Research Article

Genetic isolation by distance and landscape connectivity in the American marten (*Martes americana*)

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Abstract

Empirical studies of landscape connectivity are limited by the difficulty of directly measuring animal movement. 'Indirect' approaches involving genetic analyses provide a complementary tool to 'direct' methods such as capture–recapture or radio-tracking. Here the effect of landscape on dispersal was investigated in a forest-dwelling species, the American marten (*Martes americana*) using the genetic model of isolation by distance (IBD). This model assumes isotropic dispersal in a homogeneous environment and is characterized by increasing genetic differentiation among individuals separated by increasing geographic distances. The effect of landscape features on this genetic pattern was used to test for a departure from spatially homogeneous dispersal. This study was conducted on two populations in homogeneous vs. heterogeneous habitat in a harvested boreal forest in Ontario (Canada). A pattern of IBD was evidenced in the homogeneous landscape whereas no such pattern was found in the near-by harvested forest. To test whether landscape structure may be accountable for this difference, we used effective distances that take into account the effect of landscape features on marten movement instead of Euclidean distances in the model of isolation by distance. Effective distances computed using least-cost modeling were better correlated to genetic distances in both landscapes, thereby showing that the interaction between landscape features and dispersal in *Martes americana* may be detected through individual-based analyses of spatial genetic structure. However, the simplifying assumptions of genetic models and the low proportions in genetic differentiation explained by these models may limit their utility in quantifying the effect of landscape structure.

Introduction

The concept of landscape connectivity was introduced to designate the interaction between landscape structure and movement (Taylor et al. 1993). This interaction may strongly affect dispersal (the movement that an individual makes between its place of birth and the place where it

reproduces), a critical process shaping the evolution of populations (Wiens 2001). How to quantify connectivity remains a subject of debate (Tischendorf and Fahrig 2000, 2001; Moilanen and Hanski 2001; Goodwin and Fahrig 2002), but a number of approaches require some information on movement or immigration/emigration rates. However, empirical studies of animal movement are often severely constrained by inherent practical difficulties (e.g. limited sample sizes, extensive field work, cost of equipment, limited study area). 'Indirect' approaches of dispersal involving genetic analyses have proved increasingly useful in the recent past (reviewed in Neigel 1997; Rousset 2001a, b). A number of genetic methods in fact allow estimating either dispersal rates or distances and seem to provide suitable complementary tools to 'direct' methods. A genetic approach may therefore allow investigating the interaction of landscape features with dispersal (Castric et al. 2001; Hale et al. 2001; Michels et al. 2001; Vos et al. 2001; Arnaud 2003; Coulon et al. 2004).

In continuous populations with spatially limited dispersal, levels of gene flow tend to decrease with increasing geographic distances, which results in increasing genetic differentiation among individuals. This process called 'isolation by distance' (Wright 1943) may be detected by analysing the distribution of pair-wise estimates of genetic distances between individuals (Rousset 2000). Under a model of isolation by distance assuming genetic equilibrium (equilibrium between the genetic variability introduced by mutations and gene flow and lost through genetic drift at each generation: Rousset 2004, Chap. 3), the relationship between genetic and geographic distances allows estimating some demographic parameters (effective population density and/or dispersal distance) in the focal species (Hardy and Vekemans 1999; Rousset 2000; Hardy 2003). Another interesting property of this model is that it assumes that individuals disperse equally in all directions in a homogeneous environment. Conversely, the effect of the topography of the landscape on dispersal would cause a departure from isolation by distance (Coulon et al. 2004). Setting this model as null hypothesis, the effect of the connectivity of the landscape on dispersal may hence be tested in a continuous population framework through analyses of population genetic structure (Epperson 2003, p. 3, 31).

The American marten (*Martes americana*) is a mid-sized mustelid carnivore species inhabiting North-American forests. This species is mostly found in the Canadian boreal forest, where its habitat has been best preserved. *Martes americana* is a presumptive forest indicator species (Watt et al. 1996) typically associated with mature forest systems providing high prey availability and abundant shelter and predator-escape cover (Buskirk and Powell 1994). Very few data on marten movement are available in the literature, and conditions of dispersal remain unclear (but see Fecske and Jenks 2002). A complementary approach of dispersal employing direct and indirect methods has shown that the fine-scale population genetic structure of marten differed between optimal vs. fragmented habitats (Broquet et al. in press). A pattern of isolation by distance between individuals was evidenced in a sample of individuals inhabiting a landscape dominated by old-growth forest of fire origin (presumed optimal habitat), whereas no such pattern was found in a near-by more fragmented forest. The present study aims at testing whether the structure of the landscape may be accountable for altered dispersal in the fragmented landscape, thereby explaining the lacking isolation by distance pattern in this landscape. Some environmental features may in fact facilitate or impede marten movement in such a way that the straight-line geographic distance between individuals can not correctly describe the actual path of dispersal. This hypothesis is tested by looking for isolation by distance using some 'effective' distances taking into account the effect of landscape structures on marten movement instead of straight-line geographic distances between individuals.

