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RESEARCH ARTICLE

Habitat suitability modelling to correlate gene flow with landscape connectivity

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Abstract Landscape connectivity is important in designing corridor and reserve networks. Combining genetic distances among individuals with least-cost path (LCP) modelling helps to correlate indirect measures of gene flow with landscape connectivity. Applicability of LCP modelling, however, is reduced if knowledge on dispersal pathways or routes is lacking. Therefore, we integrated habitat suitability modelling into LCP analysis to avoid the subjectivity common in LCP analyses lacking knowledge on dispersal pathways or routes. We used presence-only data and ecological niche factor analysis to model habitat suitability for the spiny rat, *Niviventer coninga*, in a fragmented landscape of western Taiwan. We adapted the resultant habitat suitability map for incorporation into LCP analyses. Slightly increased Mantel correlations indicated that a class-weighted suitability map better explained genetic distances among individuals than did geographical distances. The integration of habitat suitability modelling into LCP analysis can thus generate information on distribution of suitable habitats, on potential routes of dispersal, for placement of corridors, and evaluate landscape connectivity.

Keywords AFLPs · Continuous Boyce index · Ecological niche factor analysis · k-Fold cross validation · Landscape genetics · Least-cost path modelling · *Niviventer coninga* · Presence-only data

Introduction

Landscape connectivity is important for animal dispersal and gene flow in fragmented landscapes (Verbeylen et al. 2003; Coulon et al. 2004; Spear et al. 2005; Vignieri 2005; Broquet et al. 2006; Stevens et al. 2006). In a continuous landscape, animal dispersal can involve back-and-forth routine movements to exploit different resources (Van Dyck and Baguette 2005; Baguette and Van Dyck 2007). Gene flow is usually restricted by distance, with individuals being genetically more related at shorter than at longer geographical distances (Wright 1943). In a fragmented landscape, animal dispersal shifts to faster, directed searches for suitable habitat or resource patches (Van Dyck and Baguette 2005; Baguette and Van Dyck 2007). Dispersal routes

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through the matrix are likely to include environments perceived by an animal as hospitable since dispersal risks or costs are increased in hostile environments (Baguette and Van Dyck 2007). Dispersal distance increases greatly when the dispersal route meanders through a fragmented landscape. Therefore, land use and habitat fragmentation affect landscape connectivity and potentially reduce gene flow (Berry et al. 2005). To provide information for designing reserve networks and planning dispersal corridors, landscape connectivity must be assessed.

Least-cost path (LCP) analysis is widely used to estimate landscape connectivity (Adriaensen et al. 2003; Verbeylen et al. 2003). Gene flow estimated through population genetics using highly polymorphic genetic markers, e.g., microsatellites or amplified fragment length polymorphisms (AFLPs; Lowe et al. 2004) helps to validate landscape connectivity modelled by LCP (European roe deer, *Carpreolus carpreolus*, Coulon et al. 2004; Pacific jumping mouse, *Zapus trinotatus*, Vignieri 2005; American marten, *Martes americana*, Broquet et al. 2006; desert bighorn sheep, *Ovis canadensis*, Epps et al. 2007). In these cases, the shortest path with the lowest accumulated cost of dispersing through different components in a landscape is traced between locations of two individuals or populations and the length of that path is calculated (Adriaensen et al. 2003; Verbeylen et al. 2003). Correlating effective landscape distances calculated from LCP analysis or straight-line geographic distances with genetic distances among individual tests whether genetic distance is better explained by LCP distance than by straight-line distance.

Before using LCP analysis, the cost or resistance of each landscape component must be weighted to generate a cost layer (Adriaensen et al. 2003). Assigning this cost, however, relies on expertise (Coulon et al. 2004; Vignieri 2005; Broquet et al. 2006; Epps et al. 2007) or experiments designed to estimate resistance values for each landscape component (Stevens et al. 2006). In studies with insufficient knowledge of dispersal or lacking experimental estimates of resistance, a solution is to repeat the LCP analysis with different combinations of cost values (Chardon et al. 2003; Verbeylen et al. 2003; Schweiger et al. 2004). Another way of weighting the cost of each landscape component might be achieved by using habitat suitability models or resource selection functions (Hirzel et al. 2006).

Habitat suitability is defined as the probability that a species uses a particular habitat. Models of habitat suitability or species distribution (Guisan and Zimmermann 2000; Guisan and Thuiller 2005; Pearce and Boyce 2006) can help select reserve networks (Tole 2006; Zielinski et al. 2006) and evaluate connectivity (Binzenhöfer et al. 2005), because these models predict the distribution of suitable habitats or resource patches in a landscape. The resultant suitability map gives the probability for each patch to be used by a given species (Boyce et al. 2002). The information in a suitability map is the distribution and configuration of resource availability for a given species in a given landscape. The cost for an animal to disperse through a landscape matrix partly includes mortality from predation and energy exhaustion (Baguette and Van Dyck 2007). The relative dispersal cost of a location can be reflected by resource availability, including cover for hiding from predators and food for energy replenishment during dispersal. Therefore, a habitat suitability map provides a basis for objectively generating cost layers for LCP analysis.

