





Final project report Reporting template

Annex B to reporting requirements and guidelines

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The value of ecological networks and different landscape management approach

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1. Short description for publicity

To counter the deleterious effect of local population isolation (extinction vortex) and hence to increase metapopulation viability, conservation strategies explicitly focus on the improvement of landscape connectivity and the establishment of ecological networks that should allow organisms to move among remnant habitats and local populations. However, network functionality has rarely been tested. The functionality of a network will largely be determined by the its' net effect on the mobility of the target organisms, which in turn depends on landscape features and on the target organism's ecological attributes, especially the rules according to which it takes its movement decisions. The TenLamas project aims at i) evaluating alternative models for assessing the value and functionality of particular ecological networks and ii) comparing different scenarios of landscape management. From simple to complex, assessed connectivity estimates are (1) synthetic parameters of structural connectivity that are function of the presence/distribution of habitat patches in the landscape, and either the area or the length of habitat corridors or stepping stones, (2) general pattern-based algorithms from least-cost paths and (3) the use of detailed simulation models of individual behaviour (generating most probable paths). In TenLamas we evaluated the relative accuracy of these concurrent connectivity estimates for selected model species (butterflies, lizards, toads and birds) in test landscapes with respect to the required level of precision in landscape and organism information.

2. Summary

One of the most significant outcomes of TenLamas has been the development of two modelling packages (SMS and RandomWalker) as well as fist steps towards more sophisticated modelling of cognitive decision processes in movement that take concepts that have been developed recently in the movement ecology literature and apply them to dispersal and connectivity. This fills a major knowledge gap and enables spatial conservation management to begin to benefit from our considerable ecological knowledge related to the movement behaviour of animals on complex landscapes. Our aim within the project has not been to demonstrate that conservation management should always utilise more complex movement models such as those we have developed. Indeed, it would be extremely pleasing if we were to have found that, for all species tested, a structural connectivity measure or a simple functional measure (i.e. least cost paths) performed as well as an individual-based model. Our message is currently a mixed one. For the butterflies, we find that a structural measure is as good as either the simple or complex functional measure. But for the natterjack toad and Cabanni's greenbill, an individual-based model (SMS) substantially outperforms the other metrics. So the question remains: how do we determine how much information is needed to specify connectivity robustly for a species. In order to provide a general answer to this question we need to test the methods on a substantially larger number of species and across a range of landscapes. Then, we may gain some rules of thumb, whereby for species with certain characteristics we can assert with some degree of confidence that a structural estimate suffices.

Another very important outcome of TenLamas has been the clear demonstration that spatial genetic data can be used to test and compare between different movement models. We have achieved this for five species now (more than we expected to be able to) and now that the method is established, it should be relatively straightforward and fast to do it for more species. A potentially very useful, if challenging, next step will be to utilise the genetic data, not as a test of the models, but as a source of data for fitting the model parameters. To the best of our knowledge this has not yet been carried out for an individual-based movement model. However, the tools that we have developed are ideal for this purpose. In subsequent work, we envisage collecting genetic data for a range of species on a given landscape to infer both the movement parameters as well as the cost values associated to the different elements composing heterogeneous landscapes. Then we can



utilise our individual-based model to test, *in silico*, the performance of alternative management strategies for multi-species and seek to optimise the design of a network across an assemblage. This is a major outstanding challenge, but is one that we are now in a much stronger position to address.

Another key issue that has emerged during the course of the contract is the insight that it should be possible to predict dispersal distances from life history traits. A first analysis on European butterflies indeed showed strong relationships between life history traits and different estimates of dispersal (emigration rates, gene flow, max dispersal distances) (Stevens et al. 2012). The next step was the demonstration of the robustness of the dispersal distance predictions based on suite of traits (Stevens et al. Evol. Appl. in press). A meta-analysis on a wide range of taxa using this procedure is ongoing. First results show that predictions of dispersal distance based on traits are always possible, but the traits involved are variable in different taxonomic groups. As dispersal distance is the missing parameter in most population viability analyses, this procedure has a strong applicability in conservation planning. Partners 1 and 3 are collaborating with Finnish colleagues in a project aiming at predicting the changes in butterfly distribution range, by incorporating such predictions of dispersal distances into the RangeShifter model.

A tempting conclusion of TenLamas may be to estimate connectivity using (increasingly cheap and sophisticated) genetic methods instead of carrying out very challenging and detailed movement/dispersal studies. A common drawback of the use of the genetic methods is that we cannot be sure whether these measures reflect actual connectivity, especially if landscapes change rapidly, just because genetic estimates of population structures reflect dispersal in the past. This is certainly true for measures based on FST that integrate dispersal over multiple generations. However, recent advances in analytical methods of allelic frequencies (re-sampling algorithms of multi-locus genotypes) give access to the number of individuals that disperse among populations over the last generation (see Baguette et al. 2013 for a review). However, without any mechanistic understanding of dispersal between habitat patches we cannot easily foresee how changes in landscape structure and configuration would modify connectivity in the future. So we firmly believe that the use of genetic methods should be complemented by mechanistic movement/dispersal models like those developed in the frame of TenLamas.

3. Objectives of the research

The main objective of TenLamas was the evaluation of alternative measures of landscape connectivity assessing the value of particular ecological networks and at comparing different scenarios of landscape management. To do this, we focussed on model species (butterflies and lizards) in test landscapes for which we had long-term data of metapopulation dynamics. We compared three different connectivity estimates based on (i) simple structural connectivity estimates, (ii) least-cost paths, and (iii) individual-based models of animal movements. The efficiency of each model was tested by comparing its predictions to measures of effective dispersal in the test landscapes assessed by the genetic structure of the metapopulations.

