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Simulated and human metapopulations created by habitat selection

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ABSTRACT

Questions: Can density-dependent habitat selection create extinction–recolonization dynamics typical of metapopulations? Does habitat selection occur at spatial scales represented by metapopulations?

Approach: Simulation models of discrete logistic population growth by two competing species occupying three habitats. Test of the prediction that resident Canadians move between cities to maximize income.

Key assumptions: Groups in different habitats can be treated as different populations. Different Canadian cities represent separate habitats. Income is a surrogate of fitness. Humans and human societies are appropriate for assessing density-dependent habitat selection.

Results: Density-dependent habitat selection by two competing species can cause frequent local extinctions and recolonization of empty habitat. Canadians disperse between cities in a way that appears to maximize median household income.

Conclusion: Local extinction and recolonization is easily created by density-dependent habitat selection. Humans select habitat at a scale corresponding to that of a typical metapopulation.

Keywords: Canada, fitness, habitat selection, *Homo sapiens*, ideal-free distribution, metapopulation.

INTRODUCTION

A metapopulation is 'any assemblage of local populations connected by migration' (Hanski and Gilpin, 1997; Gyllenberg *et al.*, 2004). Classical metapopulation models (Levins, 1969; May, 1991; Nee and May, 1992; Tilman *et al.*, 1994; Hanski, 1999) use a fixed colonization parameter that mimics the individual reproductive rate used in single-species population dynamics. More advanced theories of structured metapopulations attempt to model each population separately. While such models can clearly include as much complexity as we dare to consider, in practice they typically imagine fixed per capita emigration rates (Gyllenberg *et al.*, 2004; Parvinen, 2004).

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Constant dispersal embedded in these models reflects a much deeper assumption about the evolution of optimum dispersal strategies in spatially varying environments. There are two schools of thought. The predominant view is that evolutionarily stable dispersal rates evolve to reflect the fitness of migrating individuals among the historical distribution of patches in heterogeneous environments (e.g. McPeek and Holt, 1992). An extension of this form of reasoning evaluates the role of (fixed) gene flow on local adaptation and population persistence (e.g. Kirkpatrick and Barton, 1997; Holt and Gomulkiewicz, 2004).

There is a behavioural alternative to constant dispersal. Organisms can use a variety of cues to assess density and fitness prospects, and alter their dispersal accordingly [e.g. through density-dependent habitat selection (Fretwell and Lucas, 1969)]. While such adaptive dispersal has been used successfully to model spatial distributions in different habitats (Rosenzweig, 1974, 1981; Morris, 1987, 1988), species interactions (Rosenzweig, 1979, 1981; Morris, 1988, 1999), and the evolution of community structures (Rosenzweig, 1974, 1991, 1995; Morris, 1988, 1999; Brown and Pavlovic, 1992), it has not been generally applied to the larger spatial scales of metapopulations.

We explore the role that density-dependent habitat selection theory can play in metapopulation dynamics. We begin with a computer simulation of optimal habitat selection by two competing species, each a metapopulation, and each occupying a landscape composed of one unsuitable and three suitable habitats (patches). We demonstrate that this simple model creates local extinctions and recolonizations that would normally be considered proof for classical metapopulation dynamics. Meanwhile, an otherwise identical model using constant habitat-dependent dispersal rates failed to create any extinctions whatsoever. With this result in hand, we then ask whether habitat selection or constant dispersal best describes animal (i.e. *Homo sapiens*) movement in a large metapopulation where each individual has been marked and its movement among patches recorded.

METHODS

Computer simulations

We explored the long-term dynamics of a simple but realistic representation of a metapopulation. A target species and one competing species live in a four-habitat landscape (Fig. 1). Each species can maintain a positive population growth rate in three (A, B, C) of the habitats. The fourth (D) is unsuitable for occupation by either species.

