size and isolation for a given amount of habitat. The mean (± 1SD) correlation between patch size and amount of habitat was 0.08 (± 0.09), and between patch isolation and amount of habitat was 0.09 (± 0.06).

A significant relationship with the two metrics of configuration was detected for all three species and these occurred across all spatial scales (Fig. 2, Table 2). There was low correlation in estimates of the effects of patch size and isolation at each scale since the order in which these terms were included in the models did not change their polarity or significance for any species. Furthermore, the significance and signs of the coefficients did not change when amount of habitat was fit prior to patch size and isolation terms, suggesting that the influence of configuration exists over and above any direct relationship described by the amount of habitat (Table 2 summarizes model parameters estimated with the inclusion of the main effects of patch size and isolation). The abundance of plants per peatland (quality) was correlated with the index of point isolation
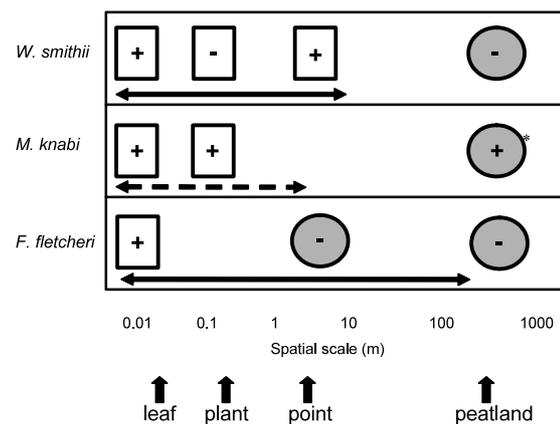
Fig. 2. The relationship between *Wyeomyia smithii*, *Metriocnemus knabi* and *Fletcherimyia fletcheri* larval density to habitat configuration at four spatial scales. The range of movement potential estimated from mark-recapture experiments with *Wyeomyia smithii* and *Fletcherimyia fletcheri* is indicated with a solid arrow. Estimated movement potential from VCA and personal observations of *Metriocnemus knabi* is indicated with a dashed arrow. Symbols represent a significant relationship with patch size (□), and patch isolation (●) summarizing parameter estimates of June and August sampling sessions (Table 2; the * indicates significance in August only). The direction of response (either + or −) is derived from parameter estimates of the GLMM statistical models. The significance of habitat configuration was species-dependent but was detected at all spatial scales. Patch size influenced distribution at relatively fine, and patch isolation at broader spatial scales, though species responded at different absolute scales.

Table 2. Coefficients and 95% confidence intervals from models describing the relationship between *Wyeomyia smithii*, *Metriocnemus knabi*, and *Fletcherimyia fletcheri* density and habitat structure (from the first (June) and second (August) sampling sessions). Values in bold indicate significance at $p<0.05$.

Species	Structural effect	Leaf		Plant		Point		Peatland (quality)		Peatland (area)	
		coef	95% ci	coef	95% ci	coef	95% ci	coef	95% ci	coef	95% ci
W. smithii	Patch size (June)	**+0.1**	**±0.03**	**−0.02**	**±0.02**	**+0.02**	**±0.01**	+0.000001	±0.00009	+3.1	±11.6
	Patch size (August)	**+0.09**	**±0.02**	**−0.03**	**±0.02**	**+0.02**	**±0.01**	+0.000001	±0.00001	−6.4	±9.9
	Patch isolation (June)	na	na	+0.02	±0.3	−0.02	±0.3	**−2.9**	**±1.6**	na	na
	Patch isolation (August)	na	na	+0.2	±0.3	+0.07	±0.2	**−2.3**	**±1.9**	na	na
M. knabi	Patch size (June)	**+0.05**	**±0.009**	**+0.01**	**±0.008**	−0.004	±0.006	+0.000004	±0.000004	+2.3	±3.8
	Patch size (August)	**+0.09**	**±0.01**	**+0.02**	**±0.07**	−0.0002	±0.003	+0.000002	±0.000002	−2.4	±4.8
	Patch isolation (June)	na	na	+0.006	±0.1	−0.07	±0.1	+0.3	±0.5	na	na
	Patch isolation (August)	na	na	+0.03	±0.08	−0.07	±0.07	**+1.1**	**±0.3**	na	na
F. fletcheri	Patch size (August)	**+0.09**	**±0.03**	−0.03	±0.03	−0.01	±0.01	−0.000008	±0.000008	+4.9	±6.6
	Patch isolation (August)	na	na	−0.4	±0.5	**−0.5**	**±0.2**	**−3.2**	**±0.9**	na	na