4. Project activities and achievements

General description of activities over the duration of the project

Partner 1

Partner 1 (Baguette) was responsible for the butterfly model species in WP 1 (Getting data),WP2 (Structural connectivity), WP3 (Least cost paths, LCP) and WP5 (Landscape genetics). In WP1 Baguette and postdocs gathered existing Capture-Mark-Recapture (CMR) data on two butterfly species (Boloria eunomia and B. aquilonaris) in different habitat networks in the Plateau des Tailles landscape in southern Belgium (see map below). It is worth mentioning here that the initial project



concerned B. eunomia only. These existing data sets were completed during the project (in 2009, 2010 and 2011) by new data collected in the same habitat networks, but also in other chosen to cover a wider habitat fragmentation gradient. Population sizes were estimated in each study population using Capture-Mark-Recapture (CMR) methods and Jolly Seber models implemented in Mark. Simultaneously, precise land cover maps were obtained from the regional agency. In WP2, Structural connectivity estimates (SCE) were extracted from these maps. Partner 1 computed two different SCE, the simplest one (the Euclidean distances between habitat patches) and the much more sophisticated Hanski connectivity index (Hanski 1994), which takes into account the distance between habitat patches but also the shape of the dispersal kernel of the species under investigation as well as the areas of the surrounding patches that is used as proxies of the densities of the surrounding populations To build LCP (WP3), the first step was to determine the grain and the resolution of the landscape to use for the model species. Therefore Partner 1 identified relevant landscape elements potentially influencing butterfly movements (by decreasing order of suitability: habitats, bogs/meadows, shrubs and forests). The next step was the experimental investigation of the resistance of each landscape elements, i.e. how the different landscape elements affect the movement of dispersing individuals. Different experiments were performed, including the collection of data on movement trajectories (step length and turning angles), and emigration rates from suitable habitat patches. Finally, three different estimates of LCP were computed: (1) the Euclidean distance weighted by the resistance of the landscape elements, (2) the length of the LCP and (3) the sum of the costs cumulated along the LCP. In WP5, partner 1 used 13 polymorphic microsatellite loci for B. eunomia and 16 for B. aquilonaris to assess the genetic structure of metapopulations and hence the effective dispersal between habitat patches, later used as a reference. Tissue samples were collected on each individual captured during the CMR experiments. Landscape genetic analyses were then conducted to measure the last generation dispersing individuals among and within the metapopulations in the landscape. Results demonstrate that even the most intensive CMR experiments drastically underestimate long distance dispersal movements. All the data (CMR, landscape structure, landscape element resistance, movement trajectory, emigration rate, genetic diversity) and analyses (population sizes, SCE, LCP, population genetic structure and matrices of movements) were transferred to partners 2 (Hovestadt) and 3 (Travis) for inputs in models.

Partner 2

Partner 2 (Hovestadt) was involved in development of individual movement models (WP 4) as well as the generation of metapopulation models capable of utilizing the different connectivity matrices provided by WPs 2, 3, and 4. Within WP 4 we followed two approaches, the first rooted in the more 'traditional' approach of modeling movement trajectories as (derivates) of correlated random-walk models. Here we extended and generalized previous approaches to model movement as 'area-concentrated search' (ACS) where the correlation of movement, e.g. of a butterfly searching for suitable egg plants, depends on past encounters with prey or other favored resources. This model provided us with important and general insights on how landscapes attributes, i.e. the spatial distribution of critical resources, affect optimal movement rules and how that in turn would affect the movement between resource aggregations (between patch dispersal) and large scale range expansion. Using this correlated-random walk framework we identified in cooperation with partner 1 the link between butterfly movement and habitat type, and determined existence of adaptive differences in movement behaviour among populations inhabiting landscapes of different structure (habitat fragmentation).

In a second approach we developed a (to our knowledge) completely new class of movement model where movement is completely controlled by the ability of the model organisms to perceive (resources), to memorize its past trajectories, to infer the location of resources based on general statistical landscape properties, and finally, to anticipate the consequences of actual movement decisions for the profitability of future movement options. Within WP 6 we completed development



of a program (METAPOP; publishes as open-source R-library under name 'ibmpm') necessary to run metapopulation simulations with different connectivity matrices generated by WP 1-4 and produce population genetic data as output (to contrast with empirical genetic information provided by WP 5). We further addressed several principle questions concerning the metapopulation framework and dispersal within spatially structured populations. We gained general insights how likely the emergence of a metapopulation dynamics in the strict sense – i.e. metapopulations showing frequent local extinction and re-colonization and certain genetic population structure – would in fact be depending on landscape conditions and how patch management might affect the dynamics of metapopulation. We further advanced our understanding of the role of 'informed' emigration in the metapopulation context, e.g. the effects of predator-induced dispersal and the effect of density-dependent emigration on dispersal distance in actively moving organisms.

Partner 3

(Travis): Our responsibility was for developing the individual-based models (WP4) and for providing alternative connectivity estimates using the models we developed parameterised with the data made available by WPs 1 & 5. In WP6 we had the responsibility for comparing these connectivity measures made by the individual-based model against those produced by structural connectivity (WP2) and least cost path estimates (WP3). At Aberdeen we developed the stochastic movement simulator, a model that relaxed some of the critical assumptions of least cost path (see details provided later in the document). This development of this model followed many discussions with the other partners, especially partners 1 and 4 who co-ordinated the case studies. It was decided that we needed a relatively simple model that would work in discrete space, such that it could utilize the same raster landscapes as LCP. Importantly, we did not want to introduce too many parameters as a key motivation in the project was to provide tools that could readily be applied to a large number of species, for which large datasets on dispersal will not often be available. The development of the algorithm took around 3 months and implementation of a working version for use by the project team a further 3 months. Subsequently, we have focused on two key activities. First, we fully tested and refined the model such that it could be published. We were delighted to be able to publish this in Methods in Ecology and Evolution in 2011. We have since added increased functionality to the model such that it can be used to simulate the dispersal behavior of a greater range of species and also such that it can be used to infer movement parameters from artificial release experiments. Following publication of the method, we have had numerous requests to use the model and have initiated several productive collaborations that are directly relevant to the goals of TenLamas. Supporting the model as it used by others has demanded some time. SMS version 2 is expected to be released in 2014 with all the additional functionality packaged within it together with an enhanced algorithm that significantly speeds the simulations up. The majority of our time in the project was spent, as expected, on producing the estimates for connectivity using the simulation and then in comparing these with those produced by other approaches. Key here was ensuring that compatible data layers were used by different partners and that we conducted fair tests. It is a non-trivial task linking the spatial genetic data to the outcome of the movement model. However, we successfully achieved this goal testing SMS against spatial genetic data for two species of butterfly as well as for natterjack toads and for an African bird species. One paper is submitted on this and another two are in preparation. Finally, we have spent time in developing proposals that ensure that the substantial progress we have made in TenLamas in developing and testing a new model for connectivity is further developed and used. This has yielded two new well-funded projects that SMS is an integral part that seek to develop robust habitat networks for forest and grassland species in the UK.