We modelled population growth using a discrete logistic equation (e.g. Case, 2000) for each species and habitat:

$$N_{ih(t+1)} = N_{ih(t)}\left(1 + R_{ih}\left(1 - \frac{[N_{ih(t)} + \alpha_{ijh} N_{jh(t)}]}{K_{ih}}\right)\right)$$

where subscripts correspond to species i and j in habitat h, N is population density, R is the discrete maximum rate of per capita population growth, α is the per capita competitive effect of species j on i in habitat h, and K is carrying capacity. Each simulation began with $K - 1$ individuals of species 1 in habitat A co-occurring with a single individual of species 2. All other habitats were empty. The simulation ensured that species 2, when rare, could invade the system.

Next, each population grew for a single generation (Fig. 2). Then it grew through a second time interval according to the geometric mean R calculated for that species and

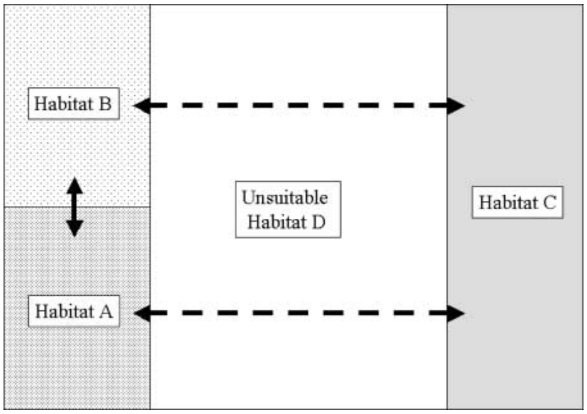


Fig. 1. A schematic of the four-habitat landscape imagined for two competing habitat-selecting species. Each species could move freely between habitats *A* and *B* (solid arrow), but incurred a mortality risk by moving from, or to, habitat *C* (dashed arrows).

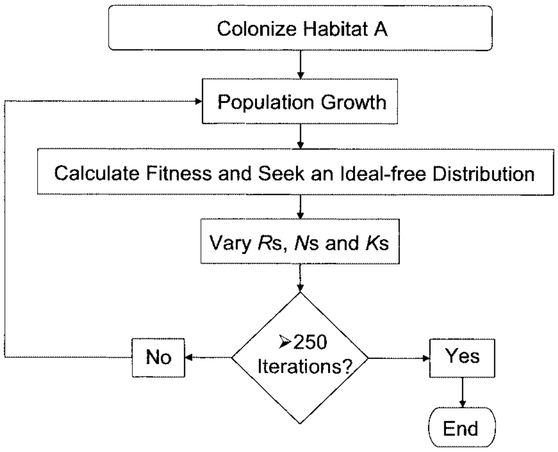


Fig. 2. A flow chart summarizing the main steps in simulations of density-dependent habitat selection of two species living in a four-habitat landscape.

habitat across all previous growth intervals. The geometric mean *R* is an appropriate density-independent fitness estimator in temporally variable environments (see, for example, Case, 2000). We calculated the per capita difference in population sizes between the two generations as an estimate of an individual's expected density-dependent fitness in each habitat. An individual was then selected at random, and if it could improve its fitness by dispersal, it moved. We recalculated all fitness estimates for the new distribution of population sizes, selected another individual at random, and repeated the process. Dispersal stopped only when no individual could improve its fitness by moving to an alternative habitat (an ideal-free distribution).

All individuals that moved between habitats *A* and *B* did so without cost. However, movement to or from habitat *C* entailed a binomial mortality risk. Expected fitness was devalued according to the binomial probability of survival. After the movement of an individual that could improve its expected fitness by dispersal to or from habitat *C*, we determined whether it survived or not by drawing values of zero (died during dispersal) and one (survived dispersal) from a binomial distribution with the appropriate probability of survival. Once an ideal-free distribution was attained, the environment was altered such that all population-growth parameters for each species and habitat (including population sizes, but not mortality risk during dispersal) varied stochastically. Then the system began another round of population growth. The simulations assumed perfect spatial autocorrelation for environmental variance (i.e. the parameters for each habitat varied in exactly the same proportion of their initial value). Stochasticity was simulated by imagining that each parameter had a maximum proportional deviation ($p_{\max}$) from its constant (R and K) or current (N) value. We then drew a random value less than or equal to that proportion from a uniform distribution. The current value of each parameter was multiplied by the proportional effect [$x_{(t+1)} = (1 \pm p)x_t$, where x represents the parameter of interest and p corresponds to the randomly drawn value $\leq p_{\max}$].