however significance level did not change with the exclusion of point isolation from the peatland-scale model for any species.

In general, relationships between larval density and patch size existed at finer scales, and between patch isolation at broader scales (Fig. 2, Table 2). Parameter estimates from the first and second sampling sessions were similar for *W. smithii* and for *M. knabi* (Fig. 3), however for the latter a significant relationship with patch isolation at the peatland scale was only detected in the August sample. For *F. fletcheri*, significant structure terms were patch size at the leaf scale, and isolation at the point and peatland scales. A quadratic point isolation term was not significant in the model. No significant interaction effects between amount of habitat and either patch isolation or patch size were detected for any species.

Variance components analysis displayed an unequal distribution of variance between the random effects leaf, plant, plot and peatland and the pattern was similar in both sample sessions. For *W. smithii*, variation was distributed as leaf > point ≈ plant > peatland. For *M. knabi*, variation was distributed as leaf > plant ≈ point > peatland. For *F. fletcheri*, variation was distributed as peatland > point ≈ plant ≈ leaf.

Discussion

Significant relationships between larval density and configuration (patch size and isolation) were detected for all three species in this study system, and existed above and beyond a relationship with amount of habitat. Moreover, the importance of the configuration effects of patch size versus isolation changed with spatial scale and in a different way for each species. We could detect no consistent evidence for interactions between habitat amount and either patch size or isolation at any spatial scale that would suggest thresholds where the influence of configuration increased with decreasing amounts of habitat.

We can consider the within-leaf density of larval *W. smithii*, *M. knabi* and *F. fletcheri* as an index of adult movement (i.e. the visitation of adult females to a leaf), since rates of oviposition are roughly equal among suitable leaves (Forsyth and Robertson 1975, Heard 1994). As such, the observed relationships between larval density and configuration infer that patch size and isolation strongly influence the accessibility or selection of habitat by adults of each species.

