Oikos 118: 67–76, 2009
doi: 10.1111/j.1600-0706.2008.16722.x,

Subject Editor: Tadashi Fukami. Accepted 15 July 2008

Evaluating the relative importance of patch quality and connectivity in a damselfly metapopulation from a one-season survey

Takehiko Yamanaka, Koichi Tanaka, Kenji Hamasaki, Yukinobu Nakatani, Nobusuke Iwasaki, David S. Sprague and Ottar N. Bjørnstad

T. Yamanaka (apple@affrc.go.jp), K. Tanaka and K. Hamasaki, Biodiversity Division, National Inst. for Agro-Environmental Sciences, 3-1-3 Kannondai, Tsukuba, JP–305-8604 Ibaraki, Japan. – Y. Nakatani, Natural Resources Inventory Center, National Inst. for Agro-Environmental Sciences, 3-1-3 Kannondai, Tsukuba, JP–305-8604 Ibaraki, Japan. – N. Iwasaki and D. S. Sprague, Ecosystem Informatics Division, National Institute for Agro-Environmental Sciences, 3-1-3 Kannondai, Tsukuba, JP–305-8604 Ibaraki, Japan. – O. N. Bjørnstad, Depts of Entomology and Biology, 501 Ag Sciences and Industries Building, The Pennsylvania State Univ., University Park, PA 16802, USA.

The area-and-isolation paradigm, which has been the primary focus of metapopulation research, may not hold in some animal metapopulations if within-patch preference is more important than patch area or connectivity. Recently, regression analyses have been used to evaluate the effect of patch connectivity and various patch qualities including area. However, their relative importance is not easy to determine, because patch qualities and connectivity are often spatially autocorrelated. In this paper, we try to evaluate the relative importance of within-patch quality, patch connectivity and spatial autocorrelation using variation partitioning methods from community ecology. We constructed three regression models: within-patch quality, PCNM (principal coordinates of neighbor matrices) and patch connectivity based on a one-season survey of a damselfly *Copera annulata* metapopulation. The contribution of within-patch quality was larger than that of connectivity. There was no prominent effect of patch area. We conclude that the area-and-isolation paradigm is not applicable to this *C. annulata* metapopulation. The spatial autocorrelation extracted by PCNM had the largest contribution; it contained almost all of the variation of connectivity and overlapped with variation explained by within-patch quality. Connectivity corresponded most closely to medium-scale spatial structure captured by PCNM (ca 640 m). The mean effective dispersal scale was estimated to be 53 m. Within-patch quality, debris accumulation and vegetation cover in the pond corresponded with the medium and small (ca 201 m) spatial scales from PCNM, though we could not clearly explain the cause of this correspondence. We believe that our method will contribute to quick and effective evaluation of spatial and non-spatial aspects of metapopulation.

The metapopulation theory is a standard and basic tool for understanding population dynamics in fragmented habitats. In the early metapopulation models, habitat patches were assumed to be identical in quality and position (Levins 1970). Though these models greatly contributed to our qualitative understanding of metapopulation dynamics, they were highly conceptual and hardly rigorous for empirical testing. This situation has improved over the last 15 years through the formulation of more realistic models that allow for quantitative prediction, facilitating important applications in the study and management of rare and endangered species (summarized by Hanski and Ovaskainen 2003). Hanski-type models, many of which inherited the basic structure of his first incidence function model (IFM, Hanski 1994), were novel in that they used patch occupancy as the state variable and patch area and isolation as predictors, achieving spatially realistic yet simple models. Researchers and conservation practitioners can apply these models to their systems relatively easily because patch area and position are easy parameters to collect (Moilanen and Hanski 1998). These models have clarified how metapopulation persistence depends on the balance between colonization and extinction rates determined by patch area and isolation. Their approach may be seen as an area-and-isolation paradigm. This paradigm has proven especially apt for butterflies: for example, Glanville fritillary *Melitaea cinxia* in Finland (Hanski et al. 1996) and dingy skipper *Erynnis tages* in North Wales (Gutiérrez 2005).

There are, however, numerous reports of patterns that are not concordant with the area-and-isolation paradigm (summarized by Harrison and Bruna 1999). Thomas et al. (2001) reported that within-patch quality was more important than patch size or isolation for three butterfly metapopulations in the UK (Dennis and Eales 1997, Hanski and Singer 2001). Krauss et al. (2005) reported that patch size was indeed more important than local covariates but of the same importance as isolation. There are contrary studies reporting that incorporation of local patch variables does not improve the predictive power of area-and-isolation models (Moilanen and Hanski 1998).

These contradictions may arise because environmental requirements and dispersal ability vary from species to species and these biological differences affect patch occupancy in metapopulations. In specialist herbivores including some butterfly species, the size of the host plant can be a surrogate for patch capacity and the area-and-isolation paradigm may hold to some degree (Dennis et al. 2003). However, in carnivores and generalist herbivores whose habitat patches are difficult to quantify, patch capacity should be evaluated not only by area but also by other factors within the patch. In addition, strong dispersers may easily cover the whole region, in which case patch isolation may not affect metapopulation structure (Harrison 1991).

Recently, applied ecologists are starting to evaluate the effect of patch isolation (or conversely, patch connectivity) and patch qualities in addition to area by various regression analyses (Thomas et al. 2001, Fleishman et al. 2002). The importance of patch connectivity or within-patch quality can be evaluated by various goodness-of-fit measures, such as coefficient of determination (R^2). These approaches offer greater insights into the processes structuring metapopulations than do the process-oriented models based on area and isolation. There has been, however, a problem in these simple uni- or multivariate regression analyses; that is, within-patch qualities are often spatially autocorrelated across the landscape. Connectivity is also autocorrelated by definition since it is calculated by a distance decay function among habitats. Consequently, it is not easy to determine the relative importance of within-patch qualities and habitat isolation.

One way to mediate this problem is to use ‘variation partitioning’, also known as ‘commonality analysis’, in the regression analysis (Kerlinger and Pedhazur 1973). Variation partitioning has been widely used in community ecology (Borcard et al. 1992, Legendre and Legendre 1998, Legendre et al. 2005), but less so in population ecology (Heikkinen et al. 2005). Using this technique, we can evaluate the contribution of patch connectivity, that of within-patch quality and the overlap of these contributions.