Partner 4

Partner 4 (Clobert) was responsible for the common lizard model species in WP 1 (Getting data), WP2 (Structural connectivity), WP3 (Least cost paths, LCP) and WP5 (Landscape genetics).



In WP1, we provided data on reproduction in different landscape on a temperature and human disturbance gradient at the level of all the massif central. In the same time, we collected genetic sample at three different scales: (1) the scales of a few hundred meters, (2) a few kilometers and (3) between plateau separated by deep valleys (supposed to function as barrier). For WP2 and WP3, we collected habitat data (from satellite images and IGN maps) together with fine scale data on temperature and humidity dynamics of different habitats elements. To understand the behavioral reactions of the common lizard to humidity, temperature and habitat coarseness (luminosity, granularity), we performed sets of experiments to both study avoidance of and attraction to these different elements in the habitats. From these results we then constructed least cost paths and compared to the genetic structuring of the population at the level of one massif (the Mont Lozere). First results showed that 1) least cots paths calculated on the combination of animal behavior and satellite images were closely matching the genetic data at the level of the Mont Lozere, 2) that it exist a fine genetic structuring at the level of less than 100 meters. Finally, partner 4 also contributed to the building of an individual based model mixing genetic, behavioral and demographic data.

Scientific outcomes

1. Scientific background (see review in Baguette et al. 2013)

Current massive species extinctions highlight how human activities negatively impact biodiversity worldwide. Among the manifold pressures inflicted by Homo sapiens on other living organisms, the destruction of natural ecosystems is undoubtedly one of the major causes of biodiversity loss due to immanent habitat loss and fragmentation. Theory predicts and empirical studies confirm that habitat loss and fragmentation both contribute to local population extinctions. The extinction of a species is indeed usually preceded by the fragmentation and shrinking of its distribution area, which reflects the progressive disappearance of local populations. By removing suitable resources, habitat loss directly affects the carrying capacity of a given area, and hence its ability to sustain large populations, while small populations are more vulnerable to genetic, demographic and environmental accidents. Further, low effective population sizes decrease the genetic variability in populations and hence their adaptability to environmental changes (the extinction vortex). Both empirical and experimental studies document the harmful interactions between genetic diversity and demographic stochasticity, dooming local populations to extinction. Besides such local processes, the loss of habitat associated with fragmentation also increases the distances among suitable habitat patches, which in turn decreases the settlement probability of immigrants. The resulting functional isolation of local populations reduces both the rescue of imperilled populations (the rescue effect) and the rate of (re)colonization of vacant habitats, which should ultimately result in wider-scale species extinctions. The best way to curb such extinctions would be to increase the carrying capacity of local populations, by increasing either habitat area or habitat quality. Implicit to the first possibility, the re-allocation of large areas to nature is rarely an option in heavily human-dominated landscapes. Improving habitat quality is feasible for those few species for which ecological requirements are sufficiently well known, but often demands extensive man-power and hence high financial support. In addition, as habitat quality is species-specific and even population-specific conservation efforts targeted for one species may prove to be detrimental to other species of the same community. An alternative (or complementary) strategy would be to increase the exchange of individuals among local populations, to reduce functional isolation. These exchanges would facilitate the maintenance of large metapopulations defined as groups of local populations where the movement of individuals among habitat patches is possible. In addition to their demographic effects [rescue and (re)colonization], movements of individuals among local populations may increase the genetic mixing among populations, hence reducing possible genetic variability erosion and thereby genetic diversity within populations, in turn sheltering these populations from extinction. The metapopulation concept thus provides a solid framework for the conservation of species in heavily fragmented landscapes. In our vision of such spatially structured populations, local populations (demes) occupy habitat patches Final report template for BiodivERsA funded projects Annex B to reporting requirements and guidelines



more or less isolated from each other in a matrix of more or less sub-optimal habitats. By explicitly considering that the matrix is composed of different landscape elements with different quality, such structures do not correspond to the binary representation of landscape composed of suitable habitats embedded in an uniformly unsuitable matrix typical of the classical metapopulation theory. Our vision of metapopulations rather integrates insights from landscape ecology into metapopulation theory. The linkage strategy, corollary of the metapopulation theory, is an appealing methodology in conservation planning that aims to facilitate the displacements of individuals among local populations, for example by the creation of corridors or stepping stones that bind local habitat patches into functional ecological networks.

However, network functionality has rarely been tested. It will largely be determined by the network's net effect on the mobility of the target organisms, which in turn depends on landscape features and on the target organism's ecological attributes, especially the rules according to which it takes its movement decisions. TenLamas evaluated alternative models for assessing the value of particular ecological networks and for comparing different scenarios of landscape management. From simple to complex, current connectivity estimates are (1) synthetic parameter of structural connectivity that is a function of the presence/distribution, and either the area or the length of, habitat corridors or stepping stones, (2) general pattern-based algorithms based on least-cost paths and (3) the use of detailed simulation models of individual movement behaviour (generating most probable paths). In TenLamas we evaluated the relative accuracy of these concurrent connectivity estimates for selected model species in test landscapes with respect to the required level of precision in landscape and organism information. Gene flow among populations (computed on first-generation migrants) was used as the ultimate empirical measurement of functional connectivity.