Habitat suitability models are based on the environmental characteristics of locations used or not used by the species in question: i.e. presence-absence or presence-only data. Models using presence–absence data are more accurate than models using presence-only data (Brotons et al. 2004). Presence-only data, however, are far easier to get from existing biodiversity databases, mainly because of the scarcity of reliable absence data (Boyce et al. 2002; Zaniewski et al. 2002; Graham et al. 2004). Field studies using radio or global positioning system (GPS) telemetry and non-systematic surveys collect presence-only data precluding habitat suitability models requiring presence-absence data. To translate a habitat suitability map into a cost layer for LCP analysis, we must first evaluate the reliability of the habitat suitability model before assigning cost weights to suitability values based on objective criteria. Hirzel et al. (2006) proposed the k-fold cross validation procedure and used the continuous Boyce index to help evaluate habitat suitability models using presence-only data. This procedure produces a curve of the ratio of predicted/expected frequency of evaluation data (P/E) versus the mean suitability value of a suitability class. The P/E curve can serve as a more objective means for reclassifying habitat suitability maps (Hirzel et al. 2006) to estimate dispersal costs.

Because the applicability of evaluating landscape connectivity by incorporating a habitat suitability model into LCP analysis has not yet been assessed (Guisan and Thuiller 2005; Broquet et al. 2006), we used ecological niche factor analysis (ENFA, Hirzel et al. 2002) on the presence-only data of an endemic forest rodent, the spiny rat (*Niviventer coninga*), to model the distribution of habitat suitable for the rat in a fragmented forest landscape in western Taiwan. We evaluated this model by k-fold cross validation and the P/E curve (Hirzel et al. 2006). We then used the P/E curve to incorporate the habitat suitability model into LCP analysis. Finally, we correlated the LCP distances with the genetic distances among individuals. The latter were considered as indirect estimates of gene flow. Our objective was to test the usefulness of a habitat suitability model for assessing landscape connectivity.

Methods

Study area

The study area was ca. 10 × 10 km^2 and included most of the Sanyi Township in Miaoli County, western Taiwan (Fig. 1), at an elevation of 200–980 m above sea level. Mean January temperature was 15°C, mean July temperature 28°C, mean annual temperature 22°C and annual precipitation 1,500–2,000 mm (http://www.sanyi.gov.tw/b/b01_3.htm). In 2004, residents in Sanyi Township numbered 17,990 (http://www.sanyi.gov.tw/b/b07_1.htm) and economic activities included agriculture, tourism, and industry. Heavy traffic on Highway No. 1 (6 lanes, traffic flow = 67,594 cars/day, speed limit = 100 km/h; http://www.freeway.gov.tw/02_01_06.asp) and Provincial Road No. 13 (4 lanes, traffic flow = 21,416 cars/day, speed limit = 60 km/h; http://www2.thb.gov.tw/download/Volume95.rar) as well as adjacent residential areas separated the area's forests into a western and eastern part (Fig. 1). Forest cover of the entire landscape was about 60% in 2001 (Fig. 1). Other types of land cover (e.g., bamboo plantations, agricultural land, additional smaller roads and buildings) further fragmented the forest cover. Because the spatial pattern of forest cover was different in the western and the eastern part, effects of landscape connectivity on gene flow may be different within each part and/or the entire landscape. Therefore, we assessed landscape connectivity by correlating genetic distances with LCP distances among individuals for each part separately as well as for the entire landscape.

Study species

The spiny rat, *Niviventer coninga*, is endemic to Taiwan. It is distributed in forests below 2,000 m and common at 1,300 m above sea level (Yu 1994; Wu and Yu 2000; Wilson and Reeder 2005). It has a low

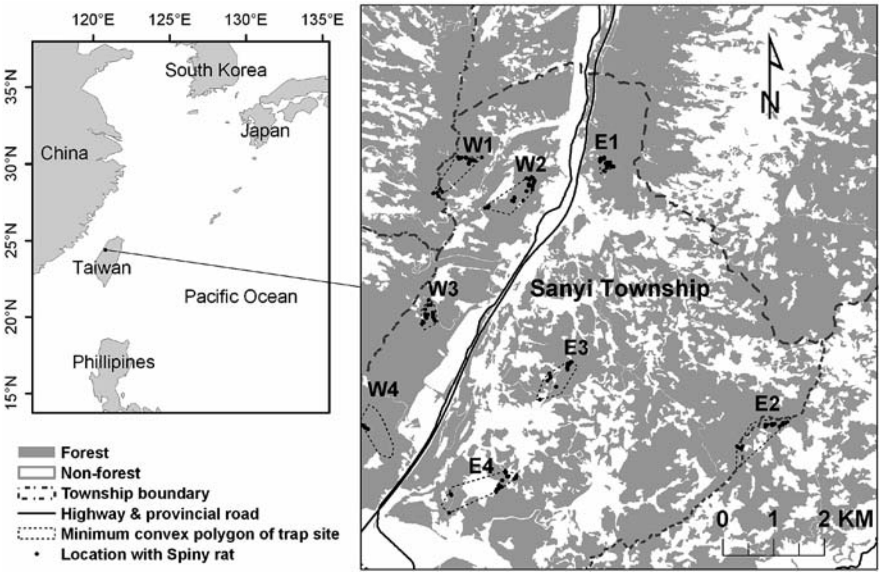


Fig. 1 Study area and trap sites of the spiny rat (*Niviventer coninga*) in the Sanyi Township, Miaoli County, Taiwan. Trap sites are numbered and labelled W or E depending on whether they were west or east of the highway and the provincial road