In this paper, we seek to evaluate the importance of within-patch quality, spatial autocorrelation and connectivity in a damselfly metapopulation from a one-season survey using variation partitioning. Connectivity was calculated based on the assumption of a Hanski-type metapopulation. Various patterns of spatial structure were extracted by a semi-parametric method: principal coordinates of neighbor matrices (PCNM) (Legendre et al. 2005, see also Statistical analysis) separate from metapopulation measures of connectivity. Though we expect connectivity and the PCNM component to be similar and to fully overlap if dispersal and metapopulation dynamics are the only sources of spatial autocorrelation, the autocorrelation can also arise from the effects of other biotic processes, such as trophic interactions (Bjørnstad and Bascompte 2001), or spatially structured environmental factors (Thomas 1991, Borcard et al. 1992). Following variation partitioning among the within-patch environment vs spatial vs connectivity models, we discuss the relative importance of within-patch quality and connectivity.

Material and methods

The study species

Copera annulata (Zygoptera: Platycnemididae) occurs in central China, Korea and Japan. It is univoltine in most parts of Japan and is typically observed in June through August. As a damselfly species, early life stages from egg to the final instar larva occur in water. After emergence, the adult insect can fly among water bodies for mating and oviposition. We chose *C. annulata* as a model species for our study because of the ease of delineating its habitat patches: namely, farm ponds. In addition, it has been reported that *C. annulata* prefers small and shady pond conditions (Sugimura et al. 1999) and, therefore, the pond area cannot simply be assumed to represent patch capacity.

Field observation

The study area is located in the northeastern Kanto plain, Ibaraki prefecture, Japan (10 × 10 km, 36°8’N, 140°8’E; Fig. 1). The typical land use in the area is a mixture of forests, fruit orchards, crop fields, rice paddy fields, golf courses and residential areas. We perused the national basic maps (1: 2500) and aerial photographs of the area from 1994 to 1999 (about 1: 10 000 scale, stored and managed by the Japan map center; <http://www.jmc.or.jp/>) to locate potential habitats for *C. annulata* such as ponds and water holes in marshy areas. Rivers and ditches were excluded from our survey because they are largely unsuitable (Sugimura et al. 1999). All potential habitats were explored to determine whether they had water year-round. Artificial ponds such as water reservoirs and swimming pools were also excluded as unsuitable. Seventy-four ponds were selected as potentially suitable habitats for *C. annulata.*

Each pond was surveyed at least once by four well-trained observers on sunny days between 16 June and 22 July, 2004 from the period of early to peak adult emergence. The margins of the pond were explored exhaustively by four observers on foot to catch adult individuals. In the first round of the survey of 74 ponds, we found *C. annulata* adults only at ponds which had aquatic and riparian vegetation. Therefore, additional capturing trials were conducted only for those ponds; we did not visit the other ponds again. As a result, 25 ponds were visited only once, 35 ponds twice and the rest three times. Though this visitation schedule could introduce a bias in which suitable ponds would have a larger detection probability, it maximized our ability to detect small populations. To evaluate our imperfect survey, we used a maximum likelihood estimation of the detection probability implemented by the software Presence ver. 2.0 (MacKenzie et al. 2002). We assumed the probability of the estimation would not change during our survey or among ponds.

The individuals captured were counted and marked by removing the right middle tibia with forceps. Those without the right middle tibiae were not counted to avoid double recording. The sample tibiae were kept in a deep freezer for future genetic analysis. In damselflies, loss of this tibia does not significantly shorten life span (Fincke and Hadrys 2001). The mean number of individuals captured

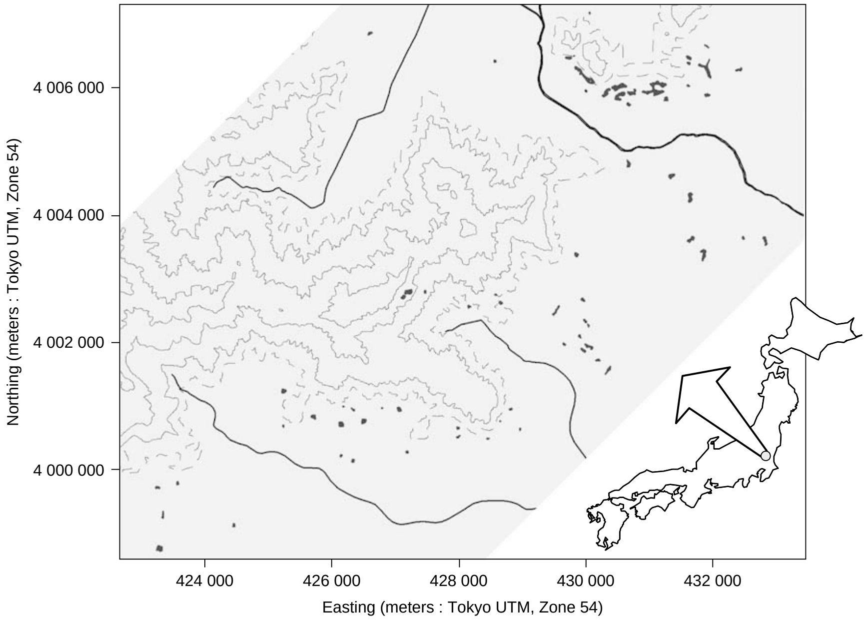

Figure 1. A summary map of the study area. The ponds surveyed are colored in black. The black and grey lines indicate rivers and the contour lines of elevation, respectively. The map was projected onto the UTM (Universal Transverse Mercator) coordinates, Tokyo UTM, Zone 54.

per observation in a pond was natural log-transformed after adding 0.5 (Yamamura 1999). Linear trends in spatial coordinates were further eliminated from the log-transformed abundance, because PCNM cannot detect broader spatial trends than those of the study area (Borcard and Legendre 2002). The detrended abundance (hereafter denoted as the 'population size' in this paper) was calculated as the residuals of the regression on XY spatial coordinates.