Each set of simulations consisted of 250 iterations (generations). We eliminated the first 50 iterations to ensure that the dynamics did not reflect initial conditions, then we summarized the number of individuals living in each habitat for the final 200 time steps.

We compared the dynamics of ideal-free habitat selection with those produced by constant habitat-dependent dispersal rates. We began by imagining that natural selection could produce a dispersal rate between each pair of habitats that reflected the ideal-free solution of our previous simulations. So we used the mean densities from the final 200 generations (selected above) as input. We ran ten additional 50-generation simulations of ideal-free habitat selection and calculated the mean number of descendants from these simulations. We compared our results with those obtained from modified bootstrapped estimates (1000 random samples of 10 similar simulations) drawn from 50 fixed dispersal-rate simulations that used the same input parameters. We also compared similar bootstrapped estimates for the total number of descendants of each species.

Habitat selection in a human metapopulation

Does habitat selection or classical metapopulation dynamics better describe migration in a large metapopulation? Populations of *Homo sapiens* allow one to pose that question because all individuals are marked and their dispersal among populations is recorded. Accordingly, we extracted anonymous summary data on more than 10×10^6 resident Canadians living in Canada's 27 largest cities from the 15 May 2001 census (Statistics Canada website, http://www12.statcan.ca/english/census01/home/index.cfm; data retrieved between 8 December 2004 and 28 February 2005). Each census takes place on a single day every 5 years. The data include the number of resident Canadians living in each city (we combined adjacent Ottawa and Hull as a single city) in 1996 who were resident in another city in 2001 (dispersing individuals). Additional city metrics that we used in our analyses included median household income of each city in 2000, employment rate (age 15 years and older), population size, and the total number of employed persons. Details of the data and their collection can be found on the Statistics Canada website. We used Microsoft Corporation's MSN Maps and Directions to calculate driving distances (our estimate of dispersal distance) by the quickest routes between Canadian cities, and weighted this metric by the number of immigrants from that distance (http://www.mapblast.com/directionsfind.aspx?&src=MP&cnty2=0; data retrieved between 3 and 13 January 2005).

Because Canadians moved between cities, the cities' collective population fits the definition of a metapopulation (Fig. 3; see Appendix). True, Canadians are also distributed in numerous smaller centres throughout the country. Although such centres can doubtless serve as stepping stones for migration, we ignore them in our analysis because we focus on movements among cities. Thus, we formulated and tested a series of hypotheses to determine whether human migration within Canada reflected constant dispersal rates or represented active habitat selection. We reasoned that if dispersal rates were constant for all cities, then the proportion of immigrants that cities received from a common source should either depend on the distance from the source city or on its population size. But if humans base their dispersal on active, adaptive choices, then the proportion of immigrants entering cities from a common source should reflect economic differences between those cities. We assume that income attracts people and represents a reasonable surrogate for human fitness. If Canadians tend to occupy cities that maximize income, and if they are free to choose the city of their choice, then migration should be biased towards cities with the highest median