population density, high winter mortality (Chang-Chien 1989; Chang 1991; Wu and Yu 2000) and slow juvenile growth (Yu 1983; Yu and Lin 1999). Among the murids of Taiwan's low elevations, *N. coninga* is the only forest species (Wu and Yu 2000). All records of *N. coninga* are from forests (Yu 1983; Chang-Chien 1989; Chang 1991; Tsai 1997; Y.-H. Wang, unpublished data). A pilot study (2002–2004, Y.-H. Wang, unpublished data) in west-central Taiwan did not trap *N. coninga* in urban, grassland, and farmland habitats. Thus, human land uses such as residential areas, farmlands and transportation infrastructure were expected to affect the dispersal of *N. coninga*.

Trapping

Since we had no prior information on the distribution of *N. coninga* in the study area, we placed trapping sites in accessible public and private land. We chose eight sites covered by forest and shrub in which we placed 758 mesh-wired live traps (Fig. 1 and S1). Neighbouring traps were 15–30 m apart. We recorded the geographical coordinate of each trap location using a global positioning system receiver (3–5 m accuracy without differential correction). We anaesthetised trapped *N. coninga* with isoflurane, recorded sex and body weight and individually marked each rat by toe clipping. Because amplified fragment length polymorphisms (AFLPs) DNA analysis demands large quantities of high quality DNA (Lowe et al. 2004), we augmented tissue from toes with snips of ear tissue or tail tissue if a rat had severely torn ears from fighting. Tissues were preserved in 99.9% alcohol.

Genetic analysis

We extracted genomic DNA using the MasterPure Complete DNA Purification Kit (Epicentre Biotechnologies), checked DNA quality and its concentration by a UV/Vis Spectrophotometer SSP-3000 (Infinigen Biotechnology). Extracted DNA was diluted to 50 ng/μl.

We followed the AFLP protocol of Vos et al. (1995) with some modifications. Combinations of EcoRI/MseI and EcoRI/Taq$^{\alpha}$I restriction enzymes digested genomic DNA. Two fluorophores, 6-FAM or NED, labelled the 5′ ends of the selective EcoRI primers. Conditions of pre-selective polymerase chain reactions (PCR) and selective PCR are described in the supplementary material S2. We used twelve selective primer combinations (S3).

We analysed fragment lengths on a 3100 Genetic Analyzer with GS500 ROX (Applied Biosystems) as internal standard and GENESCAN (Applied Biosystems). GENEMAPPER 4.0 (Applied Biosystems) was used to identify and score peaks as present or absent within a fragment-length range of 75–500 bp. The peak-height threshold was set to 50 relative fluorescent units to exclude false peaks due to background noise. To reduce genotyping error, we randomly chose fourteen individuals and independently repeated the AFLP analysis from DNA extraction to peak scoring twice. Fragments with a reproducibility $\geq$ 86% (12/14) were retained. We identified a total of 172 polymorphic AFLP loci (S3) after dismissing loci with fragment frequencies higher than 95% or lower than 5%. GENALEX (Peakall and Smouse 2006) was used to calculate pair-wise genetic distances between individuals: $D = N(1 - 2\,N_{xy}/2\,N)$, where $2\,N_{xy}$ is the number of shared loci of two individuals and N is the total number of polymorphic loci (Huff et al. 1993).

Niviventer coninga presence data

We used a geographic information system to create a 20-m buffer around each point where a *N. coninga* was trapped. The buffered area (1,257 m^2) approximated Chang's (1991) report of *N. coninga* core home range (1,550 m^2). We transformed this buffer polygon layer into a raster of 10-m grid cells to match the resolution of SPOT5 satellite images and coded the cell value as '1' for cells within buffer polygons and as '0' for cells outside buffer polygons.

Environmental variables for modelling habitat suitability

We used twelve variables in the habitat suitability model, including vegetation growth, topography, and distance to various types of human land uses (Table 1). We used two scenes of cloud-free and geo-referenced SPOT5 satellite images of the study area (recorded 16 October 2005 and 30 March 2006, processed by the Center for Space and Remote Sensing Research, Central University, Chungli, Taiwan) to calculate a mean normalized difference

Table 1 Environmental variables for ecological niche factor analysis (ENFA) for *Niviventer coninga* in Sanyi Township, Miaoli County, Taiwan, including factor scores of marginality and specialization