Within-patch quality

For within-patch quality, i.e. the pond environmental condition, six variables were selected in our study (variables are numbered, hereafter). We recorded the following three biotic factors in the ponds in August 2005: (1) predatory fish score ('fish'), (2) abundance of benthos fauna ('benthos'), and (3) cover area of aquatic and riparian vegetation in each pond ('vegetation'). For predatory fish, the combined abundance of largemouth bass *Micropterus salmoides* and bluegill sunfish *Lepomis macrochirus* was surveyed by a D-frame net and/or a casting net at the littoral area and was recorded in three categories (abundant, existing, none). For benthos, chironomid larvae and naidid worms (Oligochaeta) were collected using a plastic frame (25 × 25 cm, 20 cm height) and a hand net (mesh size about 300 µm, aperture 10 × 8.5 cm) from four sample sites of each pond. Wet weights (g) were measured and summed for the four samples from each pond. For vegetation, the total coverage area (m^2) of aquatic and riparian vegetation in each pond, including emergent plants (*Typha latifolia*, *Acorus calamus*, *Phragmites australis*, etc.) and floating plants (*Nelumbo nucifera*, *Nymphoides peltata*, etc.), was measured in the field. Adults utilize vegetation for perching and oviposition (Sugimura et al. 1999).

We also measured three physical conditions of the ponds. (4) The thickness of the debris layer ('debris'), namely dead branches and leaves, was measured at three points in the littoral area of each pond bottom and averaged. Accumulated debris has been reported as a suitable habitat for larvae (Sugimura et al. 1999). (5) The area of the ponds ('area') was also considered. Area is of primary importance in many metapopulation studies but may negatively affect *C. annulata* because they appear to prefer small shady ponds. (6) The percentage of the pond perimeter with revetment ('revetment') was also extracted using GIS (ArcView ver. 9.1) constructed specifically for our study based on the national basic maps (1:2500). Revetment was recorded because we suspected that artificial alteration of the pond bank would reduce *C. annulata* habitat.

Statistical analysis

Our data contain numerous cases with zero abundance (74 – 16 = 58 ponds). The recent advance in regression theory may provide a more sophisticated tool to analyze our raw heteroscedastic data such as logistic regression or negative binomial regression than our classical regression of transformed data. However, partial correlations, which are the bases of variation partitioning, are in turn based on variance-stable data (Gaussian) are not applicable to other regressions (Nagelkerke 1991, Shieh 2001). All analyses were performed using the function 'glm' in the statistical environment R (R Development Core Team 2006).

Regression analysis of within-patch quality

We checked for normality of all within-patch factors plotted against normal quantiles, and transformed them to stabilize variation if necessary: percentage data (revetment) were arcsine-square-root transformed, and others (benthos, debris and area) were natural log-transformed after adding 0.5.

Variable-selection procedures such as the stepwise regression have been criticized for introducing bias in parameter estimations, inconsistencies among model selection algorithms, and inappropriate reliance on a single best model (Whittingham et al. 2006). Therefore, our study takes, at least partly, the information-theoretic approach (Burnham and Anderson 2002). We constructed linear regression models of every possible combination of the six within-patch factors ($2^6 - 1 = 63$ models) assuming no interaction effect. Because our sample size was small (74 ponds), AICc instead of AIC was calculated (Hurvich and Tsai 1989):

$$\begin{aligned} \mathrm{AICc} &= \mathrm{AIC} + \frac{2 \times m \times (m+1)}{n - m - 1} \\ &= n \times \log(\hat{\sigma}^2) + \frac{2 \times m \times n}{n - m - 1} \end{aligned} \tag{1}$$

where n is the number of samples (74 ponds), m is the number of parameters to be estimated including the intercept and variance of the regression model, and $\hat{\sigma}^2$ is the estimated error variance. The model with the smallest AICc ($\mathrm{AICc}_{\mathrm{min}}$) value may be best supported by data but other models with small AICc values may also have support. Therefore we calculated Akaike weights (w_i) for all the models instead to choose a single model (Burnham and Anderson 2002):

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{i=1}^{63} \exp\left(-\frac{1}{2}\Delta_r\right)} \tag{2}$$

where $\Delta_i = \mathrm{AICc}_i - \mathrm{AICc}_{\mathrm{min}}$. The relevance of a factor was evaluated by summing all w_i's of the models including that factor (the summed Akaike weight) (Burnham and Anderson 2002). We did not use model averaging for multi-model inference, which is recommended by Burnham and Anderson (2002), because variation partitioning could not be implemented among the compounded models produced by model averaging.

Spatial autocorrelations extracted by PCNM

Principal coordinates of neighbor matrices (PCNM) is a method to extract spatial structures at various scales (Legendre and Anderson 1999, Borcard et al. 2004). The method creates a set of spatial predictors (PCNM), which are orthogonal to each other, from a geographic distance matrix. The most prominent spatial autocorrelation can be extracted by regressing population size on the PCNMs. There are some derivatives from the original method and we based our analysis on Dray et al. (2006) as follows: (1) calculate a geographic distance matrix for all pairs of ponds ($D = [d_{ij}]$). Pond positions were represented by their centroids. Nine points were added to reduce the largest distance between adjacent ponds. Providing these supplementary points enhances the detection of small spatial structures (Peres-Neto et al. 2006 in the supplementary material). (2) calculate the connectivity matrix W based on D:

$$W = [w_{ij}] = 1 - \left(\frac{d_{ij}}{4 \times th}\right)^2 \tag{3}$$

where th is the maximum distance of the minimum spanning tree (Legendre and Legendre 1998). (3) calculate the eigenvectors $\{u_i: i = 1, 2, ..., 82$ (the number of ponds + nine supplementary points − 1)$\}$ of the centered connectivity matrix,

$$\Omega = \left(I - \frac{11^T}{n}\right) W \left(I - \frac{11^T}{n}\right) \tag{4}$$