Wyeomyia smithii density is related to patch size at the finest three spatial scales (leaf, plant, point), and to patch isolation at the broadest (peatland) scale. The scales can be thought of as reflecting local through population-level processes. Local processes include interactions between individual behaviors and the structure of the habitat (oviposition decisions, local
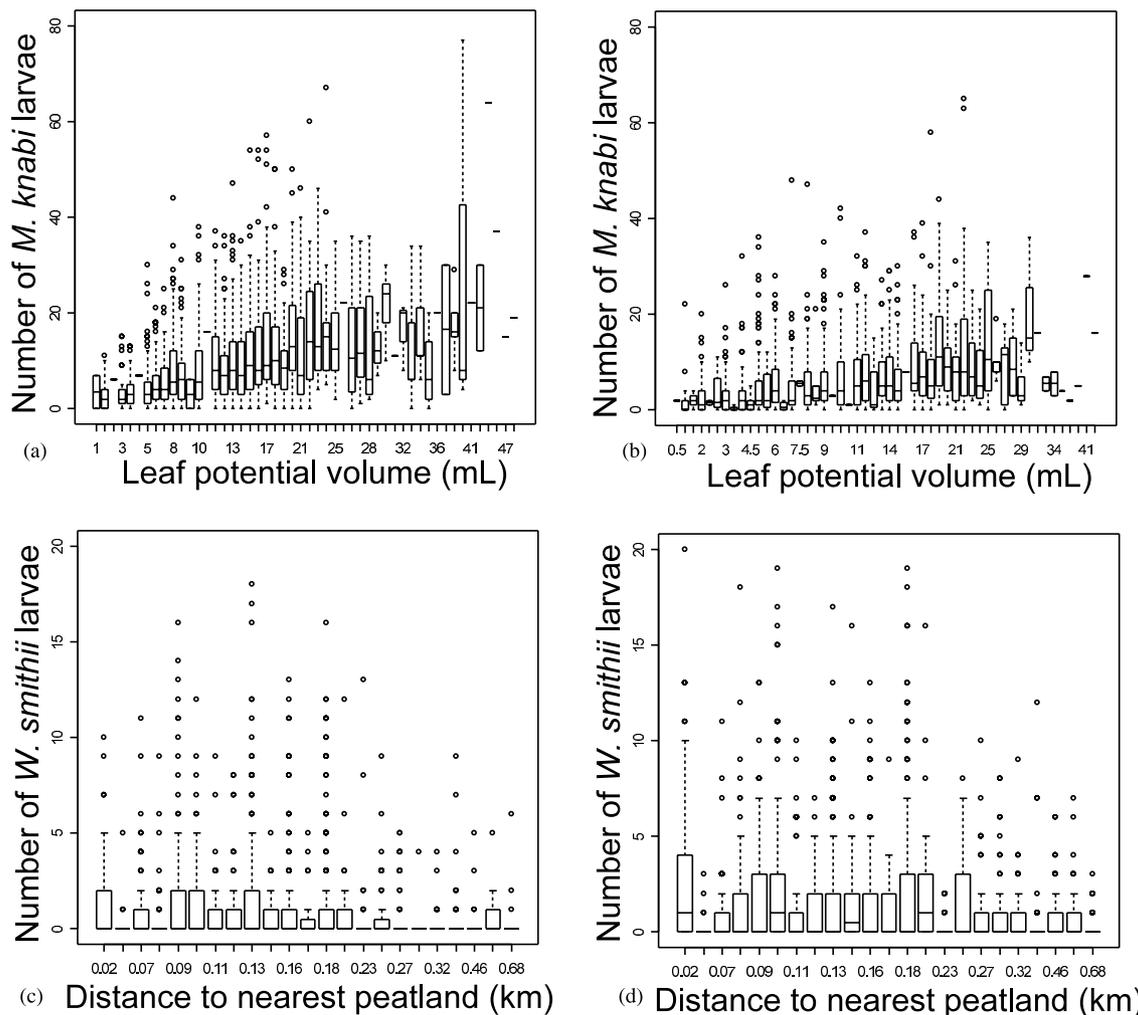
Fig. 3. An example of the similar relationships observed between the two sampling sessions. Each box within a plot illustrates the interquartile range of the data. The median is indicated by a horizontal strike, extreme points are illustrated by whiskers and outlying points. There was a significant positive relationship between *Metriocnemus knabi* larvae and the potential volume of each sample leaf in (a) June and (b) August. Similarly, a significant negative relationship between *Wyeomyia smithii* larvae and peatland isolation existed in both (c) June and (d) August. Note that these plots simply illustrate patterns in raw abundance.

movement abilities), while population-level processes include broader-scale movement or effects of environment (Miner and Taylor 2002). Movement distances observed in release-recapture experiments run simultaneously to the census work indicated a mean move distance of 11 m (± 3 m (± 1 SE); 840 released, 35 recaptured) and a maximum of 84 m suggesting that most *W. smithii* move within portions of a single peatland throughout their life time (both dispersal and adult movement). Genetic work has inferred movement at a similar order of magnitude by showing that panmixis occurs within a peatland but not among peatlands (Istock and Weisburg 1987). The negative relationship with peatland isolation suggests that successful movement among peatlands varies inversely with between-peatland distance, manifested as a de-

creased density in more isolated peatlands. Further, VCA of the census data showed greatest variation at the leaf scale indicating greater independence of distribution among leaves than among plants and points within peatlands. Overall, these data suggest that individual *W. smithii* likely oviposit in one leaf per plant, frequently move among plants and points, but rarely among peatlands. Incidental observations of weak and erratic flying by adult *W. smithii* concur (Bradshaw 1983, Krawchuk pers. obs).