Environmental variable	Transformation	Value range	Marginality factor (60%)	Specialization Factor 1 (11%)	Specialization Factor 2 (11%)	Specialization Factor 3 (5%)
Mean NDVI[a]	None	−0.321–0.476	0.226	0.116	−0.161	−0.728[b]
Aspect	Square root	0.017–18.974	−0.038	0.039	−0.019	−0.054
Slope	Box-Cox	−1.789–16.721	−0.191	0.086	0.149	0.032
Distance to forest	Plus 0.5	0.5–475.9	−0.315[b]	−0.494[b]	−0.628[b]	−0.226
Distance to bamboo plantation	Box-Cox	0–30.641	0.414[b]	0.217	−0.389[b]	0.244
Distance to bare land	Box-Cox	0–52.756	0.301[b]	0.514[b]	−0.465[b]	−0.042
Distance to building	Box-Cox	0–44.568	0.442[b]	−0.477[b]	0.093	0.134
Distance to shrub	Box-Cox	0–34.395	0.103	−0.29	−0.04	−0.093
Distance to farmland	Box-Cox	0–30.412	0.276	−0.182	0.168	0.37[b]
Distance to orchard	Box-Cox	0–24.981	0.472[b]	−0.257	0.017	−0.315[b]
Distance to road	Box-Cox	0–31.564	0.123	0.096	0.076	0.26
Distance to water	Box-Cox	0–57.532	0.174	−0.043	0.38[b]	−0.153

[a] Mean normalized difference vegetation index (indicates vegetation growth)

[b] Indicates variables with factor scores ≤ -0.3 or ≥ 0.3

vegetation index (NDVI; Bawa et al. 2002), which averaged the seasonal variation of NDVI in the study area to indicate vegetation growth of each location. We derived aspect and slope layers from a digital elevation model (DEM) created by the Aerial Survey Office, Forestry Bureau, Taipei, Taiwan. The DEM was resampled to 10 m with nearest neighbour without interpolation. Additionally, we used a land cover map (Y.-H. Wang, unpublished data) digitised from ortho-rectified images photographed in 2001 by the Aerial Survey Office, Forestry Bureau, Taipei, Taiwan, to calculate nine distance layers (Table 1). To match the resolution of SPOT5 satellite images, we transformed the polygon layer of the land cover map of the study area into a raster with 10-m cell size by the rule of maximum combined area of a cover type in one cell. All distance layers were calculated from this raster layer of the land cover map. Methods used to normalise the variables for factor analysis are listed in Table 1. Box-Cox transformation was a robust way to normalise most of these variables.

Habitat suitability model

We used ENFA (Hirzel et al. 2002) as implemented in BIOMAPPER (http://www2.unil.ch/biomapper/) to develop and validate a habitat suitability model for *N. coninga*. Based on the ecological niche concept, ENFA extracts factors of marginality and specialization to quantify the environmental variation of locations with the species compared to the environmental variation of the entire study area (Hirzel et al. 2002). Global marginality measures how the average environmental conditions of locations occupied by a species differ from the average of the entire study area (Hirzel et al. 2002). Tolerance, i.e., reciprocal of global specialization, measures the range of a species' distribution along environmental gradients (Hirzel et al. 2002).

We used an algorithm of geometric mean distance (Hirzel and Arlettaz 2003) to produce the habitat suitability map. To validate this model, we divided the presence data into 10 partitions with zero randomness for k-fold cross validation (Hirzel et al. 2006). We used the continuous Boyce index and a curve of the P/E ratio versus habitat suitability values (Hirzel et al. 2006) to evaluate model quality. The continuous Boyce index is the Spearman rank correlation of the P/E ratio with the habitat suitability value (Hirzel et al. 2006). If the P/E ratio increases with increasing habitat suitability (Fig. 2), the model has a good predictive ability (Hirzel et al. 2006).

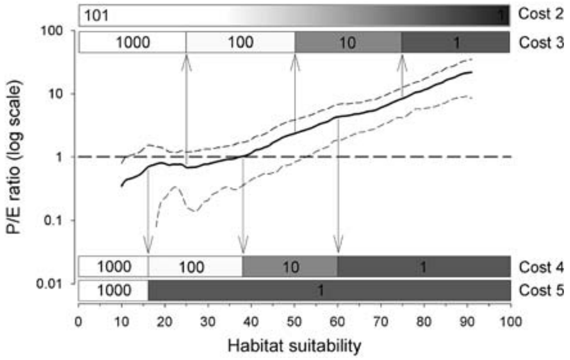


Fig. 2 The ratio of predicted/expected (P/E) frequency of evaluation data versus values of mean suitability. Trends in the P/E curve help with reclassifying habitat suitability and weighting costs. Solid line indicates mean P/E ratio. Short dashed lines are standard deviations of P/E. Long dashed line (P/E = 1) indicates a random model. Grey scale bars indicate four cost weighting methods (Cost 2–5) for each suitability value or class. Numbers in the bars indicate relative dispersal cost for each suitability value or class