where I is the identity matrix and 1 is a vector whose elements are all ones. The eigenvectors of Ω are PCNM themselves and represent various spatial scales. Those corresponding to large eigenvalues represent the global scale of the spatial trend; those with medium eigenvalues, the regional scale; and those with small eigenvalues, the local or fine spatial trends. The eigenvectors associated with negative eigenvalues represent negative spatial autocorrelation. In this study, only eigenvectors having positive eigenvalues $\{\mathrm{PCNM}_i: i = 1$ (the largest), $2, \ldots, 32$ (the smallest)$\}$ were used to model spatial autocorrelation, since we were primarily interested in detection of positive spatial autocorrelation. PCNM values were calculated using the R library 'spacemakeR' developed by Dray et al. (2006). (4) Select relevant spatial autocorrelation structures by linear regression analyses of PCNMs. Here again, we took the information-theoretic approach. Thirty-two PCNMs were equally divided into four subsets of spatial categories, that is, large (PCNM_1, $\mathrm{PCNM}_2, \ldots, \mathrm{PCNM}_8$), medium ($\mathrm{PCNM}_9$, $\mathrm{PCNM}_{10}, \ldots, \mathrm{PCNM}_{16}$), medium-small ($\mathrm{PCNM}_{17}$, $\mathrm{PCNM}_{18}, \ldots, \mathrm{PCNM}_{24}$) and small ($\mathrm{PCNM}_{25}$, $\mathrm{PCNM}_{26}, \ldots, \mathrm{PCNM}_{32}$). It was impossible to execute regression analyses for all combinations of the 32 PCNMs, and we were interested in spatial categories, which are biologically interpretable, rather than individual PCNMs. Every combination of the four spatial categories was regressed to population size. The Akaike weights were calculated for all the regression models and summed across each category. The inclusion or exclusion of each spatial category was determined by this summed Akaike weight.

The spatial scale of each category was further measured by a non-parametric correlogram function (NCF) developed by Bjørnstad and Falck (2001). Visual determination is difficult when the data are taken from irregularly allocated sites. The population size predicted by the regression model of each spatial category was used to evaluate the spatial scale of the category. The spline correlogram of the predicted population size was then calculated. The x-intercept of the correlograms was used as our estimate of the scale. Confidence intervals of estimated spatial scales were calculated by 1000-time bootstrapping of the data. NCF was executed using the R library 'ncf' developed by Bjørnstad and Falck (2001).

Estimation and evaluation of connectivity

We defined the connectivity strength of pond i according to the model of Hanski and Singer (2001):

$$S_i = \sum_{i \neq j} N_j \times \exp\left(-\frac{d_{ij}}{\alpha}\right) \qquad (5)$$

where N_j represents the actual abundance in pond j (the row average number of individuals before the transformation). The equation represents the total summation of the product of population size in the emigration patch and an exponential dispersal kernel from pond j to pond i. Each product can be seen as the number of propagules reaching pond i from pond j (Moilanen 1999). Though other fat-tailed dispersal kernels are possible (Moilanen 2004), Eq. 5 was chosen because it is tractable and easy to interpret: α is the mean generational dispersal distance. To estimate α we used a modification of the profile likelihood method of Havel et al. (2002); that is, the population size was regressed for connectivity defined in Eq. 5 assuming a sequence of values for the parameter α (increased at 1.0 m intervals), and the value of α that gave the minimum residual sum of squares (RSS) was selected. The minimum RSS corresponds to the maximum likelihood estimate for Gaussian regression models (Venables and Ripley 1998).

Variation partitioning for three components

So far, three regression models have been described: those for (1) within-patch quality, (2) spatial autocorrelation by PCNM and (3) connectivity. In addition to these three models, we conducted regressions on all predictors simultaneously and all pairs. The R^2 (coefficient of determinations) was calculated and transformed by Ezekiel's adjustment to make them comparable among models having different numbers of predictors (Peres-Neto et al. 2006),

$$R^2_{adj} = 1 - \frac{n-1}{n-p-1}(1 - R^2) \qquad (6)$$

where n is the number of samples (74 ponds) and p is the number of predictors excluding the y-intercept, and R^2 is the original coefficient of determination, i.e. the residual sum of squares standardized by total variance of the data. Variation partitioning was then conducted to determine the contribution of the pure components, the paired components, and the full suite of explanatory variables using R^2_{adj} (Økland 2003).

Although it was impossible to further decompose the overlapping fraction into each factor by variation partitioning, a correlation matrix was calculated among the factors. This helped to interpret the merged effects in the overlapped fractions, especially in conjunction with the spatial autocorrelation. Overlapped fractions represent correlation structures among factors (Legendre and Legendre 1998). The fish score was not incorporated in the matrix because it was an ordered score. The medium-small spatial category was removed for the final PCNM model (Results) and was also discarded for the calculations.

Results

Copera annulata was found in 16 out of the 74 ponds surveyed. The largest number of *C. annulata* captured was 41; the smallest was one (at one pond). The detection probability for the data of the ponds visited three times was 1.0 and that of the ponds visited twice (including those visited three times, but for which only the first two data were incorporated) was 0.904. This high probability, which is partly due to the conspicuousness of *C. annulata*, verifies the data for further analyses in spite of our imperfect survey schedule. Only two ponds having one or two individuals were absent in the first survey but present in the second survey. Removing these two ponds did not affect the results (not shown); therefore, we concluded that our approach was robust for minor detection failures.

Regression result of within-patch quality

The regression model including within-patch quality indicated that debris, vegetation and benthos had positive effects while revetment, area and fish had negative effects on the population size (Table 1, fish results are not shown but their effect was observed by plotting against the population size). Judging from the total Akaike weights in Table 1, debris had the most prominent effect (0.975). Vegetation was also of secondary relevance (0.597). Though the other four were not relevant compared to debris and vegetation, even fish (0.200) would be selected in 20 times out of 100 similar data sets if they had been virtually available. Since there is no clear-cut criterion like the α-level to remove factors in the information-theoretic approach and we judged that they all had substantial effects, we did not remove any of them. The adjusted R^2 for the regression model with six factors was 0.193.

Spatial structure estimated by PCNM

Our procedure decomposed spatial autocorrelation into four spatial scales which were measured as 1696 m, 640 m, 392 m and 201 m by NCF, respectively (Table 2). The large spatial category was highly relevant, as the summed Akaike weight was 0.973. While the other three categories, medium, medium-small and small, were less relevant than the large, the medium-small scale was the most trivial (less than 10 times less information-retaining than the other two). Therefore, we removed the PCNMs of the medium-small category. The final spatial autocorrelation including large, medium and small spatial categories had an adjusted R^2 of 0.407.