In general, we attribute positive relationships with patch size to individual mechanisms such as recruitment and/or survivorship (see Fahrig and Jonsen 1998 for a thorough discussion of mechanisms driving such relationships) though these processes were not addressed in this study. However, the observed higher *W. smithii*

density in smaller plants may result from repeated oviposition within suitable leaves if neighbouring plants are too distant to detect. Alternatively, very large plants (e.g. with 47 leaves, Table 1) may provide overwhelming resources relative the the population of ovipositing *W. smithii* within the area resulting in decreased numbers when only three leaves are sampled per plant. These hypotheses deserve further testing.

The *M. knabi* data similarly illustrate changes in the significance of relationships with habitat configuration at increasing scales. There is a positive effect of patch size at the leaf and plant scale, and patch isolation is important at the peatland scale (August sample). Variance components analysis of the census data illustrated greater variation among leaves than plants and points for *M. knabi*. This suggests that individual midges have limited movement potential and cluster around plants and points similarly to *W. smithii*. If we match relative biological scales, *W. smithii* and *M. knabi* both respond to patch size locally (individually) and patch isolation at broader (aggregation) scales. The positive relationship at the peatland scale suggests that there are additional higher-level regional processes at work.

A significant relationship between *F. fletcheri* larval density and patch size only occurred at the finer, leaf scale suggesting larger leaves are preferable larviposition sites for the fly. Patch isolation was significant at the broader point and peatland scales. Unlike *W. smithii* and *M. knabi* whose larvae over-winter in the leaves of *S. purpurea* (Heard 1994), *F. fletcheri* larvae move from the plant, and pupate in the surrounding sphagnum moss where they over-winter and from which they emerge as adults (Forsyth and Robertson 1975). Adult *F. fletcheri* roost and mate within the flower heads of *S. purpurea* (Krawchuk and Taylor 1999) so they may function as pollinators for the plant. We speculate that the relationship with habitat isolation at the point scale might be linked to mechanisms influencing survivorship of individual pupae and tenerals and/or the mating success of adults. Patch isolation was also significant at the peatland scale. A small mark-recapture experiment of *F. fletcheri* performed simultaneously to the census work showed a mean movement distance of 34 m (± 19 m (± 1 SE); marked $= 35$, recaptured $= 9$), with a maximum recorded move distance of 184 m. This may underestimate the adult movement potential of *F. fletcheri* (and also dispersal) since this record represents the length of the peatland, and we did not sample beyond its edge. This suggests the potential for fluent cross-peatland movement by adults and consequently more frequent inter-peatland movement than with the smaller species. However, the negative relationship suggests that distance among peatlands may still restrict *F. fletcheri* movement. Further, the distribution of *F. fletcheri* may be regulated by additional variables, since larvae were detected in only 5 % of the leaf samples.