Dispersal distances among individuals in a fragmented landscape

We used LCP modelling in ARCVIEW 3.2 (Environmental System Research Institute) and PATHMATRIX script (Ray 2005) to calculate the pair-wise LCP distances among individuals. Six cost layers (Cost 1–Cost 6) were used to model the least-cost dispersal paths among individuals. In the Cost 1 layer, each cell had the same cost value of one (Fig. 3a), assumed that landscape had no effect on the dispersal of *N. coninga*. This resulted in straight-line geographical paths among individuals. In the Cost 2 layer, the cost value of each cell was weighted between 1 and 101 by subtracting the habitat suitability value from 101 (Figs. 2 and 3b). Since Hirzel et al. (2006) pointed out that uncertainty in a model may make continuous habitat suitability values too accurate to reflect actual habitat conditions, we produced Cost 3–Cost 5 layers by reclassifying the habitat suitability into 2–4 classes. For the Cost 3 layer, we reclassified habitat suitability (HS) into four equal interval classes (class 1: $0 \leq \text{HS} < 25$; class 2: $25 \leq \text{HS} < 50$; class 3: $50 \leq \text{HS} < 75$; class 4: $75 \leq \text{HS} \leq 100$) and gave each class a respective cost weight of 1,000, 100, 10, and 1 (Figs. 2 and 3c). Hirzel et al. (2006) also suggested using the line P/E = 1 and steps in the P/E curve to define the class boundaries (Fig. 2). Hence, we produced Cost 4 by reclassifying habitat suitability into four classes according to the defined boundaries (class 1: $0 \leq \text{HS} < 16$; class 2: $16 \leq \text{HS} < 38$; class 3: $38 \leq \text{HS} < 60$; class 4: $60 \leq \text{HS} \leq 100$) and weighted cost of each class as 1000, 100, 10, and 1, respectively (Figs. 2 and 3d). We overlaid the land-cover map onto the habitat suitability map and found that most land-cover types had low mean suitability values (S4). Because our habitat suitability model used presence-only data recorded within or close to forest cover, it mainly reflected suitability of forest habitat. Therefore, we developed the Cost 5 and Cost 6 layers to examine landscape connectivity if habitat suitability above a threshold (Cost 5 layer: cost = 1 if $\text{HS} \geq 16$ or cost = 1,000 if $\text{HS} < 16$; Fig. 3e) or if all forested patches (Cost 6 layer: cost value of forest = 1; cost value of all other land cover types = 1000; Fig. 3f) were suitable for *N. coninga* dispersal. We modelled the among-individual LCP within each part and within the entire landscape to assess the landscape connectivity at two spatial scales.

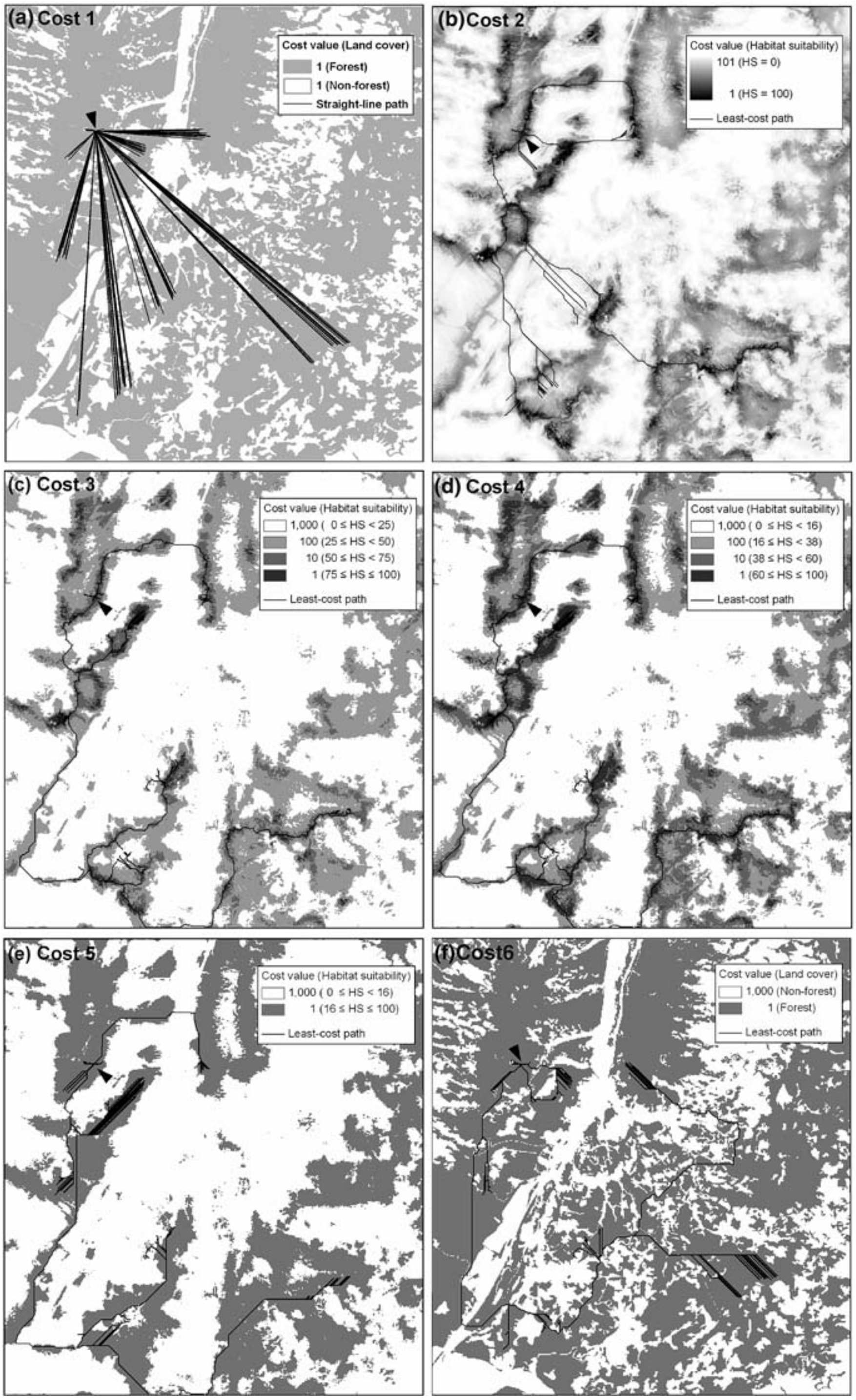
Correlating indirect estimate of gene flow with landscape connectivity