Table 1. Regression analysis for within-patch factors and their relevance estimated by their summed Akaike weights.

Factor	Estimated coefficients[†]	Summed Akaike weight[§]
y-intercept	−0.018	–
Debris	0.461	0.975
Vegetation	0.261	0.597
Benthos	0.106	0.293
Revetment	−0.030	0.279
Area	−0.037	0.239
Fish	–	0.200

[†] The coefficients were calculated for the full model. It was not reported for the fish as this factor had an ordered score.

[§] A summed Akaike weight for each factor was calculated as the summation of Akaike weights in all the models including the factor (see Statistical Analysis for details).

Table 2. Spatial autocorrelation extracted by PCNM and its relevance for population size. PCNMs were decomposed into four spatial scales, large, medium (Mid), medium-small (MidS) and small.

Spatial categories	Spatial scale (m)[†]	Summed Akaike weight[§]
Large ($PCNM_1 \sim PCNM_8$)	1696.4 (1076.9 ~2614.2)	0.973
Mid ($PCNM_9 \sim PCNM_{16}$)	640.2 (423.6 ~1211.2)	0.116
MidS ($PCNM_{17} \sim PCNM_{24}$)	392.2 (0 ~877.4)	0.007
Small ($PCNM_{25} \sim PCNM_{32}$)	200.7 (0 ~592.4)	0.099

[†] The population size predicted by each regression model (large, medium, medium-small and small) was used to evaluate its spatial scale. The spatial scale was estimated as the x-intercept of the non-parametric correlogram function (NCF) of the predicted abundance of each spatial category. Confidence intervals (ranges in the parentheses) of estimated spatial scales were calculated by 1000 times bootstrapping. See text and Bjørnstad and Falck (2001) for details.

[§] A summed Akaike weight for every category was calculated as the summation of the Akaike weights in all the models including the set of PCNMs in it. Notice that regression analyses were not based on the PCNM individually but on each spatial scale including eight PCNMs, respectively.

Effect of connectivity

The profile likelihood estimated α (i.e. the generational mean dispersal distance) to be 53 m (Fig. 2a). Though this value may seem small for damselflies, another mark-recapture study in another area confirmed that this species seldom migrates more than 100 m (Yamanaka unpubl.). Such short-distance dispersal behavior has also been reported for other damselfly species (McPeek 1989, Rouquette and Thompson 2007). The adjusted R^2 for the connectivity model based on $\alpha = 53$ m was 0.157.

The mean nearest-neighbor distance was 357m (±44 m SE) among 52 pairs of ponds and was greater than $\alpha = 53$ m. However, because there were still enough nearest-neighbor distances in closer ranges (seven pairs < 100 m, 15 pairs < 200 m), we postulated that the pond configuration in our study area was suitable for estimation of a valid α. If more ponds had been clustered in a smaller region, the damselfly could have move in a stepping-stone fashion and could have dispersed much further. Consequently, connectivity might be estimated as greater than 53 m or its effect might be estimated as less important than 0.157. If ponds were separated by much greater distances, *C. annulata* might not have lived in this region.

Variation partitioning and interpretation of the spatial structure

For simplicity, each adjusted R^2 was renamed as R^2_S (= 0.407, S represents spatial autocorrelation extracted by PCNM), R^2_E (=0.193, E represents within-patch quality) and R^2_C (=0.157, C represents connectivity), respectively. The variation of all three combined models was calculated as $R^2_{S \cup C} = 0.435$ and those of all pairs were $R^2_{S \cup E} = 0.430$, $R^2_{S \cup C} = 0.418$ and $R^2_{E \cup C} = 0.290$. Following Økland (2003), the pure contributions of the three regression models were $R^2_{S|(E \cup C)} = 0.144$, $R^2_{E|(S \cup C)} = 0.016$ and $R^2_{C|(S \cup E)} = 0.005$, respectively. The overlapping contributions were $R^2_{S \cap C|E} = 0.092$, $R^2_{S \cap E|C} = 0.117$ and $R^2_{E \cap C|S} = 0.006$ and $R^2_{P \cap E \cap C} = 0.053$. When small fractions (less than 0.01) were neglected, the contributions could be depicted as in Fig. 3. The contribution of spatial autocorrelation extracted by PCNM was the largest, and it contained almost all of the variation of connectivity and also of within-patch quality. One-third of its contribution overlapped with the contribution of connectivity. Another one-third of its contribution overlapped with within-patch quality (not overlapping with connectivity). The rest of its