Considering a number of landscape features interacting with marten movement, the effective distance between two individuals may be represented by the length of the most likely path that an individual would follow to join the other one. This path avoiding some elements of the landscape more resistant to movement and preferentially going through more permeable features can be approximated by the path minimizing the sum of the 'costs' of every feature crossed on the way (Chardon et al. 2003; Verbeylen et al. 2003). In this study, least-cost modeling was used to determine such paths among individuals. The length of these paths was then used to test for isolation by

distance in two contrasted landscapes in order to assess whether landscape connectivity affects gene flow in *Martes americana*. An additional aim of this study was to investigate the robustness of combining least-cost modeling and genetic analyses in connectivity studies. Accordingly, we tested for the effect of the arbitrary choice of resolution of grid-based representations of landscapes employed in least-cost modeling on the resulting effective distances and on their correlation with genetic distances. Hence, the objectives of this study were: (i) to test whether the structure of the landscape may be accountable for differing dispersal in *M. americana* and (ii) to assess the robustness and limits of least-cost IBD models.

Methods

Study area

The study site was located in a black spruce/jack pine-dominated boreal forest in the region of Ear Falls (50°38′ N, 93°13′ W), northwestern Ontario, Canada (Figure 1). The study area was divided into two landscapes differing in harvesting history (hereafter referred to as 'logged' and 'unlogged' landscapes). The unlogged landscape (ca. 500 km^2) was dominated by old-growth forest of fire origin, whereas the logged landscape (ca. 800 km^2) was composed of regenerating forest, with a mixture of second-growth stands of different ages and types.

Sampling and microsatellite analyses

Martens were live-trapped in both landscapes in 2001, 2002 and 2003. Live-trapping and handling procedures are described in Broquet et al. (in press). Trapping locations were recorded using a hand held GPS (accuracy 5–10 m). Samples of hair were taken on every live-trapped individual and used as a source of DNA for the genetic analyses. A set of seven microsatellite markers (hyper-variable nuclear DNA sequences: Avise 2004, p. 92) previously isolated by Davis and Strobeck (1998) were used to examine the spatial distribution of genetic variability. Conditions of DNA extraction and genotyping are described in Broquet et al. (in press). Expected heterozygosity (*He*) and allelic

richness per locus (*A*) were calculated for each population using the software FSTAT (Goudet 1995, 2001).

Genetic distance between individuals

A hierarchical analysis of marten genetic structure in the study area revealed an homogeneous genetic composition within each landscape, and little but significant divergence between landscapes (Broquet 2004). Accordingly, the two landscapes were considered as distinct populations, and the genetic structure used in this paper is based on the spatial distribution of genetic variation among individuals, as described in Broquet et al. (in press). Genetic distances between individuals (*a*) were computed with the program SPAGeDI (Hardy and Vekemans 2002).

Euclidean distance between individuals

Pair-wise Euclidean distances (*r*) correspond to straight-line geographic distances between pairs of individuals. These distances were calculated in Arcview 3.2 (Environmental Systems Research Institute, Redlands, USA) using Universal Transverse Mercator (UTM) coordinates of the original capture site of each individual.