2. Connectivity for butterflies

We focussed on two butterfly species (*Boloria aquilonaris*, Ba and *B. eunomia*, Be) whose metapopulation biology was investigated since 1992 in the 'Plateau des Tailles' landscape (PT) (southern Belgium, see below). This work was realized in close connection with the Quantitative Conservation Biology team from the Univ. Louvain (N. Schtickzelle, C. Turlure, S. Vandewoestijne).

2.1 Species natural history

Both species have a boreo-mountane relict distribution, in the Palearctic and the Nearctic for Ba and Be, respectively. Both species are specialists: larvae feed on only one host plant (the cranberry *Vaccinium oxycoccos* for Ba and the bistort *Persicaria bistorta* for Be) in the study area. Moreover, Be adults feed exclusively on bistort flowers. Adults are on the wing 3-4 weeks a year, in May-June for Be and in June July for Ba. Networks of habitat patches of both species are well delineated in PT and are interspersed among forests, pastures and shrubs. Human infrastructures are poorly developed at PT and are expected of not significantly affecting habitat connectivity and were therefore grouped with shrubs.

2.2 Study systems

PT area is 15 X 17 km. For Ba we investigated the 14 populations existing in the PT area. For Be, we selected 3 different habitat networks with contrasted fragmentation level (Figure 1).





Figure 1. Map of the study locations in the Plateau des Tailles in Belgian Ardenne (circles; one circle may cover several patches) for Ba (left panel) and Be (right panel).

Prés de la Lienne (PL) is a compacted network of 7 patches along 1km. Vallée de Bihain (VB) is an aggregated network of 7 populations. Vallée de Wibrin (VW) is a fragmented network of 5 populations. Previous intensive CMR experiments in PT showed that (1) for Ba, long distance interpopulation movements [up to 13 km] were observed (Baguette 2003), whereas (2) for Be the PL network was isolated from other metapopulations (no dispersing individuals detected in 18 yr, e.g. Baguette et al. 2011).

2.3 Study methods

During the project (2009-2011), we sampled all the patches within the study area using standard CMR protocols. Butterflies were individually marked using an alphanumeric code (a letter for the population and a unique number for each individual) at capture and recaptured along standardized transects in each patch. CMR data were used both to compute the size of the populations in each population with relevant methods (either Jolly Seber models implemented in Mark or, when the low number of recapture prevented the use of such models, a new methods we developed in the context of TenLamas) and to monitor the movements of individuals across the landscape. Besides, experimental work was conducted to infer the resistance of the 4 landscape elements listed previously to displacements (Turlure et al. 2011). In the cage experiment, an enclosure (10m X 5m X 1.5m) was built in a habitat patch. The vegetation was kept unchanged on one half of the cage, whereas it was modified on the other half, to mimic meadows or shrubs vegetation. The behaviour of flying individuals released in the cage was mapped on a grid of 32 1.25m² cells. Besides, the trajectory of naturally flying individuals was monitored with a standardized protocol in meadows, shrubs and forests. Emigration rate was computed by monitoring the behaviour of naturally flying at the border of habitat patches and meadows or shrubs. Finally, we investigated the density of naturally flying individuals in habitats, meadows, shrubs and forests along a large number of standardized transects. With these 4 experiments we built a scale of the resistances of the 4 landscape elements that was used in a next step to build the maps of the costs of the movements of dispersing individuals for both species. During CMR experiments, tissues were also collected for genetic analyses. We used 16 and 12 polymorphic microsatellite loci to genotype 1530 individuals of Ba and 1482 individuals of Be over the 3 years, respectively.

2.4 Results

In this section we focus mainly on results related to connectivity. Many other results on individual variability in behaviour, population sizes, metapopulation dynamics and the role of inbreeding were also collected and will be addressed/released in publications.



2.4.1 Structural connectivity estimates

Euclidean distances and the Hanski connectivity index provided perfectly correlated estimates of structural connectivity of the habitats in the PT landscape for the two species. We used then the more intuitive and simplest one: the Euclidean distance.

2.4.2 Movement-based connectivity

Figure 2 shows the frequency of within- and between- habitat network movements as assessed with CMR data for Ba and Be. The frequent movements between habitat patches in the PL network are not figured at this scale, as well as the . In the two other networks, movements are (1) frequent in the aggregated network (VB; one arrow may actually represent movement of several individuals), (2) not that frequent in the fragmented network (VW), even at such a small spatial scale, and (3) variable from one year to the other. Only one inter-network movement was observed over 3 yr of intensive CMR experiments. Similarly, movements are relatively rare or undetected between Ba habitats and greatly differed between sampled years.



Figure 2. Movement-based connectivity inferred from CMR data for Ba (left panel) and Be (right panel) over 3 yr (2009: red arrows, 2010: orange arrows, 2011: yellow arrows)

2.4.3 Landscape resistance estimates

The four experiments described in section 2.3 provided resistance values for different combination of landscape elements: habitat, meadow and shrub for the cage experiment, habitat, meadow, shrub and to a lesser extent forest for both the trajectory monitoring and the emigration rate, and all the four landscape elements for the transects. The absolute values of resistance were different among the four elements. But in both species, the relative ranking provided by the experiments was similar, and provided the scale that was subsequently used to build the resistance map of the landscape (Table 1).