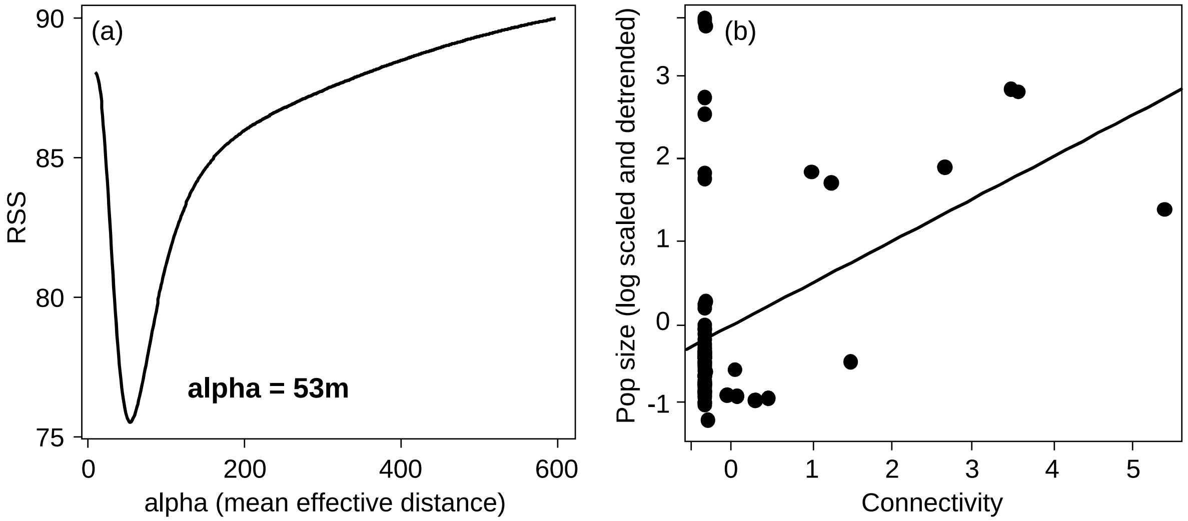

Figure 2. (a) The profile likelihood analysis of connectivity in relation to parameter α. (b) The relationships of connectivity with the estimated α (=53 m) and *C. annulata* population size. Population sizes were natural log-transformed after adding 0.5. They were also linearly detrended to remove the global trend, and there were some negative points jittering around $\log_e(0.5) = -0.693$. The straight line in (b) represents the regression line in our study (see text).

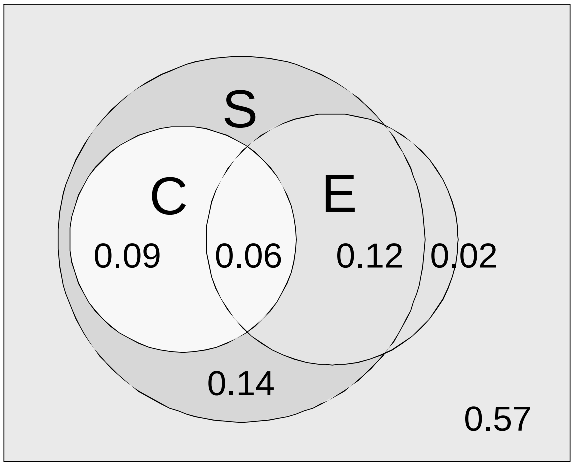

Figure 3. Schematic diagram of the contributions. S, the spatial autocorrelation extracted by PCNM; C, the connectivity effect; E, the environmental effects (debris and vegetation). The numbers in the figure represent the relative contributions of the fractions to the total variation (= 1.0).

contribution was not explained by connectivity or within-patch quality. The contribution of connectivity was substantial but fully embodied within spatial autocorrelation as we had expected. Because PCNM expresses various spatial scales of autocorrelation, the one created by the connectivity effect should be totally enveloped within the PCNM spatial scales if the method works properly. Within-patch quality also largely overlapped with spatial autocorrelation, which represents that a large portion of the environmental variation is spatially structured.

To gain further insights on the overlapping variations in Fig. 3, correlations among factors were calculated in Table 3. None of the correlations was high; this represents the fact that there were no strong complementary relationships among factors. Connectivity had the largest correlation with the medium spatial category (Table 3). Though there was no strong relationship between spatial autocorrelation and within-patch quality, debris was slightly correlated with the medium (0.23) and small scales (0.25) and vegetation with the small scale (0.23). Debris and vegetation were somewhat correlated but both were negatively correlated to revetment. This result is easy to interpret in a biological sense. The more vegetation exists, the more debris accumulates. If revetment is installed in a pond, vegetation will be destroyed and consequently debris will be reduced.

Discussion

From a one-season survey of the damselfly *Copera annulata*, we successfully evaluated the relative importance of within-patch quality, connectivity (as quantify using standard metapopulation methods) and various spatial structures (quantified using PCNM) (Fig. 3). The contribution of within-patch quality was larger than that of connectivity. Moreover, the area of the ponds was much less important than debris and vegetation. From this result, we conclude that the classic area-and-isolation paradigm from metapopulation theory will not hold for the *C. annulata* metapopulation. Though the contribution of connectivity was the smallest among three regression models, it was still substantial (0.157). Therefore, we cannot ignore the importance of pond configuration when studying the distribution of this species.

There is a caveat for interpreting the modest importance of connectivity; that is, we only considered the Euclidean distances among ponds. Recent studies have revealed that the effective distance, which is calculated from the cost surface of the land-use mosaic between patches, can be a better measure of distance than the Euclidean distance (summarized by Taylor et al. 2006). A greater part of the variation of spatial autocorrelation might have been attributed to connectivity if the connectivity had been calculated based on effective rather than Euclidian distance. To do so was, however, impossible in our study because its calculation requires behavioral data or mark-and-recapture experiments.

Though spatial autocorrelation extracted by PCNM was found to have the largest contribution in explaining local abundance, this fact tells us little about the underlying metapopulation processes since PCNM is too flexible to pick up spatial structures at various scales. Therefore, the correlations among factors were calculated to determine which spatial scale each factor had. We found that connectivity had the most correspondence with the medium spatial scale. We postulated that the dispersal behavior of 53 m on average connects neighboring patches and that these patches make clusters at the scale of the medium spatial category (640 m). Though we could not detect a clear

Table 3. Correlation matrix among all the factors, connectivity (C), within-patch quality (debris, vegetation, benthos, revetment and area) and spatial scale (large, mid and small).

	C[†]	Debris	Vegetation	Benthos	Revetment	Area	Large[§]	Mid[§]	Small[§]
C	1.0	0.22	0.11	0.07	−0.12	−0.02	0.18	**0.42**	0.19
Debris	–	1.0	**0.48**	0.19	**−0.44**	−0.05	0.16	0.23	0.25
Vegetation	–	–	1.0	0.09	**−0.45**	−0.11	0.18	0.14	0.23
Benthos	–	–	–	1.0	−0.19	−0.19	0.17	0.14	−0.03
Revetment	–	–	–	–	1.0	**0.29**	−0.27	0.0	−0.13
Area	–	–	–	–	–	1.0	−0.09	−0.05	0.06
Large	–	–	–	–	–	–	1.0	0.02	−0.01
Mid	–	–	–	–	–	–	–	1.0	0.01
Small	–	–	–	–	–	–	–	–	1.0

[†] Connectivity was calculated for every pond using Eq. 5 with the estimated α (= 53 m).