Effective distance between individuals

The least-cost modeling procedure involves two steps (see Adriaensen et al. 2003; Chardon et al. 2003; Verbeylen et al. 2003 for a detailed description). First, the landscape is modeled as a friction map (grid) describing the resistance to marten movement of each type of land cover. Second, a least-cost algorithm is used to determine the least-cost path between locations. Friction maps for the logged and the unlogged landscapes were built from forest resource inventory (FRI) digital maps, which provide detailed descriptions of timber resources (e.g. stand age and species composition) and other types of land cover (e.g. water areas, swamps). Because least-cost modeling is based on a grid-based representation of landscapes (array of equal-size square cells), we first converted FRI
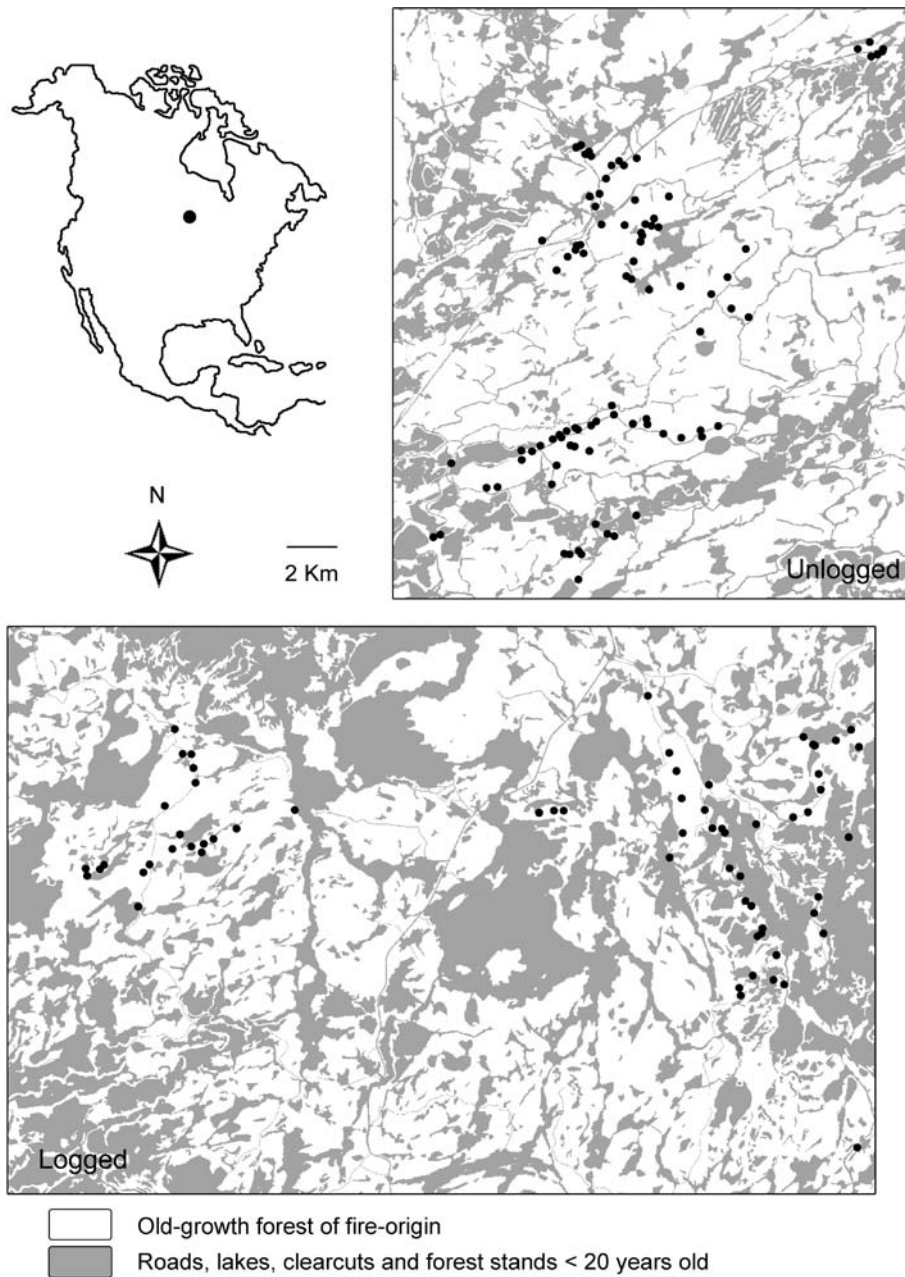
Figure 1. The study area located near Ear Falls, Ontario (50°38′ N, 93°13′ W), was divided into an 'unlogged' (above) and a 'logged' (below) landscape located approximately 50 km apart. White areas represent old-growth forest of fire-origin and regenerating stands ≥20 years old. Younger forest stands and unforested areas are represented in grey. Black dots represent original trapping sites of 118 and 73 American marten live-trapped in the unlogged and the logged landscapes, respectively.

maps into raster grids using the Arcview module Spatial Analyst 1.1. The effect of the choice of resolution on least-cost modeling and on the relationship between genetic and effective distances was investigated by repeating the procedure with six resolutions (grid cell sizes of 10, 25, 50, 75, 100 and 500 m) for the friction map of the logged landscape. The raster representation of the unlogged landscape was then built using a resolution of 75 m.

The choice of cell values depicting local resistance to marten movement was based on existing knowledge of marten biology. *Martes americana* avoids unforested areas such as clear-cuts and lakes, as well as young or unproductive stands presenting a low forest cover (Soutiere 1979; Buskirk and Powell 1994; Payer and Harrison 2003; Poole et al. 2004). Very little is known on the relative permeability of other forest stands varying in ages and dominant tree species. Accordingly, we used a simplistic distribution of friction values to build the raster maps of the study site. Each cell of unforested area (recent clear-cut, lake or road) or of young forest stand regenerating from logging (<20 years old) was given a friction coefficient of 50, while the friction of every other type of land cover (forested areas) was unchanged (friction coefficient = 1). These values were arbitrarily chosen such as to allow narrow elements (e.g. <100 m) like rivers, roads or small clear-cuts to be easily crossed while large unforested areas (e.g. >1 km) would always be skirted (accordingly to observations of marten movement realized during this study). These coefficients were chosen in such a way that the sum of costs of a straight-line crossing a large non-permeable area would necessarily be higher than the sum of costs along the path going around this zone. Conversely, linear structures like roads would easily be crossed since the sum of costs of a path trying to avoid crossing roads would become very high.

Least-cost paths were computed with the program Pathmatrix (Ray 2004). Pathmatrix uses a friction map representing the cost of movement for a given species and applies the 'cost distance' algorithm implemented in Arcview 3.2 to minimize the sum of resistances of all cells along the path between pairs of locations. Here, effective distances were not measured as the total sum of costs along the paths ('least-cost distance' *sensu stricto*), but as the lengths of the least-cost paths between each pair of individuals.