Gene flow of *N. coninga* would be restricted by distance if dispersal is spatially homogeneous (Rousset 2004). To test whether indirect estimates of gene flow of *N. coninga* were correlated with landscape connectivity in western and eastern parts and the entire landscape, we used Mantel tests (9,999 permutations) in GENALEX (Peakall and Smouse 2006) to correlate pair-wise genetic distance matrices with logarithmic landscape distance matrices calculated from the six LCP models (Cost 1–Cost 6).

Results

A total of 134 *N. coninga* were trapped during 6,098 trap-nights. Global marginality and tolerance for *N. coninga* in the study area were 0.745 and 0.279, respectively. The four marginality and specialization factors retained to calculate the habitat suitability map explained 87% of the variation in twelve environmental variables describing *N. coninga* distribution (Table 1). The marginality factor explained 60% of the variation (Table 1). Distance to forest,

Fig. 3 Dispersal paths of a *Niviventer coninga* (arrow) to all others trapped in the Sanyi Township, Miaoli County, Taiwan, as delineated by least-cost path (LCP) models using six different cost layers: (**a**) Cost 1, forest and non-forest received same cost of one, resulting straight-line dispersal paths; (**b**) Cost 2, each cell received a cost between 1 and 101 that was opposite its habitat suitability (HS); (**c–d**) Cost 3 and Cost 4, cost value of 1, 10, 100, and 1,000 assigned to each of four HS classes; (**e**) Cost 5, cost value was one if HS $\geq$ 16 or 1,000 if HS $<$ 16; and (**f**) Cost 6, forest received a cost value of one and non-forest was 1,000



bamboo plantation, bare land, buildings and orchards contributed most to the marginality factor (factor scores ≤ -0.3 or ≥ 0.3; Table 1). Specialization factors 1–3 explained another 27% of the variation (Table 1). Distance to forest, bare land, buildings, bamboo plantations and water contributed most to specialization factors 1 and 2 (Table 1). Distance to farmland and orchards and the mean NDVI

Table 2 Mantel tests of a pair-wise genetic distance matrix against six least-cost path (LCP) distance matrices (Cost 1–Cost 6) among individuals of *Niviventer coninga* within the western and eastern parts and the entire landscape covering the Sanyi Township, Miaoli County, Taiwan

LCP model[a]	Mantel r (P-value)[b]		
	Entire landscape	Western part	Eastern part
Cost 1	0.123 ($P < 0.0001$)	0.115 ($P = 0.0012$)	0.151 ($P < 0.0001$)
Cost 2	0.127 ($P < 0.0001$)	0.116 ($P = 0.0016$)	0.160 ($P < 0.0001$)
Cost 3	0.147 ($P < 0.0001$)	0.138 ($P < 0.0001$)	0.162 ($P < 0.0001$)
Cost 4	0.161 ($P < 0.0001$)	0.142 ($P < 0.0001$)	0.169 ($P < 0.0001$)
Cost 5	0.158 ($P < 0.0001$)	0.139 ($P < 0.0001$)	0.159 ($P < 0.0001$)
Cost 6	0.154 ($P < 0.0001$)	0.120 ($P = 0.0008$)	0.149 ($P < 0.0001$)

[a] Models defined in text and Figs. 2 and 3

[b] Mantel r is the Pearson correlation coefficient

contributed most to specialization factor 3 (Table 1). The continuous Boyce index (window size = 20) was 0.888 ± 0.168. The P/E ratio increased with habitat suitability in an exponential way (Fig. 2).

Figure 3 illustrates the least cost paths traced from six LCP models (Cost 1–Cost 6) that one *N. coninga* could use to disperse to other locations with *N. coninga*. Mantel correlation in the entire landscape as well as within each of the two parts separately slightly increased. The LCP distances of Cost 4 exhibited the strongest correlation with genetic distances in entire landscape and in both parts (Table 2).