Table 1. Relative scale of the resistance of four landscape elements to individual movements					
Resistance Ba	Landscape element	Resistance Be			
1	Habitat	1			
1.5	Meadow	1.1			
3.9	Shrub	1.1			
12	Forest	2.2			

Table 1. Relative scale of the resistance of four landscape elements to individual movements

With regards to landscape grain, we tested the changes in the connectivity estimates using 7 resolutions in a subsample of habitat patches. Grid cells of the landscape maps tested were then 1m



x 1m (the most precise resolution we could use given the precision of the vectorial maps), 5m x 5m, 10m x 10m, 25m x 25m, 50m x 50m, 100m x 100m (the resolution corresponding to the EUNIS maps) and 250m x 250m. This exercise shows that choosing the right resolution is challenging as the changes in connectivity estimates with increasing resolution is highly non linear for Be (Figure 3). Further investigations revealed that resolution lower than 25 m allowed considering narrow forest paths in the landscape, while resolution higher than 25 m did not. To take this non-linear response into account, we kept resistance maps with two grid sizes for the next steps of the project, namely the 10m X 10m and 50m X 50m resolutions. For Ba the increase in dispersal costs associated with an increase in resolution showed a monotonic increase. We kept thus a single resistance maps with a 10m X 10m resolution, for the sake of comparison with Be.



Figure 3. The graph on the left panel shows the change in the connectivity estimates (here LCP length) for 6 pairs of Be habitat (from A to F) according to the resolution of the resistance maps. The central figure represents the path (black line) linking patch 16 to patch 27 (pair E) for a 1m x 1m resolution map. The right figure represents the path linking patch 16 to patch 27 (pair E) for a 50m x 50m resolution map.

2.4.4 Genetic-based landscape connectivity

Ba populations were organized in two clusters (Figure 4, clusters represented in orange and blue) grouping respectively the west and the east populations of PT, with a stepping stone in the middle.



Figure 4. Upper panel: probability of each individual in the 14 populations to belong to one of the two clusters. Lower panel: spatial repartition of the two clusters.



The populations of Be had a more complex structure: genetic differentiation was detected both among networks and within network (except for PL). But both the gene flow among populations and the effective population sizes were stable in space and time. Matrices of first generation migrants showed the existence of long-distance movements between networks (Table 2).

Table 2. Matrix of first generation migrants in Be for 2010. White, grey and black populations pertain to VW, VB and PL networks respectively

To From	Bérismenil	Chapons	Mormont	Pisserotte	Bihain	Grande Fange	Bievres	Langlire	Prés de la Lienne
Berismenil	-		1						
Chapons	1	-						1	
Mormont			-	1					
Pisserotte				-		1	2		2
Bihain		1	1		-		2	1	
Grande Fange	1				2	-		1	1
Bievres				1	1		-	1	
Langlire								-	
Prés de la Lienne		1							-

2.4.5 Correlation among structural connectivity, least cost paths, movements and gene flow In Ba, movements had a similar correlation with Euclidean distances and least cost paths (r=0.32 and 0.33, respectively). Gene flow had similar, and higher correlation, with Euclidean distances and least cost paths (r=0.51 and 0.53, respectively). In Be, movements had a high correlation with Euclidean distances and least cost paths (r=0.62 and 0.59, respectively).

2.4.6 Application of SMS to butterfly populations

Functional connectivity estimates using SMS were made for various combinations of the two key parameters (perceptual range, PR, and directional persistence, DP) at each of the cell sizes. PR for these species is estimated to be only a few tens of metres, but a constraint of the model is that PR must be set to an integer multiple of the cell size. Moreover, as cell size increases, DP must be reduced to achieve the same degree of auto-correlation in realised paths.

A fixed number of 10,000 virtual butterflies were released individually from each breeding site, and allowed to move freely through the landscape until they reached any one of the other sites in the network or exceeded 5000 steps (10,000 at 5 m grain size). The numbers of successful movements between each pair of sites in each direction were used to derive connectivity estimates for the particular combination of cell size, PR and DP.

Two estimates of connectivity were derived from genetic samples collected from the populations of the two species: F_{ST} (symmetrical between sites) and the estimated numbers of migrants per generation N_M between sites as predicted by the MIGRATE model (asymmetrical between sites). Separate estimates were derived from the three years 2009-2011. The relationships between connectivity matrices were examined using Mantel tests, and, where appropriate, partial Mantel tests controlling for Euclidean distance.

2.4.7 Comparing SMS performance against LCP and Euclidean performance For both species, connectivity matrices estimated by SMS were either less well correlated than were structural (Euclidean) estimates with genetic estimates, or only slightly more strongly correlated. The same pattern held true with the estimates of connectivity based on the LCP approach (i.e. no improvement of correlation when using LCP cost or distance compared to Euclidean distance). There was therefore no clear evidence that, in the case of these two butterfly species in the landscape studied, the additional complexity present in the individual-based modelling approach afforded any substantial advantage, nor that connectivity affected gene flow. However, it must be noted that the relatively poor performance of SMS could be due either to the fact that individual movements cannot be approximated by correlated random walk (CRW), or to the limited range of cost values determined for the study landscape; an alternative approach would be to attempt to use an optimization procedure to estimate the cost values of the habitats present within the landscape.

2.4.8 Small scale movement analysis



In a further approach and a cooperative initiative of partner 1 and 2 we analysed small scale movement characteristics (see 2.3) of the two butterfly species described above, Be and Ba, from individual movement tracks recorded with high precision GPS. We examined differences between movement manners inside and outside of habitat patches. We looked at: (1) differences between populations (single patch and isolated population vs. multiple connected patch population), in terms of emigration and frequency of looping flights; (2) differences between species subjected to different habitat fragmentation regime (Ba in naturally and long term fragmented ecosystems vs. Be in recently and increasingly fragmented ecosystems); (3) differences between sexes; and (4) difference in morphological traits related to flight capabilities.

Examination of the butterfly trajectories within CRW framework (differences of net squared displacement) revealed that the observed flight paths are generally straighter than expected with a CRW (Figure 5). Moreover, the trajectories cover more habitat patches than those expected with theoretical CRW paths (Figure 5). The results suggest that movement cannot be well approximated by (simple) CRW. The proportion of steps spent in- and outside the habitat was similar in both species. It was not linked to population, sex or the population x sex interaction for both species. Flight manner differed between sexes, populations and habitats, and in some cases, the distance from habitat. Males generally moved in a fairly straight manner, with little differences between movement inside and outside habitat. Females exhibited a wider range of movements. Flight manner changed with distance to habitat - most prominently in Be females from Berismenil population, which flew in a straighter manner as distance from habitat increased. Flights generally were recorded within small distances from habitat. Emigration probability did not differ between species and sex. Mean loop size was larger for Ba than for Be. The loop size differed between populations and sexes for both species. The decay in distance was affected by the population and sex in Be and by sex only in Ba.