Relationship between genetic and geographic distances

Local polynomial regression (Cleveland et al. 1992) may be used to visualize the spatial distribution of genetic divergence produced by large pair-wise data sets (Coulon et al. 2004). The software R 2.0.1 (R Development Core Team 2005) was used to compute smoothed curves based on local polynomial regressions of pair-wise genetic distance against Euclidean or effective distances (polynomial regression of second degree fitted locally at 50 evaluation points using 2/3 of the total number of points) following Coulon et al. (2004). The null hypothesis of isolation by distance is characterized by the linear relationship between pair-wise genetic distances and the logarithm of geographic distances (Rousset 1997, 2000). This relationship was tested using Mantel tests based on 10,000 permutations implemented in FSTAT. Because under isolation by distance this linear relationship is expected to hold best at distances greater than the effective dispersal distance (σ) in the population (Rousset 1997, 2000), regressions were performed using only pair-wise comparisons for individuals separated by a distance ≥ 3.8 km (value of σ estimated for *M. americana* in the unlogged landscape: Broquet et al. in press). To do so, all points corresponding to pair-wise effective geographic distance data for individuals closer than 3800 m (i.e. $\ln(r) < 8.24$) were given the genetic and geographic values of the barycentre of all other points. This transformation allows removing from the distance matrices all variability introduced by the data points that should not be included in the analysis. The transformed matrices were then used in the Mantel tests.

Landscape connectivity

The resistance of landscape to movement along least-cost paths may be represented by the residuals of the regression of effective distances against Euclidean distances (Verbeylen et al. 2003). These residuals therefore express the effect of landscape features independently of the effect of distance. The software R (version 2.0.1) was used to regress effective distances against Euclidean distances in the logged and the unlogged landscapes, and residuals were plotted against Euclidean distances to visualize and compare the overall connectivity of each landscape. The distribution of the standard deviation of these residuals was also plotted to visualize the effect of landscape heterogeneity in logged vs. unlogged landscapes.

Results

Sampling and genetic variability

A total of 191 marten ($n_{Unlogged} = 118$, $n_{Logged} = 73$) were sampled. The gene diversity and allelic richness of the seven microsatellite markers used in this study to investigate the genetic structure of marten populations respectively found in the logged and the unlogged landscapes are presented in Table 1.

Effective distance between individuals

Pair-wise least-cost paths computed using friction maps of different resolutions appeared to differ in shape and length. The permeability of local landscape structures was highly dependent on the resolution of friction maps (Figure 2). However the global evolution of effective distances against Euclidean distances did not differ among resolutions, except for the largest grid cell size (500 m), which led to slightly lower effective distances than obtained at finer resolutions (Figure 3). The choice of the resolution for the friction maps used to model the resistance of the landscape to marten movement nonetheless greatly influenced the results of least-cost modeling and the ensuing relationship between genetic distances and effective distances (see below).

Relationship between genetic and geographic distances

Pair-wise genetic distances among individuals in the unlogged landscape were significantly correlated with both the Euclidean and the effective distances between individuals (Table 2). In this landscape, the polynomial regressions based on Euclidean and effective distances showed very similar patterns illustrating the increase of genetic differentiation with increasing geographic distance characteristic of isolation by distance (Figure 4a, b). In contrast, genetic distances among individuals in the logged landscape were correlated only with effective distances (Table 2), and polynomial regressions based on Euclidean vs. effective distances, respectively, showed opposite trends (Figure 4c, d). However, the pattern of isolation by distance detected in the logged landscape using effective distances was much less pronounced than in the unlogged landscape (Figure 4b, d).