Discussion

HS model and characteristics of *N. coninga* habitat

Niviventer coninga had specific habitat requirements: forests and areas distant from human activities (factor scores ≤ -0.3 or ≥ 0.3 in Table 1). As shown by high global marginality (0.745) and low tolerance (0.279), suitable habitat was not common in the study area. Although *N. coninga* inhabits low elevation forests, its presence within these forests is hard to predict (Wu and Yu 2000; Wang, unpublished data). Dense shrub cover is an important habitat variable determining the species' habitat use and spatial distribution (Chang-Chien 1989; Chang 1991; Tsai 1997). For *N. coninga* nesting on ground or in trees, shrub cover may provide shelter and access to tree canopy (Chang 1991; Tsai 1997). According to our habitat suitability map, some habitats of low suitability were in the interior of large forest patches (Fig. 3b), even though *N. coninga* is considered a forest species (Wu and Yu 2000; Wilson and Reeder 2005). Dense shrub cover is unevenly distributed in canopy gaps within forests. This heterogeneous distribution may result in low capture rates at locations away from canopy gaps. The continuous Boyce index and P/E curve showed that our model reflected the general distribution of suitable habitats and indicated its high predictive ability.

However, to refine the model's predictive ability for forest interiors, we would need to incorporate micro-environmental variables characterizing complex three-dimensional forest structures at a landscape scale. Point surveys measuring height and coverage of shrubs under canopy cannot be extrapolated to the entire area without the help of remote sensing. Recent advances in remote sensing technology using light detection and ranging (LiDAR) promise to map forest structure accurately at the landscape scale (Zimble et al. 2003; Hyde et al. 2005; Nelson et al. 2005).

Landscape connectivity and *Niviventer coninga* gene flow

Niviventer coninga gene flow may be partially affected by fragmentation in Sanyi's forests. This is because the dispersal distance estimated from Cost 1 LCP model (Fig. 3a), which gave the same cost weight to all land cover types, had the lowest correlation with genetic distance (Table 2). Path distances of other LCP models (Fig. 3c–f; Table 2), giving different cost weights to each location according to habitat suitability, improved the correlations with genetic distance. The Cost 2 model (Fig. 3b) showed almost the same correlation as Cost 1 (Table 2), indicating that weighting dispersal cost for each location according to habitat suitability produced a contrast too weak to reflect the potential dispersal routes and did not have a better predictive ability than straight lines. Reclassifying habitat suitability into few classes (Figs. 2 and 3) produced a better contrast of relative dispersal cost of each location, as indicated by the correlations of models Cost 3 to Cost 5 (Fig. 3c–e; Table 2).

When reclassifying a habitat suitability map it is important to determine thresholds of class boundaries based on the quality of a habitat suitability model as shown in Figure 2: an ideal model should have a linearly increasing trend and small uncertainty (low variance of P/E ratio) in the P/E curve (Hirzel et al. 2006). If a model has large uncertainty, it is impractical to reclassify habitat suitability into a large number of classes, because adjacent classes would have a similar P/E ratio. If a model's predictive ability does not linearly increase with habitat suitability, adjacent classes also have similar P/E ratios: these situations would erroneously weight different dispersal costs of adjacent classes with similar P/E ratios. Therefore, we determined class boundaries based on the line P/E = 1 and steps in the P/E curve (Hirzel et al. 2006) to weight classes in the Cost 4 model (Fig. 2). The correlation of genetic distance with the Cost 4 LCP distance was the highest of all models for both spatial scales, the entire landscape and its western and eastern parts (Table 2).

Because we used presence-only data sampled from forests or locations close to forests to build a habitat suitability model for *N. coninga*, our model mainly contrasted the habitat suitability with respect to forest cover (Fig. 3b). Although the study area was about 60% forest cover, the model showed that many small forest patches were unsuitable for *N. coninga* (small fragments in Fig. 3a are shown as unsuitable in Fig. 3b). When correlated with genetic distance, the landscape connectivity estimated by Cost 5 better explained estimated gene flow than the Cost 6, which assumed all forest patches were suitable. Among the six LCP models, the LCP distances in Cost 4 best explained estimated gene flow. This showed that reclassifying a habitat suitability map based on trends in the P/E curve helped to objectively weight the cost of dispersing through each location with a given habitat quality. Although the area of a specific land cover type is not necessarily equal to the area of suitable habitat for a species (Lindenmayer et al. 2008), the distribution and amount of suitable habitat can be mapped through habitat suitability modelling to reclassify the suitability map.

LCP analyses of previous studies had two main problems when assigning dispersal costs to land cover types. First, they did not consider patch size and shape. Expert opinions (Spear et al. 2005; Vignieri 2005; Broquet et al. 2006; Compton et al. 2007) or experiment-based resistance values (Stevens et al. 2006) give the same cost to a particular land cover type regardless of patch size, shape, and edge effects. Since small, complexly shaped patches may have low suitability due to edge effects, the relative cost of dispersing through these patches should be higher (e.g., small fragments of forest in Fig. 3a are shown as unsuitable in Fig. 3b–e). By including distance or proximity variables, habitat suitability modelling takes edge effects into account. A reclassified suitability map may hence more objectively reflect dispersal costs. The second problem with assigning dispersal costs is incorporating knowledge from other studies on the species' dispersal behaviour. This information may not be transferable from one area to another because of variation in environment, differences in landscape history, and local adaptation of animal behaviour. Because habitat suitability models are based on information of local environmental conditions and species presence (and absence) in the landscape of the study area, translating habitat suitability into dispersal cost can sidestep problems of patch size, patch shape, and transferring dispersal knowledge from other areas.