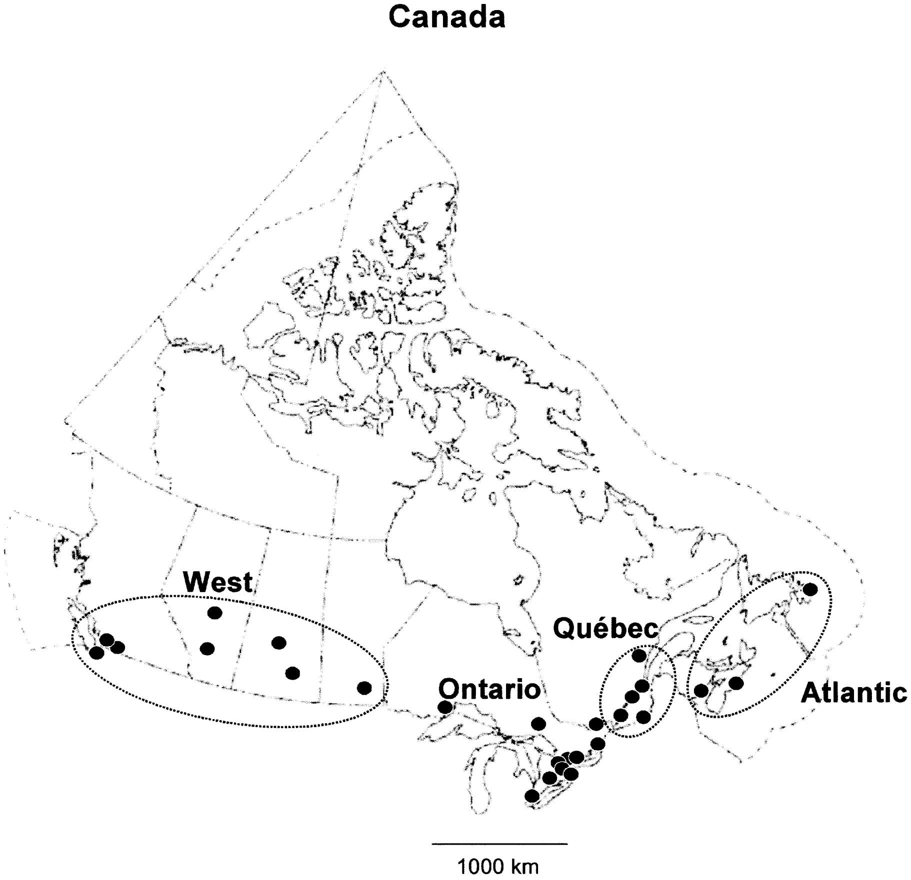


Fig. 3. A map illustrating the spatial distribution of the metapopulation composed of Canada's 27 largest cities (regions correspond to those recognized by many Canadians; after map available at: http://atlas.gc.ca/site/english/maps/reference/outlinecanada/canada01/map.pdf; accessed 7 December 2005).

income. Canadians should preferentially move to those cities that provide the greatest economic reward. We recognize that the costs of housing and other expenses vary from city to city. Even so, income should be a reliable predictor of lifetime monetary value.

Economic demographers have long analysed patterns of human migration (Greenwood, 1985). Human migration among the co-terminous United States, for example, is well described by an econometric model that includes population size, per capita income, unemployment rates, migration distance, and state-specific amenities (Davies *et al.*, 2001). The model assumes that individual humans maximize the economic utility of either staying in the state where they currently reside, or moving to another state. The utility-function maximization is analogous to fitness maximization incorporated in theories of density-dependent habitat selection, and sets a clear precedent for using economic indicators as fitness correlates.

Our analysis of human habitat selection carries several assumptions. We address the most restrictive of these in turn:

1. Economic indicators such as median household income and employment rates represent reliable cues of habitat (city) quality. Although we assume that Canadians may base dispersal on expected income, we acknowledge that the decision to migrate will also be based on a complex of social, economic, and biological variables. Regardless of the complexity, opportunities for humans to raise and provision offspring successfully depend, in large part, on income.
2. All Canadian cities are assumed equal. This assumption is patently false. Canada is a confederation of ten provinces and three territories. Our sample includes cities in nine of the provinces that Canadians recognize as four distinct regions (Fig. 3). The provinces differ in geography, climate, ecosystems, history, language, ethnicity, industry, taxation, social programmes, health-care delivery, educational opportunities, and numerous other areas under provincial jurisdiction. But all Canadians have equal rights and share numerous values and responsibilities, including universal health care, a federal pension programme, freedom of movement, assembly, and expression, and an unrivalled passion for hockey.
3. All Canadians moving between cities are assumed equal. This assumption is also false. Emigrants from Canadian cities span the gamut of demographic, economic, social, ethnic, and educational backgrounds. But such differences should tend to reduce our ability to detect nationwide patterns of dispersal related to simple economic indicators.