In all cases, the proportion of variance (R^2) explained by the model was very low. This is an expected results from IBD, where genetic drift and sampling error in individual genetic estimators result in high variance in spatial genetic structure. However, the regression of genetic vs. geographic distances is biologically meaningful as it directly depends on the distribution of dispersal distance.
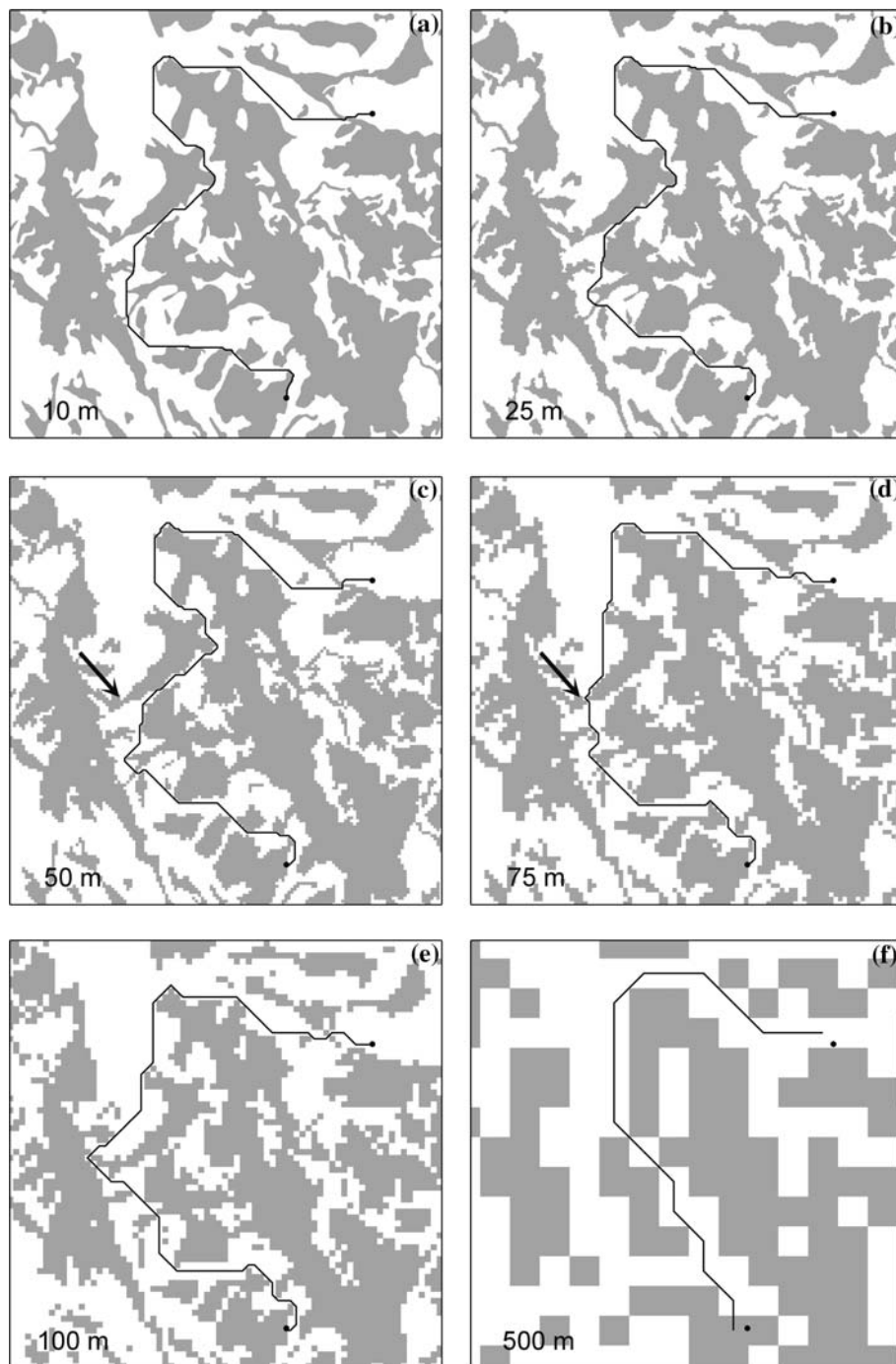
Landscape connectivity

The residuals of the regression of effective distances on Euclidean distances express the net effect, i.e. independent of the effect of distance, of landscape structures on simulated marten paths (Figure 5). The distribution of these residuals against Euclidean distances drastically differed between the unlogged (Figure 5a) and the logged landscape (Figure 5b). In the logged landscape, the residuals were much more dispersed and their variance increased more rapidly with increasing Euclidean distances.

Discussion

Correlation between genetic and geographic distances

In homogeneous environments, spatially limited dispersal causes an increase in genetic differentiation among individuals separated by increasing geographic distances. This isolation by distance was revealed in the unlogged landscape by the

Table 1. Summary of genetic diversity at seven microsatellite loci in two American marten populations inhabiting contrasting landscapes; allelic richness (*A*); expected heterozygosity (*He*).

Locus	forest		Logged forest	
	A	*He*	*A*	*He*
Ma2	5.0	0.726	5.9	0.693
Ma5	7.0	0.781	6.0	0.719
Ma8	7.7	0.795	7.0	0.794
Ma9	4.0	0.647	4.0	0.592
Ma11	3.0	0.540	4.0	0.550
Ma19	6.8	0.777	6.9	0.752
Gg7	7.0	0.717	8.0	0.764

Figure 2. Effect of the resolution of friction maps on the length of the least-cost path between two individuals of American marten (dots connected by black line) in the logged landscape. Cell size for maps a–f is 10, 25, 50, 75, 100 or 500 m. Black arrows on maps c and d show an example of a structure acting as a barrier or as a permeable element, respectively, depending on the resolution adopted. Accordingly, the resulting length of the least-cost path was decreased (e.g. from c to d) or increased (e.g. from d to e) with decreasing resolution.
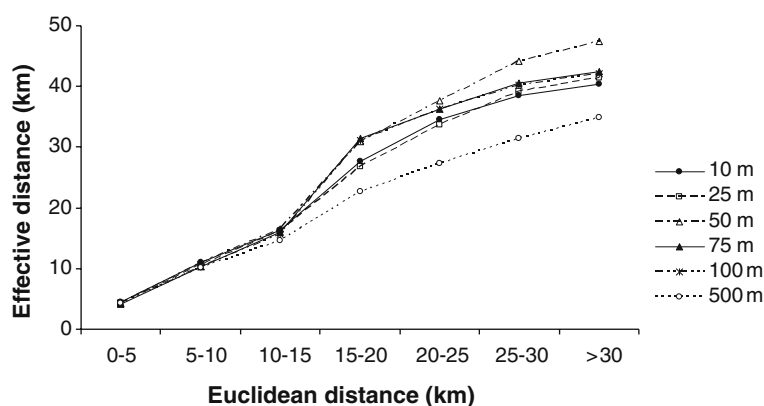
Figure 3. Evolution of effective distances against Euclidean distances calculated for 73 individuals of American marten in the logged landscape using different resolutions of friction map. Resolution is expressed as grid cell size.