This study system provides a range of natural structural scenarios varying patch configuration within many contexts (amount of habitat) at multiple scales. It does not include large, continuous tracts of habitat consistent with studies of forest fragmentation where a landscape can include up to 100 % habitat. Thus it is possible that configuration effects at a given scale could decrease if surveys were performed in landscapes with even more plants or peatlands, or increase/decrease if the matrix among peatlands changed from forest as a result of forest harvest. However, based on the movement ability of the three species, we suggest that at finer spatial scales the habitat measured here is relatively continuous, and still we detect configuration effects above and beyond general relationships with amount of habitat. Depending on the characteristics of the organism and the structure of the landscape (e.g. matrix type Fahrig 2001, Ricketts 2001), attention to configuration of habitat may be influential even in landscapes containing large amounts of habitat. Here, we illustrate that for specialized species living where habitat in the landscape is abundant but discontinuous, the ecological value of the amount of habitat available in the landscape can be affected by its configuration. We argue that both amount and configuration of habitat are likely important for many species, but may be manifested differently among spatial scales and may be masked by our inability to measure habitat effectively. By using a multi-scale framework we show that both the amount and configuration of suitable habitat are important to organisms, and that their relative importance changes with increasing spatial scale. In addition, the level of these changes is different for various organisms and can be related to scales of critical processes – here we postulate a link with movement potential (Ludwig et al. 2000). This study further reinforces the notion that not only does broader-scale structural information increase our understanding of local patterns (Mazerolle and Villard 1999) but, that local-scale information increases our understanding of broad-scale phenomena.

The issue of scale has been increasingly addressed in ecology throughout the past decade (Kotliar and Wiens 1990, Holling 1992, Levin 1992, Wu and Loucks 1995). Studies addressing broad scale (e.g. ecosystem) questions are becoming more common (Kline et al. 2001), however, we argue that many studies are still not being conducted at either multiple or sufficiently large spatial scales to capture the important processes and patterns that are governing population structure and ecosystem dynamics. In this study, movement potential of all three species of insects is much less than that of most birds and mammals. Yet, the smallest species (*M. knabi* is roughly 3 mm in body length) appears to be influenced by spatial patterns at scales measured in kilometers. To this we add a call for researchers to strive to explore attributes relating to both process and pattern at very broad scales in future studies.

160

References

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

Bender, D. J., Contreras, T. A. and Fahrig, L. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. – Ecology 79: 517–533.

Bowers, M. A. and Dooley Jr., J. L. 1999. A controlled, hierarchical study of habitat fragmentation: responses at the individual, patch, and landscape scale. – Landscape Ecol. 14: 381–389.

Bradshaw, W. E. 1983. Interaction between the mosquito *Wyeomyia smithii*, the midge *Metriocnemus knabi*, and their carnivorous host *Sarracenia purpurea*. – In: Frank, J.H. and Lounibos, L.P. (eds), Phytotelmata: terrestrial plants as hosts for aquatic insect communities. Plexus Publishing, Medford, NJ.

Drolet, B., Desrochers, A. and Fortin, M.-J. 1999. Effects of landscape structure on nesting songbird distribution in a harvested boreal forest. – Condor 101: 699–704.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. – J. Wildl. Manage. 61: 603–610.

Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? – Ecol. Model. 105: 273–292.

Fahrig, L. 2001. How much habitat is enough? – Biol. Conserv. 100: 65–74.

Fahrig, L. and Jonsen, I. 1998. Effect of habitat patch characteristics on abundance and diversity of insects in an agricultural landscape. – Ecosystems 1: 197–205.

Flather, C. H. and Bevers, M. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. – Am. Nat. 159: 40–56.

Forsyth, A. B. and Robertson, R. J. 1975. K reproductive strategy and larval behavior of the pitcher plant sarcophagid fly, *Blaesoxipha fletcheri*. – Can. J. Zool. 53: 174–179.

Greig-Smith, P. 1979. Pattern in vegetation. – J. Ecol. 67: 755–779.

Gustafson, E. J. and Parker, G. R. 1992. Relationships between landcover proportion and indices of landscape spatial pattern. – Landscape Ecol. 7: 101–110.

Hanski, I. 1999. Metapopulation ecology. – Oxford Univ. Press.

Harlow, L. L., Mulaik, S. A. and Steiger, J. H. 1997. What if there were no significance tests. – Lawrence Erlbaum Associates.

Harvey, E. and Miller, T. E. 1996. Variance in composition of inquiline communities in leaves of *Sarracenia purpurea* L. on multiple spatial scales. – Oecologia 108: 562–566.