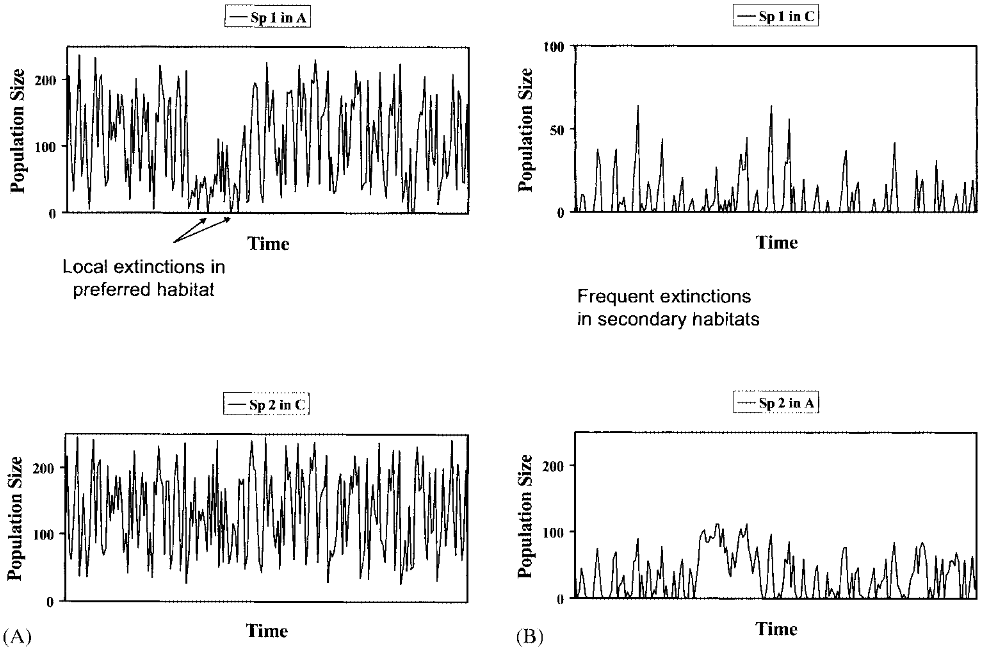
In fact, every false assumption we make places the theory of habitat selection at higher risk and increases the difficulty of detecting dispersal based on habitat selection. Thus, if patterns of Canadian dispersal are related to cues that represent habitat (city) quality, we can be assured that habitat selection plays a role in Canadians' dispersal decisions. And we remind readers that our objective is different from that of many economists and human demographers. We wish to evaluate whether habitat selection operates at a scale where ecologists would normally invoke metapopulation dynamics. We are not interested in building the best model to describe human dispersal. We focus on humans merely because in no other animal species from so vast an area is virtually every individual tagged and every metapopulation-scale movement recorded.

RESULTS

Habitat selection yields extinction and recolonization patterns consistent with metapopulation dynamics

The population simulations revealed fluctuating densities with a clear signature of underlying stochasticity (Fig. 4). Species 1 often faced extinction, even in its best habitat (Fig. 4A). Both species became extinct frequently in their secondary habitat (Fig. 4B). Species 2 never became extinct in either habitat *B* or habitat *C* where it maintained a competitive advantage over species 1.