Table 2. Correlation between genetic and geographic distances in the unlogged and the logged landscapes in two American marten populations.

Landscape	Distance	Grid cell size (m)	Size of the friction map[a]	p[b]	R^{2}[c]
Unlogged	Euclidean	–	–	0.0001	0.0032
	Effective	75	315×277	0.0001	0.0043
Logged	Euclidean	–	–	0.438	0.0002
	Effective	10	2273×3473	0.061	0.0013
		25	909×1389	0.088	0.0011
		50	455×695	0.068	0.0013
		75	303×463	0.026	0.0019
		100	227×347	0.050	0.0015
		500	45×69	0.071	0.0012

Pair-wise effective distances in the unlogged landscape were calculated using a resolution of 75 m (grid cell size), whereas six resolutions were used in the logged landscape.
[a]The size of friction maps is reported as number of rows×number of columns for each resolution.
[b]p-Values were calculated using 10,000 permutations in Mantel tests.
[c]R^2 expresses the proportion of variance in genetic distances explained by the variation in geographic distance.

relationship observed between pair-wise genetic and Euclidean distances. Such a correlation was also detected in the logged landscape, but only by replacing Euclidean distances by effective distances, which took the effect of landscape structures on marten movement into account. This result supported the hypotheses that gene flow in *Martes americana* is affected by landscape features and that this interaction may be detected through individual-based analyses of spatial genetic structure.

Whether the effect that we observed in the present study was caused by current or older landscape configuration remains an open question. In the logged landscape, the forest harvested during the last 40 years (∼20 generations of marten) represented 20% of the total area, whereas other perturbations were older. Depending on the rate of evolution of IBD, it is possible that the most recent alterations of the landscape did not yet affect marten spatial genetic structure. However, Leblois et al (2004) showed that strong temporal heterogeneity in dispersal had a limited influence on the estimation of current demographic parameters from IBD pattern. Modeling studies investigating the rate of evolution of IBD in response to modifications in dispersal would help identifying relevant landscape features in such landscape genetics approaches.

Similar results were recently obtained by Coulon et al. (2004) in a study of connectivity in roe deer (*Capreolus capreolus*). They computed least-cost distances using a slightly different modeling approach based on the distribution of
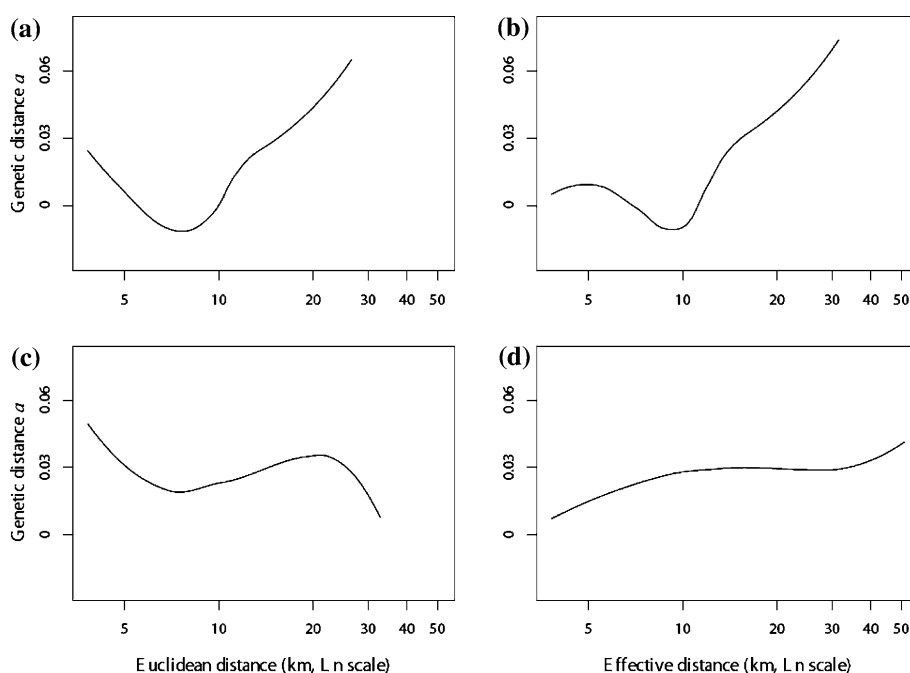
Figure 4. Smoothed curves of local polynomial regression of pair-wise genetic distances against geographic distances in the unlogged (a, b) and the logged landscape (c, d), respectively, using Euclidean (a, c) or effective (b, d) distances in American marten (for details of curve fitting see text).
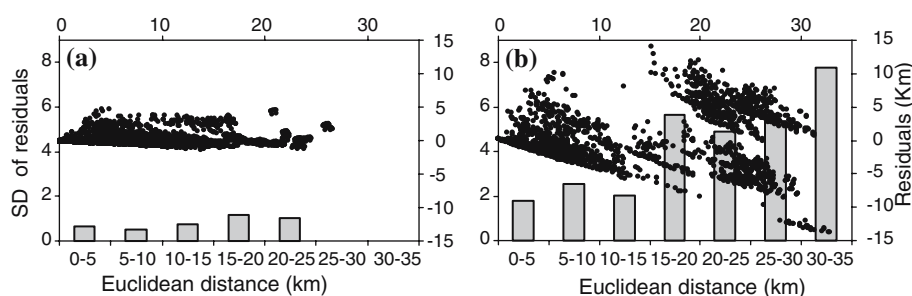