Table 3 correlated pair-wise genetic distances with landscape connectivity, even though they varied with respect to the mobility of the species studied and size of study area. The correlation coefficient of the genetic distance and Cost 4 LCP distance of *N. coninga* (0.161; Table 3) was almost five times larger than that for the European roe deer (Coulon et al. 2004) and five times smaller than that for the natterjack toad (Stevens et al. 2006). Studies showing low correlation with landscape connectivity may result from the assumptions that genetic structure

Table 3 Mantel tests of genetic distances against least-cost path distances for selected species in fragmented landscapes

Species	*R*	*P*	Level of analysis	Study area (km^2)	Reference
European roe deer (*Carpreolus carpreolus*)	0.031	0.005	Individual	2,200	Coulon et al. 2004
American marten (*Martes americana*)	0.043	0.026	Individual	800	Broquet et al. 2006
Spiny rat (*Niviventer coninga*)	0.161	<0.0001	Individual	100	This study
Land snail (*Cepaea nemoralis*)	0.374	0.007	Population	16	Schweiger et al. 2004
Mountain vizcacha (*Lagidium viscasia*)	0.40	0.008	Population	12,000	Walker et al. 2007
Pacific jumping mouse (*Zapus trinotatus*)	0.420	0.029	Individual	945	Vignieri 2005
Natterjack toad (*Bufo calamita*)	0.75[a]	0.036	Population	100	Stevens et al. 2006

[a] Partial Mantel test

reflects gene flow without considering differential dispersal by sex, age, and social status (Broquet et al. 2006). It is also possible that landscape structure is not correlated with gene flow because of landscape history.

Advantages and disadvantages of ENFA in LCP modelling

We incorporated ENFA into LCP analysis to assess landscape connectivity for *N. coninga*. Factor scores from ENFA quantified the contribution of environmental variables to the habitat suitability model (Table 1). Understanding the importance of each environmental variable is necessary for habitat management, but such quantification is not available from other models using presence-only data (Sérgio et al. 2007). Furthermore, the P/E curve from k-fold cross validation (Hirzel et al. 2006) not only helped with describing the predictive ability of our model based on presence-only data, but it also provided an objective basis for reclassifying the habitat suitability map.

Using presence-only data, ENFA can overestimate suitable habitat (Hirzel et al. 2001; Pearce and Boyce 2006) and may be less accurate than models including absence or pseudo-absence data, e.g., generalized linear models (GLM; Hirzel et al. 2001; Brotons et al. 2004; Engler et al. 2004) and generalized additive models (GAM; Zaniewski et al. 2002). In cases where reliable absence data are not available, pseudo-absence data may be acceptable, provided they are adequately generated. Researchers can more objectively select pseudo-absence data points from locations predicted as unsuitable by ENFA and then use these data for GLM (Engler et al. 2004; Chefaoui and Lobo 2007, 2008) or GAM. By including ENFA-generated pseudo-absence data and modelling approaches, GLM or GAM may also help to contrast habitat suitability and dispersal costs in all land cover types. We did not adopt this approach because validation of GLM and GAM using the method of area under curve (AUC) does not provide convenient and objective basis for reclassifying habitat suitability as compared with k-fold cross validation and P/E curve (Hirzel et al. 2006). Although the k-fold cross validation and P/E curve are applicable to validate GLM and GAM (Hirzel et al. 2006), the complexity of these techniques may prevent general users of geographic information systems from performing this validation procedure. Hence, a program imbedded in geographic information system software that automatically cross validates GLM or GAM and generates a P/E curve would greatly facilitate incorporation of habitat suitability modelling using presence/pseudo-absence data into LCP analysis.

Integrating habitat suitability model, LCP, and genetic analysis to conserve biodiversity in fragmented landscapes

The LCP analysis in a geographic information system is routinely used to assess landscape connectivity by modelling animal dispersal and corridor use. The effectiveness of these models can be validated by population- or individual-based genetic analyses (Coulon et al. 2004; Vignieri 2005; Broquet et al. 2006; Epps et al. 2007). If knowledge of a species' habitat preference and dispersal is lacking, LCP analysis loses effectiveness. This is because the costs of dispersing through a landscape matrix must be weighted subjectively. When collecting genetic samples, the collection locations can be mapped. If the result of random sampling, these presence data are useful for habitat suitability modelling, especially in areas, lacking information of a species' distribution. Through habitat suitability modelling, it is possible to identify potentially suitable habitats not yet sampled within the study area. This technique also allows quantification of a study species' ecological niche and habitat requirements (Guisan and Thuiller 2005). Here, we showed how habitat suitability modelling can be adapted for LCP analysis to assess landscape connectivity and validated the usefulness of LCP models by using landscape genetics.

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