Could our system also produce local extinctions in the case of constant dispersal? We used the results of our two-species simulation to calculate each habitat's mean density as well as the mean dispersal rate between each pair of habitats (including individuals that died during dispersal to and from habitat *C*). We imagined that natural selection fixed the dispersal rates between each pair of habitats in a way that mimicked, as closely as possible, the ideal-free distribution. Then we replicated our simulations of habitat selection for



Local extinctions in preferred habitat

Frequent extinctions in secondary habitats

Fig. 4. Illustrations of results from computer simulations evaluating the pattern of population dynamics of two species living in a four-habitat landscape over 200 generations. (A) An illustration of the dynamics of the two species in their separate preferred habitats (habitat *A* for species 1, habitat *C* for species 2). Both species persisted in the landscape for all 200 generations, but note that species 1 faced several episodes of extinction even in its 'best' habitat. (B) An illustration of the dynamics of the two species in their secondary habitats. Both species became extinct in these habitats on several occasions. A similar (but less pronounced) pattern existed for species 1 in habitat *B*. Habitat *D* was unsuitable for either species. Parameter values as in Table 1.

10 series of 50 generations using those mean densities as starting points. We compared our results with bootstrapped estimates from another suite of 50 simulations that simply allowed the expected number of individuals to move between each habitat (with the same initial conditions).

Four effects predominate in the analysis (Table 1):

1. Habitat selection yielded more descendants than did constant habitat-dependent dispersal rates (species 2, $P = 0.01$; species 1, $P = 0.06$).
2. The differences between habitat selection and constant dispersal also differed among habitats (habitat selection produced more descendants than constant dispersal for species 1 in habitats *B* and *C*, and for species 2 in habitat *C*, but fewer descendants for species 2 in habitats *A* and *B*).
3. Extinction was common with habitat selection.
4. However, with constant dispersal, extinction was absent entirely.

We repeated the simulations by imagining that the emigration rate was constant for each habitat. We allowed the expected number of emigrants from each habitat to move to the remaining two suitable habitats at random. Again, there was no extinction in any of the 50 simulations.

Table 1. A comparison of mean population sizes, and the number of extinctions, in three habitats

Measurement*	Habitat selection	Constant dispersal	*P*
Mean number of species 1 in *A*	6 233	6 146	0.22
Mean number of species 1 in *B*	**1 556**	1 456	<0.001
Mean number of species 1 in *C*	**385**	346	<0.001
Mean number of species 2 in *A*	1 298	**1 345**	<0.001
Mean number of species 2 in *B*	4 095	**4 214**	<0.001
Mean number of species 2 in *C*	**7 195**	6 805	0.001
Mean total in all habitats for species 1	8 174	7 951	0.06
Mean total in all habitats for species 2	**12 588**	12 365	0.01
Mean extinctions of species 1 in *A*	1	0	
Mean extinctions of species 1 in *B*	4	0	
Mean extinctions of species 1 in *C*	32	0	
Mean extinctions of species 2 in *A*	19	0	
Mean extinctions of species 2 in *B*	0	0	
Mean extinctions of species 2 in *C*	0	0	

Note: Data represent simulations lasting a total of 500 generations assuming either ideal-free habitat selection or constant inter-habitat dispersal rates based on the ideal-free solution. Significantly larger values are in **bold** font. Parameter values as follows: $R_{1(A)} = R_{2(C)} = 1.6$; $R_{1(B)} = R_{2(B)} = 1.2$; $R_{1(C)} = R_{2(A)} = 1.4$; $K_{1(A)} = K_{2(C)} = 160$; $K_{1(B)} = K_{2(B)} = 120$; $K_{1(C)} = K_{2(A)} = 140$; $\alpha_{1,2(A)} = \alpha_{2,1(B)} = \alpha_{2,1(C)} = 0.8$; $\alpha_{2,1(A)} = \alpha_{1,2(B)} = \alpha_{1,2(C)} = 0.85$; stochastic variation in *R* constant for both species and all habitats at 0.2; stochastic variation in population densities constant for both species and all habitats at 0.2; stochastic variation in $K_{1(A)}$ and $K_{2(C)} = 0.5$; stochastic variation in all other carrying capacities = 0.2; binomial survival probability of species 1 moving to or from $C = 0.6$; binomial survival probability of species 2 moving to or from $C = 0.8$.