Forewing length, thorax volume and wing loading differed between sexes and populations for Be and only between sexes for Ba. In Be, females have longer forewing, bigger thoraxes and hence higher wing loading than males and individuals from the isolated population have higher wing loading than individuals from the connected population suggesting higher mobility of individuals from connected populations. In Ba, females have higher wing loading than males.



Figure 5. Relationship between distance to habitat and path straightness (directional persistency of flight trajectory). Points depict values of p for path segments of length 30 steps, and lines prediction of linear models



with 95% confidence intervals (dashed lines). Vertical dashed line marks habitat border. Density of location occurrences is shown at the bottom of each plot.

2.5 Conclusions from the butterfly case study

The most striking results is the lack of power of (detailed) movement-based connectivity estimators (either LCP, SMS or CRW) to predict effectively the (net) dispersal events assessed by genetic methods. This suggests that intensive CMR experiments are unable to provide reliable, respectively improved dispersal and connectivity estimates in butterflies. Divergence in dispersal estimates between demographic and genetic methods were already shown in butterflies (Stevens et al. 2010). Several factors were invoked as causes of these divergences, like differences in time scales or the lack of reproduction of dispersing immigrants in the population of arrival. Here we show that the underestimation of dispersal events by CMR method could be the principal factor explaining this discrepancy. Besides, we show that in the PT landscape, structural connectivity estimates perform as well as LCP and SMS to predict effective dispersal events assessed by genetic methods. This unexpected result comes from the strong, unexpected correlation between structural connectivity estimates and both LCP and SMS. Accordingly, in this particular situation, neither LCP nor SMS thus provide extra-information compared to the use of simple Euclidean distances.

3. Connectivity for lizards

3.1 Species natural history

Lacerta vivipara is a small lacertid species (50-70 mm adult snout-vent length) inhabiting peat bog and heathland. This species is widely distributed across Europe and Asia (from Spain to the Pacific coast of Russia and from Scandinavia to southern Romania). It is a live-bearing species, except in the extreme south of Europe where oviparous populations occur (37). It reproduces once a year. In the populations we studied, mating takes place in May. After 2 months of gestation, parturition usually starts mid-July and last for 3 weeks, when young are fully developed. Five eggs, with a thin and transparent shell, are laid on average (range 1-13). Hatchlings are independent of their mother from birth. The common lizard displays dorsal patterns which are generally grey brown to dark brown with black lines (linear individual: L) running from head to the base of the tail and/or spots (reticulated individual: R) scattered throughout the back.

3.2 Study systems

We selected many populations in Southern France (scattered through the Massif Central), which were contrasted by their altitude (all the sites were at an average of 1055 m to 1440 m), man use and temperature levels of their habitat. They were selected at three levels: regional (22 populations), at the level of one plateau (the Mont Lozere) and at the local level (one population on a 100x70 meter square). This last local population was followed for more than 24 years.

3.3 Study methods

We captured pregnant females from 20 sites situated throughout the Massif Central between mid – late June 2007 and 2008. The sites varied in elevation (~1000 - ~1500 m) and habitat quality (moisture, vegetation coverage and perturbation). We kept females in captivity under standard conditions until parturition. Each lizard was individually housed in a plastic terrarium with damp soil and a shelter. Individuals were exposed to natural daylight and exposed to a heat source for 6 hours per day (25W lamp; temperature gradient from 25 to 30°C). Water was provided by daily spray. Lizards were fed once a week with one small larva of *Pyralis farinalis* (average live weight \pm SD =0.189 \pm 0.051 g, n = 30), according to standardized rearing conditions (Massot & Clobert, 2000). After giving birth, females and their hatchlings were weighed and released in their population. We recorded snout-vent length (SVL, mm), mass (mg), and condition (mass corrected by snout-vent length).



We used the protocol described in Lepetz et al. (2009) to categorize individual female dorsal patterns. Briefly, the dorsal patterns were evaluated by dividing the dorsum of each individual into four areas: anterior median, anterior lateral, posterior median, and posterior lateral. Individuals that had melanin arranged linearly were designated as the L-morphotype, whereas individuals that had melanin in unaligned dots were classified as reticulate, R-morphotype. A low frequency of females displayed dots in a regular arrangement, which we designated as RL. However, for the purpose of this study we collapsed RL and R females into the R-morphotype.

We determined habitat quality using three categories, moisture, perturbation, and openness. All categories were given a score of 1 - 4. The moisture category describes a gradient going from dry habitats without water (1) to wet habitats having standing water (4). Perturbation describes the degree of habitat degradation due to livestock grazing. Heavily degraded sites were scored (1) whereas minimally impacted sites were scored as (4). Collecting localities varied in openness, with sites being open and little canopy structure (1) to those occurring in closed forest (4). We then derived a single index of habitat quality by applying a principal coordinate analysis using Gower's distance metric as input. The first axis explained 61% of the total variation among the sites and described a contrast between perturbation (loading = -0.88) and openness (0.49). Moisture was weakly associated with the first axis (-0.29). Highly perturbed sites, open sites had negative scores, whereas sites with more vegetation structure and low grazing disturbance had positive scores. Genetic samples and location of each capture have also been recorded in 20 points all over the Mont Lozere to estimate genetic structure at the level of one plateau.