Figure 5. Standardized residuals of the regression of effective distances against Euclidean distances in the unlogged (a) and the logged landscape (b) in American marten. The residuals (black dots, right *y*-axis) and their standard deviation for seven classes (histogram, left *y*-axis) are plotted against Euclidean distances to visualize the difference of connectivity between the logged vs. unlogged landscape.

wooded habitat and obtained a better correlation of genetic distances with least-cost distances than with Euclidean distances. Implicitly setting isolation by distance as the null hypothesis, they concluded that the distribution of wooded habitat determines movement pathways during roe deer dispersal. Several other studies had previously demonstrated that the interaction of landscape structure on dispersal may be evidenced in a metapopulation framework by investigating the relationship between genetic differentiation among populations and a variety of indices of structural or functional connectivity among habitat patches (Castric et al. 2001; Hale et al. 2001; Michels et al. 2001; Vos et al. 2001; Arnaud 2003). The present paper confirms the previous results of Coulon et al. (2004) suggesting that the expected spatial genetic structure characterizing isolation by distance between individuals may also be used as a null model to detect the effect of habitat structure on dispersal within populations.

*Landscape connectivity and genetic
isolation by distance*

We described connectivity in *Martes americana* in
two different ways. First, least-cost modeling was
used to compute effective distances including
available knowledge of marten movement behav-
iour. The length of least-cost paths was then used
as a measure of the functional connectivity
between individuals within a population
(Adriaensen et al. 2003). This measure character-
izes pairs of individuals (or locations), therefore
differing from patch-based (Hanski 1999; D'Eon
et al. 2002) and landscape-based measures of
connectivity (Tischendorf and Fahrig 2000).

Second, a descriptive analysis of the residuals
of effective distances against Euclidean distances
was used to visualize differences in connectivity
between landscapes and their effect on genetic
isolation by distance. These residuals express the
net effect of landscape structure, independently of
the straight-line distance between data points
(Adriaensen et al. 2003; Verbeylen et al. 2003). A
visual inspection of the scatterplot of residuals vs.
Euclidean distances revealed the drastic difference
in overall connectivity in logged vs. unlogged
landscapes (Figure 5). In the logged landscape the
variance of the residuals (hence the variance of
the effect of landscape structure) was higher than
in the unlogged, and this variance increased much
more rapidly with increasing geographic dis-
tances. The variance of the residuals illustrates
the fact that pairs of individuals separated by
similar Euclidean distances may be differentially
affected by the structure of the landscape and,
therefore, that the effective distances between
pairs of points may be very different. The evo-
lution of the variance of the residuals in logged
vs. unlogged landscapes showed that this differ-
ential effect is much stronger in the logged land-
scape and supports the hypothesis that the
pattern of isolation by distance obtained using
effective distances in the logged landscape was
due to the differential reclassification of indi-
viduals originally separated by similar Euclidean
distances. Such differences in reclassification were
more limited in the unlogged landscape, which is
more homogeneous, but nonetheless contributed
to increase slightly the strength of the pattern of
isolation by distance.

*Effect of resistance values and resolution
of friction maps*

In this paper the functional connectivity between
pairs of individuals was treated as an independent
variable (Goodwin 2003) and examined by relying
on somewhat arbitrary choices of resistance values
and resolution of friction maps. These two
parameters were set in order to simulate marten
paths according to field observations, and were
both shown to have a great impact on the overall
correlation between genetic vs. effective distances.

Resistance coefficients set to 1 for forested areas
and 50 for other types of land cover and recently
cut forest stands were chosen such as to obtain the
presumptive, most likely pathways between pairs
of locations. A strong modification of these values
would have led to unrealistic least-cost paths. For
instance, two other scenarios tested in this study
(1/20 and 1/100), respectively, permitted pathways
to cross large areas of unforested areas or con-
strained pathways to follow large detours to avoid
narrow rivers or roads. Such paths are unrealistic
regarding available information on marten dis-
persal (see Material and methods). The first
scenario led to effective distances similar to
straight-line distances, whereas the second led to
extremely long and sinuous paths. As expected, the
effective distances obtained using these resistance
values were not significantly correlated with pair-
wise genetic distances (data not shown). Only by
using independent data on dispersal behaviour in
heterogeneous environments, we could determine
evidence-based rather than arbitrary friction val-
ues. However, such data are very difficult to obtain
in secretive species. Delineating friction values
based on an index of habitat quality as determined
by presence–absence or abundance data would be
a first step in this direction, provided landscape
permeability to dispersal can be approximated
from habitat quality.