[§] The spatial autocorrelation effects were the predicted population abundances by the categorized regression models, like those in Table 2. The numbers in bold are the top five largest absolute correlation values. Fish is an ordered score and was excluded from the analysis.

relationship between the within-habitat quality and the scales of autocorrelation, debris and vegetation seemed to have some correspondence with the medium and the small scales. If there is a regional trend for pond management and utilization, and we suspected such was the case in our study, the environment in the ponds (i.e. debris and vegetation) might have some spatial trends.

The overlapping area between connectivity and within-patch quality is rather difficult to explain. Connectivity should technically be segregated from environmental factors because it is based on the mechanistic assumption of a Hanski-type metapopulation (IFM). In some steam-fish metapopulations, the position in the stream gradient has a great influence on the local population incidence (Gotelli and Taylor 1999), and connectivity calculated by Eq. 5 might represent some spatially autocorrelated environmental condition rather than the dispersal-induced spatial structure. The environmental conditions were, however, assumed to have a different spatial effect than that of connectivity in our two-dimensional study area where damselflies can fly without structural limitations to their pathways though the overlapping fraction between connectivity and within-habitat quality (0.06 in Table 3) may reflect how they share some similar scales of autocorrelation.

Our method provides a tool to elucidate processes structuring a metapopulation from a one-season survey. It will be beneficial especially for species whose biology has not been well studied and also especially in cases in which patch area cannot be used as an indicator of patch capacity because our method uses a multi-regression model to evaluate within-patch quality and we can incorporate any suspected factors. Though it might also be possible to incorporate patch qualities into the more process-oriented approaches (e.g. SPOMs, Moilanen and Hanski 1998, Ozgul et al. 2006), such models require much deeper knowledge of how the factors affect the processes. In addition, even a simple IFM requires many years' accumulation of the population census for robust estimates of the parameters (Moilanen 1999) and for valid future predictions (Thomas et al. 2002). However, it should be noted that mechanistic metapopulation models may provide us more information about the biological consequences of the metapopulation and are much more robust for future predictions than our approach because our method evaluates the 'relative' effect of factors. Our approach will not provide absolute biological estimations but can evaluate their relative importance. Particularly if all patches were equally good quality or conversely equally poor quality, the relative effect of within-patch quality would be reduced. Our approach constructs the most parsimonious regression models in a specific location and can be used to evaluate the current conditions of a specific species in a focal area. A new population census and environmental data collection would be required for the same species in a different situation.

Like the IFM models, our method does not require extra experiments to infer dispersal ability (α) such as mark-and-recapture. Every applied ecologist who has undertaken mark-and recapture in the field recognizes that it is an arduous task and that it sometimes takes several years. There is, however, one caveat. Our method (as well as the IFM models) is based on a strong hidden assumption of the stationarity of metapopulation processes (Moilanen 1999); that is, a long-term colonization effect is estimated from a snapshot of spatial pattern data. However, ter Braak et al. (1997) conducted a power analysis of the regression model of metapopulations using simulated data and concluded that the coefficient of connectivity can be estimated relatively well from snapshot surveys. Therefore, our dispersal estimate may in practice correctly reflect the underlying biology despite these theoretical concerns.

The variation here attributed to connectivity and dispersal may conceivably be due to underlying spatial structures other than metapopulation processes. However, the particular model of spatial decay (exponential, in this case, though for example Gaussian or Bessel functions would also be appropriate; Bjørnstad and Bolker 2000) is derived from fundamental models for animal movement (Levin et al. 2003). This variation may therefore be parsimoniously attributed to movement processes. Subsequent to the statistical calculations it is of course necessary to check that the estimated range of connectivity represents a plausible scale given the mobility of the species in the study (as is the case for our analysis of *C. annulata*). We believe that partitioning out the 'connectivity' portion of the pattern separate from the broader spatial structures is useful because it provides a meeting ground for the geostatistical and the metapopulation branches of spatial ecology.

Since our method can only be applied to a specific landscape and a specific species, it may seem less attractive in basic ecology and is phenomenological at a glance. However, every metapopulation is formed by an integrated effect of the behavior of the specific species and the characteristics of the focal landscape configuration (Calabrese and Fagan 2004, Fagan and Calabrese 2006). We hope our method can contribute to quick and effective evaluation for a specific metapopulation system before more specialized mechanistic simulations are conducted.

Acknowledgements – We appreciate the suggestions of the tough editor for forging both the logic and methodology of our study. We are grateful to Segovia Golf Club in Chiyoda, Chiyoda Country Club, Niihari Golf Club and owners of the surveyed farm ponds in Niihari, Chiyoda, Sitsuku and Yasato district for their kind support in conducting the odonate census. We thank Eelke Jongejans and Lidewij Keser, the botanists in PSU and TY's best friends in Long Meadow Lane, who kindly gave us useful comments on an early draft. This study was founded by a project titled 'Shizen-kyousei (Developing Technology for Coexisting with Nature within Agro-forest and Aquatic Watershed Landscapes)' of the Japanese Ministry of Agriculture, Forestry and Fisheries of Japan (TY, KT, NI and DSS) and the US Dept of Agriculture National Research Initiative Grants no. 2002-35302-12656 and 2006-35302-17419 (ONB).

References

Bjørnstad, O. N. and Bolker, B. 2000. Canonical functions for dispersal-induced synchrony. – Proc. R. Soc. Lond. B 267: 1787–1794.

Bjørnstad, O. N. and Bascompte, J. 2001. Synchrony and second-order spatial correlation in host–parasitoid systems. – J. Anim. Ecol. 70: 924–933.

Bjørnstad, O. N. and Falck, W. 2001. Nonparametric spatial covariance functions: estimation and testing. – Environ. Ecol. Stat. 8: 53–70.

Borcard, D. and Legendre, P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. – Ecol. Modell. 153: 51–68.

Borcard, D. et al. 1992. Partialling out the spatial component of ecological variation. – Ecology 73: 1045–1055.

Borcard, D. et al. 2004. Dissecting the spatial structure of ecological data at multiple scales. – Ecology 85: 1826–1832.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer Science + Business Media, LLC.

Calabrese, J. M. and Fagan, W. F. 2004. A comparison-shopper's guide to connectivity metrics. – Front. Ecol. Environ. 2: 529–536.