We then turn to the attraction to and avoidance of different habitat elements method. We employed a cross-over design in which each animal was tested in 12 trials (corresponding to 12 treatments) in a randomly assigned order. For this, we built experimental units consisting of two terraria (18 x 12 x 11 cm) that were connected with a channel (80 x 5 cm, with 10 cm high sidewalls) made out of clear plastic sheet that was open at the top. The opening through which a lizard was able to enter and exit each terrarium, and move into and out of the channel, was 2 x 2 cm large and at a same level position as the surface of the terrarium and the channel. This allowed for a seamless movement between terraria and channel, unimpeded by any height inequalities of the surface. We manipulated light/heat, substrate, cover and humidity conditions as follows. For light/heat conditions, there either was a lamp ('with light'; 25 W Osram Concentra lamp, 20 cm above the surface) or no lamp ('no light') provided in the starting terrarium. In the other three treatments we manipulated conditions in the dispersing channel only. Channels either contained substrate ('with substrate') or no substrate ('no substrate'), the substrate was either wetted before the trial ('humid') or left dry ('dry'), and channels were either covered ('with cover') or left open ('no cover'). For the cover treatment, we put a grey opaque plastic pipe (r = 5 cm), cut in half lengthwise, in the channel so that the whole channel length was covered and completely shaded. We crossed treatments factorially, except substrate and humidity: when there was no substrate in the channel, we always left the channel dry. This resulted in 12 treatment groups in total (instead of 16 for the full factorial crossing). Before the beginning of each trial, we slightly wetted the substrate in the starting terrarium by spraying a specific amount of water on it. At the start of each trial, an individual lizard was put in the starting terrarium that always contained 1 cm of earth as substrate, without any other structures. We measured the time it took the lizard to find the opening to the channel and move at least his head completely into the channel (starting time, ts). The time it took the lizard to finish the trial (t) was defined as the time it took the lizard to pass the channel all the way through to the receiving terrarium. Hence time to finish included cases where a lizard would move right through the channel, and cases in which it did not move all the way through but went back to the starting terrarium or stayed somewhere in the channel, until it arrived at the receiving terrarium. All experimental animals crossed the channels in all trials, with maximum values of 129 mins for t and a maximum of 84 mins for ts.



3.4. Results

3.4.1. Large geographical variation of dispersal related physiological performance The goal of this analysis was to investigate factors that could explain geographic variation in three measures of locomotor performance among populations of *Lacerta vivipara* using a macrophysiological approach. Our study decomposed observed variation in performance using three prominent ecological categories. We initially considered two aspects of the morphotypes. We first evaluated whether there was an overall difference in performance between linear and reticulate morphs. Second, we evaluated whether the habitat quality used by morphs covaried with elevation. Our analyses revealed significant differentiation in body size and physiological performance among populations inhabiting bog habitats in the Massif Central.

3.4.2 Behaviour

We found that propensity to disperse is fine-tuned to the starting conditions of individuals, and depends on the physical properties of the dispersal pathway and on the individuals' phenotype. Specifically, the presence of cover and substrate providing suitable traction had positive effects on the individual movement decisions. Additionally, we find high phenotypic variation in propensity to move dependent on the presence of cover, as well as a strong correlation of back pattern with movement tendencies.

3.4.3 Genetics

We found high level of genetic structuring even at the smallest scale (the level of one population). The resistance map calculated on habitat repartition and resistance measure to the different habitat elements was predicting quite closely the genetic structuring at the landscape level.

4. Connectivity for additional species.

In our initial proposal we had emphasised two case-studies upon which we would both test the new models we developed and compare the results they provided against established connectivity indices. During the project data on additional species became available which provided an ideal opportunity to test the efficacy of the range of methods for a greater number of species. This is a key step in developing a general understanding of when greater detail in movement modelling (and thus greater requirement for data) is required. Below we briefly detail results from two of these species, for which exciting results are already available and being written up for what we believe will be an important publication. They are for the natterjack toad in a Belgian landscape using data gathered within the TenLamas group by Baguette and colleagues and for Cabani's greenbull, an African bird species living in fragmented Kenyan forests (data gathered by Erik Matthysen's group at Antwerp). Significantly, for both these species we found that SMS performs substantially better in terms of predicting spatial genetic structure than either LCP or Euclidean distances. This contrasts with the findings for the butterflies presented above and thus the results are important to emphasise here and especially in current recommendations to stakeholders.

SMS was applied to estimate connectivity between four breeding sites of the natterjack toad *Bufo calamita* in a valley landscape in southern Belgium, for which estimates of dispersal from genetic data were published and shown to be better correlated with LCP estimates than with structural estimates of distance (Stevens *et al.* 2006). The original two experimentally-determined cost landscapes (one based on preference and the other on resistance of habitat types, and both gridded at 3m cell size) were used, it was assumed that dispersing juvenile toads have a perceptual range (PR) of 30m, and SMS was run for a range of directional persistence (DP) values. Initial estimates of connectivity predicted by SMS were no better than structural estimates, but, following a simple enhancement to the model, which assumed that young toads would be attracted to breeding sites by vocalisations of mature male toads during the breeding season over a distance of 1000m (in effect, a secondary, temporary, auditory PR), correlations of genetic estimates. For example, at the optimum DP value for the preference landscape, not only did the SMS correlation (r = 0.82) exceed



that of LCP (r = 0.64) and Euclidean distance (r = 0.61), but the margin of improvement over LCP was much greater than that of LCP over Euclidean distance. Moreover, additional simulations showed that this result was robust to the choice of landscape spatial grain (6m, 10m 15m and 30m) and to the assumed PR of the toads (varied between 9m and 42m).

In collaboration with researchers at the University of Antwerp, Belgium, SMS was used to estimate connectivity between four populations of Cabani's greenbul *Phyllastrephus cabanisi*, a threatened passerine species of remnant indigenous forest in the Taita Hills, Kenya. Habitat cost values and the SMS parameters PR and DP were first estimated from a radio-tracking study of the species (Aben *et al.* submitted), and then they were applied to the estimation of connectivity for comparison with genetic estimates. Again, it was necessary to make a single enhancement to the SMS model to improve its predictions, but, in this case, it was the addition of a dispersal bias parameter which acted to add a component to the trajectory taken by each simulated individual in the direction away from its natal site. The resulting improved performance of SMS with the optimum parameters (r = 0.86) was substantially greater than that of both LCP (r = 0.44) and Euclidean distance (r = 0.56).