At first sight the choice of resolution seems to be
less arbitrary. Adriaensen (2003, p. 242) pointed
out that one may fail to detect the effect of bio-
logically significant small elements in the land-
scape if the resolution is too coarse (large grid cell
size), suggesting that 'grid cell size must be clearly
smaller than the width of the narrowest element in
the landscape'. However in our study, the finest
resolutions appeared to reduce the correlation

between effective and genetic distances. The chosen resolution determined whether small elements were considered biologically significant or not (simply by representing them on the map or not). For example, in contrast to a large lake, a river is unlikely to constitute a barrier for a dispersing marten (considering that all water areas are frozen in winter in our study area). But if all cells representing water areas are given a particular resistance value, then the resolution may determine whether rivers are represented or not, and therefore whether rivers are considered biologically significant. A more precise distribution of resistance values would definitely constitute a better way to represent landscape elements (e.g. by defining the resistance value of landscape features not only according to land cover but also according to their width, shape and orientation relative to other elements). More information about individual marten behaviour in the wild (e.g. through fine-scale radio-tracking) would hence be required to improve the precision of landscape models.

Effective distances

The effect of the landscape on marten ability to move was represented using the length of least-cost paths as effective distances between locations. Although functional, this measure of connectivity is incomplete since it does not encapsulate other important parameters such as the species' habitat preferences (probability of settlement) and risk of mortality. Both of these factors are likely to have an impact on successful dispersal in *M. americana* and, thereby, on the resultant spatial genetic structure. In this species, the selection of resting sites is very important and may drive successful dispersal (Buskirk et al. 1989). Moreover, a modeling study of dispersal also demonstrated that the spatial arrangement of habitats strongly affected the fate of dispersing marten, and not only the way they move (Gardner and Gustafson 2004). Hence, it is likely that a functional measure of connectivity taking into account these parameters would be more informative than the length of least-cost paths. The total sum of costs along the least-cost path (generally referred to as 'least-cost distance') could potentially constitute such a measure (Chardon et al. 2003). For example,

Verbeylen et al. (2003) reported that the presence/absence of red squirrels was better explained by least-cost distances than by the length of least-cost paths. However, the biological meaning of least-cost distances remains largely unclear (it may integrate a number of factors such as energy expended, predation risks, intraspecific interactions).

Assessing landscape connectivity using genetic markers

In this study, we showed that the individual-based spatial genetic structure of *Martes americana* populations was affected by the connectivity of the landscape. May spatial patterns of genetic structure be used to detect and quantify the effect of landscape features on dispersal?

The use of analyses of genetic structure to quantify the effects of landscape structure may prove very useful, especially regarding species in which direct investigations of dispersal remains hardly realizable. In fact, empirical measures of functional connectivity at the landscape scale or in the context of meta-populations were generally realized using insects, amphibians or small mammals as model species, and modeling approaches remain preponderant in the literature (reviewed in Goodwin 2003). Genetic analyses provide a promising complementary approach to this problem. However, several points regarding this landscape genetic approach have to be considered.

First, the genetic models that may be used necessarily rely on simplifying demographic assumptions. In this paper for instance, setting isolation by distance as the null hypothesis implies that the focal population is at drift-dispersal-mutation equilibrium (but see Leblois et al. 2004). In a study of genetic diversity in the Brook charr (a salmonid fish species), Castric et al. (2001) showed that non-equilibrium conditions may hinder detecting the effects of landscape structures on genetic patterns. Assessing the effect of landscape structures on dispersal using a genetic model, therefore, implies that every other parameter of the model is controlled for, which may not be easily verified in any case.

Second, assessing the relative effects of a number of landscape features using genetic isolation by distance would require being able to test for the effect of various landscape models and evaluate

their relative relevance. In this study, the results of the Mantel test indicated that the logging history of the landscape played a preponderant role on marten gene flow. However, only the proportion of variance explained by the model could potentially help distinguishing between various landscape models. Under isolation by distance models, this proportion is expected to be very low (Rousset 2000; Sumner et al. 2001; Fenster et al. 2003; Coulon et al. 2004), and it is not obvious whether one could select the best model in a range of landscape models based on R^2.

Finally, dispersal polymorphism may induce an additional level of complexity. Dispersal dependent on age or social conditions as well as sex-biased dispersal are common features in many taxa, and there is growing evidence for other sources of behavioural polymorphism such as natal experience (Davis and Stamps 2004), public information (Danchin et al. 2001) or individual decision on short vs. long-distance dispersal (Selonen 2004). Landscape features may hence have different effects on different individuals within a species. Using genetic isolation by distance between individuals, Coulon et al. (2004) distinguished between the effects of landscape features on male and female roe deer. In *Martes americana*, Steventon and Major (1982) suggested that movement patterns in males and females is differentially affected by the presence of clear-cuts. Individual-based approaches could potentially allow testing for such effects. But how much of this complexity may be perceived using genetic models has yet to be explored.

Acknowledgements

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