Heard, S. B. 1994. Imperfect oviposition decisions by the pitcher plant mosquito (*Wyeomyia smithii*). – Evol. Ecol. 8: 493–502.

Hoenig, J. M. and Heisey, M. 2001. The abuse of power: the pervasive fallacy of power calculations for data analysis. – Am. Stat. 55: 19–24.

Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. – Ecol. Monogr. 62: 447–502.

Hughes, T. P., Baird, A. H., Dinsdale, E. A. et al. 1999. Patterns of recruitment and abundance of corals along the Great Barrier Reef. – Nature 397: 59–62.

Istock, C. A. and Weisburg, W. G. 1987. Strong habitat selection and the development of population structure in a mosquito. – Evol. Ecol. 1: 348–362.

Jonsen, I. and Taylor, P. D. 2000. Calopteryx damselfly dispersion arising from multi-scale response to landscape structure. – Conserv. Ecol. 4(2): 4. [online] URL: http://www.consecol.org/vol4/iss2/art4.

Kline, J. D., Moses, A. and Alig, R. J. 2001. Integrating urbanization into landscape-level ecological assessments. – Ecosystems 4: 3–18.

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

Krawchuk, M. A. and Taylor, P. D. 1999. Roosting behaviour by *Fletcherimyia fletcheri* (Diptera: Sarcophagidae) in *Sarracenia purpurea* (Sarraceniacea). – Can. Entomol. 131: 829–830.

Levin, S. A. 1992. The problem of pattern and scale in ecology. – Ecology 73: 1943–1967.

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

Matter, S. F. 1997. Population density and area: the role of between- and within-patch processes. – Oecologia 110: 533–538.

Mazerolle, M. J. and Villard, M-A. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. – Ecoscience 6: 117–124.

McCarthy, J. 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. – Environ. Rev. 9: 1–59.

McGarigal, K. and McComb, W. C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. – Ecol. Monogr. 65: 235–260.

Menéndez, R. and Thomas, C. D. 2000. Metapopulation structure depends on spatial scale in the host-specific moth *Wheeleria spilodactylus* (Lepidoptera: Pterophoridae). – J. Anim. Ecol. 69: 935–951.

Miner, J. A. and Taylor, P. D. 2002. Effects of peatland size and exposure on two species of Diptera inhabiting the pitcher plant *Sarracenia purpurea* L. – Ecoscience 9: 347–354.

Nastase, A. J., de la Rosa, C. and Newell, S. J. 1995. Abundance of pitcher-plant mosquitoes, *Wyeomyia smithii* Coq. (Diptera: Culicidae) and midges, *Metriocnemus knabi* Coq. (Diptera: Chironomidae), in relation to pitcher characteristics of *Sarracenia purpurea* L. – Am. Midl. Nat. 133: 44–51.

Nielsen, A. and Ims, R. A. 2000. Bumble bee pollination of the sticky catchfly in a fragmented agricultural landscape. – Ecoscience 7: 157–165.

Pinheiro, J. C. and Bates, D. M. 2000. Mixed effects models in S and S-Plus. – Springer-Verlag.

Ray, C. and Hastings, A. 1996. Density dependence: are we searching at the wrong spatial scale. – J. Anim. Ecol. 65: 556–566.

Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. – Am. Nat. 158: 87–99.

Rukke, B. A. and Midtgaard, F. 1998. The importance of scale and spatial variables for the fungivorous beetle *Bolitophagus reticulatus* (Coleoptera, Tenebrionidae) in a fragmented forest landscape. – Ecography 21: 561–572.

Trzcinski, M. K., Fahrig, L. and Merriam, G. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. – Ecol. Appl. 9: 586–593.

Villard, M.-A., Trzcinski, M. K. and Merriam, G. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. – Conserv. Biol. 13: 774–783.

Wiens, J. A. 1989. Spatial scaling in ecology. – Funct. Ecol. 3: 385–397.

Wu, J. and Loucks, O. L. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. – Q. Rev. Biol. 70: 439–466.