* Mean values calculated for 10 replicates of 50 generations each.

Migration among Canadian cities was non-random

The proportion of immigrants moving into a Canadian city between 1996 and 2001 was decidedly non-random. The observed immigration pattern bore no resemblance to that expected if all cities had the same immigration rate [none of 27 different single classification goodness-of-fit tests (*G*-tests) had a significance value > 0.0001].

The migration pattern of Canadians did not depend on distance or population size

We included the distance to source as well as population size in a stepwise multiple regression predicting the proportion of Canadians immigrating into a target city (number of immigrants/number of city residents). We also included emigration rate, population size in 2001, median household income, number of people employed, and employment rate. Since each city received immigrants from all others, and because potential source populations varied in population size, we weighted distance according to the expected number of emigrants assuming a constant dispersal rate across the country. We created the weighting by multiplying the distance from each other city (km) times the average emigration rate, summing those values, and dividing by 26 (total number of cities minus 1). Neither distance nor population size was significant alone or in combination with other variables.

Resident Canadians dispersed to cities with higher income potential

The proportion of Canadians that immigrated into a city did increase with the median household income of that city and with its emigration rate:

$$\text{ArcSin SqRt[ProportionImmigrating]} =$$

$$-0.196 + 0.56 \times \text{MedianHouseholdIncome} \times 10^5 + 0.593 \times \text{ArcSin SqRt[ProportionEmigrating]}$$

($F_{2,23} = 11.07$, $P < 0.001$, $R^2 = 0.49$; the analysis excludes Victoria, which lacked employment data for the stepwise model). Our interpretation is that Canadians actively chose to move to cities with high income potential that also had a high population turnover.

DISCUSSION

Our simulations do document that habitat selection, maximizing individual fitness in a heterogeneous environment, can maintain persistent populations characterized by numerous local extinctions. The resulting extinction–recolonization dynamics might typically serve as evidence supporting classical models of metapopulations. Yet when we simulated the constant rates of dispersal assumed by those models, the extinction–recolonization dynamics disappeared. So we need to explore why our simulations of habitat selection caused adaptive local extinctions, and why our simulations using constant dispersal rates did not.

The extinction of species 1 in its preferred habitat was caused by a lower rate of mortality during dispersal by species 2, and by a much higher variance in carrying capacities of the two species in their preferred (high R) habitats than elsewhere. Thus, when both species faced periods of a low carrying capacity in their preferred habitats, species 2 could preferentially invade habitat *B* where it had a competitive advantage over species 1, as well as habitat *A* where its carrying capacity was less variable. Meanwhile, species 1 faced not only the threat of a low carrying capacity but also invaders of species 2 that exacerbated the low quality of habitat *A*. Species 1 abandoned its preferred habitat during these hard times and maintained low densities in at least one of the other two habitats where its carrying capacity was relatively high.

Both species lived at high density in their preferred habitats when conditions were relatively benign. To reap the rewards of those high carrying capacities, however, they often abandoned their secondary habitat choices. Habitat selection in this simple but realistic community and landscape can thereby create patterns of extinction and recolonization typical of classical metapopulation dynamics.

The converse is not true. When we imagined fixed adaptive dispersal rates between pairs of habitats, or constant emigration rates out of all habitats, our simulations revealed no extinctions whatsoever. The absence of extinction was caused by two interacting effects: (1) There was a repeating flux of individuals among habitats each generation. When a habitat lost emigrants it also received immigrants. (2) Our simulations rounded all 'partial' individuals to integers. The last remaining individual in a habitat would disperse only if the emigration rate was greater than 0.5. Because all ideal-free emigration rates out of a habitat were less than 0.5, except for species 1 in habitat *C*, the use of integers eliminated dispersal as a sole cause of local extinction in most cases.