Dennis, R. L. H. and Eales, H. T. 1997. Patch occupancy in *Coenonympha tullia* (Muller, 1764) (Lepidoptera: Satyrinae): habitat quality matters as much as patch size and isolation. – J. Insect Conserv. 1: 167–176.

Dennis, R. L. H. et al. 2003. Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. – Oikos 102: 417–426.

Dray, S. et al. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). – Ecol. Modell. 196: 483–493.

Fagan, W. F. and Calabrese, J. M. 2006. Quantifying connectivity: balancing metric performance with data requirements. – In: Crooks, K. R. and Sanjayan, M. (eds), Connectivity conservation. Cambridge Univ. Press, pp. 297–317.

Fincke, O. M. and Hadrys, H. 2001. Unpredictable offspring survivorship in the damselfly, *Megaloprepus coerulatus*, shapes parental behavior, constrains sexual selection, and challenges traditional fitness estimates. – Evolution 55: 762–772.

Fleishman, E. et al. 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. – Conserv. Biol. 16: 706–716.

Gotelli, N. J. and Taylor, C. M. 1999. Testing metapopulation models with stream-fish assemblages. – Evol. Ecol. Res. 1: 835–845.

Gutiérrez, D. 2005. Effectiveness of existing reserves in the long-term protection of a regionally rare butterfly. – Conserv. Biol. 19: 1586–1597.

Hanski, I. 1994. A practical model of metapopulation dynamics. – J. Anim. Ecol. 63: 151–162.

Hanski, I. and Singer, M. C. 2001. Extinction–colonization dynamics and host-plant choice in butterfly metapopulations. – Am. Nat. 158: 341–353.

Hanski, I. and Ovaskainen, O. 2003. Metapopulation theory for fragmented landscapes. – Theor. Popul. Biol. 64: 119–127.

Hanski, I. et al. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. – Conserv. Biol. 10: 578–590.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. – Biol. J. Linn. Soc. 42: 73–88.

Harrison, S. and Bruna, E. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? – Ecography 22: 225–232.

Havel, J. E. et al. 2002. Estimating dispersal from patterns of spread: spatial and local control of lake invasions. – Ecology 83: 3306–3318.

Heikkinen, R. K. et al. 2005. New insights into butterfly-environment relationships using partitioning methods. – Proc. R. Soc. Lond. B 272: 2203–2210.

Hurvich, C. M. and Tsai, C. L. 1989. Regression and time-series model selection in small samples. – Biometrika 76: 297–307.

Kerlinger, F. N. and Pedhazur, E. J. 1973. Multiple regression in behavioral research. – Rinehart and Winston.

Krauss, J. et al. 2005. Relative importance of resource quantity, isolation and habitat quality for landscape distribution of a monophagous butterfly. – Ecography 28: 465–474.

Legendre, P. and Legendre, L. 1998. Numerical ecology. – Elsevier.

Legendre, P. and Anderson, M. J. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. – Ecol. Monogr. 69: 1–24.

Legendre, P. et al. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. – Ecol. Monogr. 75: 435–450.

Levin, S. A. et al. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. – Annu. Rev. Ecol. Evol. Syst. 34: 575–604.

Levins, R. 1970. Extinction. – Lect. Notes Math. 2: 75–107.

MacKenzie, D. I. et al. 2002. Estimating site occupancy rates when detection probabilities are less than one. – Ecology 83: 2248–2255.

McPeek, M. A. 1989. Differential dispersal tendencies among *Enallagma* damselflies (Odonata) inhabiting different habitats. – Oikos 56: 187–195.

Moilanen, A. 1999. Patch occupancy models of metapopulation dynamics: efficient parameter estimation using implicit statistical inference. – Ecology 80: 1031–1043.

Moilanen, A. 2004. SPOMSIM: software for stochastic patch occupancy models of metapopulation dynamics. – Ecol. Modell. 179: 533–550.

Moilanen, A. and Hanski, I. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. – Ecology 79: 2503–2515.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. – Biometrika 78: 691–692.

Økland, R. H. 2003. Partitioning the variation in a plot-by-species data matrix that is related to n sets of explanatory variables. – J. Veg. Sci. 14: 693–700.

Ozgul, A. et al. 2006. Effects of patch quality and network structure on patch occupancy dynamics of a yellow-bellied marmot metapopulation. – J. Anim. Ecol. 75: 191–202.

Peres-Neto, P. R. et al. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. – Ecology 87: 2614–2625.

Rouquette, J. R. and Thompson, D. J. 2007. Patterns of movement and dispersal in an endangered damselfly and the consequences for its management. – J. Appl. Ecol. 44: 692–701.

Shieh, G. 2001. The inequality between the coefficient of determination and the sum of squared simple correlation coefficients. – Am. Stat. 55: 121–124.

Sugimura, M. et al. 1999. Dragonflies of the Japanese archipelago in color. – Hokkaido Univ. Press.

Taylor, P. D. et al. 2006. Landscape connectivity: a return to the basic. – In: Crooks, K. R. and Sanjayan, M. (eds), Connectivity conservation. Cambridge Univ. Press, pp. 29–43.

ter Braak, C. F. F. et al. 1997. The incident function approach to modeling of metapopulation dynamics. – In: Bascompte, J. and Solé, R. V. (eds), Modeling spatiotemporal dynamics in ecology. Springer, p. 230.

Thomas, C. D. 1991. Spatial and temporal variability in a butterfly population. – Oecologia 87: 577–580.

Thomas, C. D. et al. 2002. Short-term studies underestimate 30-generation changes in a butterfly metapopulation. – Proc. R. Soc. Lond. B 269: 563–569.

Thomas, J. A. et al. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. – Proc. R. Soc. Lond. B 268: 1791–1796.

Venables, W. N. and Ripley, B. D. 1998. Modern applied statistics with S-PLUS. – Springer.

Whittingham, M. J. et al. 2006. Why do we still use stepwise modelling in ecology and behavior? – J. Anim. Ecol. 75: 1182–1189.

Yamamura, K. 1999. Transformation using $(x+0.5)$ to stabilize the variance of populations. – Res. Popul. Ecol. 41: 229–234.