But more than one-half of all extinctions with ideal-free habitat selection involved species 1 in habitat *C*. Extinction in habitat *C* by dispersal alone was also possible with constant dispersal because the emigration rate out of *C* by species 1 was greater than 0.5. So absence of extinctions of species 1 in habitat *C* in the second set of simulations is crucially significant. A switch from variable to fixed dispersal rates reduced the probability of local extinction caused by adaptive habitat selection.

Ideal habitat selectors choose the best habitat to live in. Dispersal rates fluctuate dramatically in time and among habitats as individuals select the best of their options in stochastic environments. Local extinctions occur frequently. The alternative strategies of constant emigration rates, or constant rates of dispersal directed towards specific habitats, guarantee a flux of individuals among habitats that buffers their occupants from extinction.

The potential importance of habitat selection as a significant contributor to metapopulation dynamics is also evident in our analysis of human migration among Canadian cities. 'Obvious' predictors of metapopulation dispersal such as distance and population size (e.g. Johnson, 2005) failed to correlate with migration rates from one Canadian city to another. Rather, Canadians moved preferentially to cities where they could, on average, increase their expected household income. Such an active strategy is clearly consistent with habitat selection. Exclusion of other variables such as distance and population size is clearly inconsistent with the constant migration assumed by many metapopulation models.

A substantial amount of the variance in Canadian migration rates remains unexplained. There are at least two likely causes. First, median household income is only a correlate of the full economic advantages achieved through dispersal. Second, Canadians include more than financial gain in assessing their options on dispersal.

But we did not intend to evaluate all of the reasons that can account for dispersal of resident Canadians from one city to another. Rather, we wished to use those remarkable data to evaluate whether habitat selection plays a role in migration on a scale where it might normally be unexpected. The answer is an unequivocal 'yes'.

Adaptive habitat selection is an important potential cause of dispersal among populations. Habitat selection must be incorporated into metapopulation theory. But it is obvious that habitat selection entails costs, and it is reasonable to speculate that those costs increase with dispersal distance. Thus we must aim to integrate theories on the cost–benefit analysis of dispersal (e.g. Morris, 1992) into those of structured metapopulations (e.g. Hanski, 1999) and landscape ecology (Fahrig, 1997). Only then are we likely to truly understand spatial population dynamics.

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APPENDIX

Canadian cities used in the metapopulation analysis

City	Province	Income*	Immigration rate
Abbotsford	British Columbia	48,721	0.11
Calgary	Alberta	58,861	0.08
Chicoutimi-Jonquière	Québec	41,854	0.03
Edmonton	Alberta	51,685	0.05
Sudbury	Ontario	45,206	0.03
Halifax	Nova Scotia	46,941	0.05
Hamilton	Ontario	52,786	0.07
Kingston	Ontario	47,979	0.08
Kitchener	Ontario	55,528	0.06
London	Ontario	48,026	0.05
Montréal	Québec	42,123	0.02
Oshawa	Ontario	62,956	0.12
Ottawa-Hull	Ontario-Québec	59,009	0.06
Québec City	Québec	41,864	0.03
Regina	Saskatchewan	47,757	0.04
Saskatoon	Saskatchewan	43,392	0.04
Sherbrooke	Québec	36,744	0.04
St. Catherines-Niagara	Ontario	45,881	0.05
St. John's	Newfoundland	45,675	0.02
Saint John	New Brunswick	41,596	0.03
Thunder Bay	Ontario	47,849	0.02
Toronto	Ontario	59,502	0.03
Trois Rivières	Québec	35,969	0.03
Vancouver	British Columbia	49,940	0.04
Victoria	British Columbia	46,387	0.07
Windsor	Ontario	54,442	0.04
Winnipeg	Manitoba	44,562	0.03

* Median household income ($ CAN) in 2000.