5. Models

A central aim of the TenLamas project was to develop novel, mechanistically based modelling approaches that might better model animal movement and thus connectivity between habitat patches by accounting for the interaction between movement behaviours and landscape structure (both habitat and matrix). Within the project two complementary modelling approaches were developed for this objective.

At Aberdeen, Travis and his group focused on raster-based movement model that sought to minimise the number of parameters required. This model, the Stochastic Movement Simulator (SMS) was published during the project (Palmer, Coulon & Travis 2011) and has subsequently been applied to several case study species. Subsequently, there has been a substantial time investment in embedding this movement model in a spatially-realistic, individual-based population model that can simulate population dynamics in fragmented landscapes at regional spatial scales. This model, titled RangeShifter, results both from the TenLamas funding, from SCALES funding and from University of Aberdeen funding. A first release-version of this model will be submitted for publication by April 2013 and we are already finding there to be substantial demand for it within academic and stakeholder communities.

At Würzburg, Hovestadt and his team focused on developing higher spatial and temporal resolution, continuous time and space models. A family of models incorporating a broad range of functionality were packaged together in an R library named RandomWalker (currently under revision before finale release as R package). Where sufficient data are available for a species to parameterise a more complex model, there can be substantial benefit in utilising this modelling approach and additionally it facilitates the development of behavioural eco-evolutionary theory related to dispersal. The team in Würzburg further drafted a first version of a completely new class of movement models that is much more 'mechanistic' in nature accounting for the (potential) abilities of species to perceive their environment, memorize past experience, infer likely targets based on known statistical properties of landscapes and to anticipate the consequences of movement decisions for future options. The development of this model (Fronhofer et al.2012) class is still in an early stage but appears to be a very promising route to generate insights on the rules underlying movement.

Finally, partner 2 also developed a general metapopulation model to utilize connectivity matrices provided and generate predictions about metapopulation dynamics and population genetic attributes. In this context we also advanced general metapopulation theory and insights on the evolution of dispersal in spatially structured populations.



Below, we provide some further details on the models constructed during TenLamas. Above, we provide information on the use of the models within this project as well as highlighting how they are already being used for an increasing range of species and on a variety of landscapes in a growing number of other projects.

5.1 Movement model: Stochastic Movement Simulator (SMS)

The Stochastic Movement Simulator (SMS) is a simple individual-based model for predicting the movements of dispersing animals between breeding habitat patches through a heterogeneous landscape (Palmer, Coulon & Travis 2011). The landscape is represented as a gridded cost surface, i.e. the same raster format as is used for the least cost path (LCP) approach. Estimates of functional connectivity made by SMS and LCP are therefore directly comparable. However, the assumption of omniscience implicit in the LCP approach is relaxed in SMS, and it is assumed that dispersers can assess landscape permeability only within a limited perceptual range. In SMS, an individual animal's path through the landscape is modelled in a step-wise manner from its current grid cell to one of the eight neighbouring cells. It selects one of the neighbouring cells at random, but on the basis of probabilities based on the costs involved and its directional persistence. Other than the LCP approach the SMS thus generates most-probable paths that may – depending on landscape attributes - greatly deviate from LC paths.

The effective cost of the neighbouring cell in a given direction is calculated as an average of the costs of all cells in that direction within the perceptual range (PR). The probability of movement in a given direction is inversely related to the effective cost, i.e. directions with relatively low effective cost are more likely to be chosen than those with high cost. The PR parameter would normally take values in the range 1-10, depending on the cell size at which the landscape is represented and the presumed PR of the species being modelled. Directional persistence (DP) weights the probability of cell selection towards cells in the current direction of movement (calculated over the previous 1-14 steps), and therefore against those which have just been traversed. The higher the DP, the more a path will tend to follow a straight line and become more strongly auto-correlated.

5.2 Movement model: RandomWalker

This model is an attempt to generalize a number of Correlated Random Walk variants in an unified framework and may be especially useful for modelling small-scalemovements. These variants range from basic Brownian motion, through Lévy flights (a form of scale-free movement), to more complex biased CRW, where the moving individual responds to the surrounding landscape and its internal state. This has been included in a R package 'randomwalker', being a collection of useful tools for simulation and analysis of movement trajectories (both simulated and real data). The statistical tools include methods to identify classical CRW and Lévy patterns via fitting alternative step-length distributions with Maximum Likelihood and visual examination of survival function. In addition, various trajectory manipulation algorithms, useful in these types of analyses are included, such as splitting into equal-length step and detecting straight-line segments for path simplification. The toolbox is implemented as a library for the R environment.

Utilizing this generalized CRW modelling approach we investigated how resource distribution (patterns) would affect optimal movement decision rules. Searching individuals need to take decisions on where and how long to search. When food is spatially aggregated, detection of a food item signals an probability for the presence of further prey items in its surrounding. Organisms can thus intensify search effort upon detecting a prey item, but after unsuccessfully searching for a while, return to the previous, extensive search, this strategy is known as 'area-concentrated-search' (ACS). Switching between intensive and extensive search (with respectively low and high directional persistence) is a function of searcher's internal state depending on preceding consumption of prey items ((Barton & Hovestadt, 2013; Figure 6).



We explored the effect of this function's control parameters on searching efficiency in dependence of (i) prey items' spatial distribution ranging from randomly uniform to highly contagious, (ii) overall prey density, and (iii) prey 'caloric' value. Our main conclusions are: (1) The form of the adopted switchover exerts an effect on searching efficiency, and this effect is most pronounced in landscapes with highly aggregated resources typically with a clear optimum in movement parameter space, yielding highest efficiency. (2) The optimal switching level is larger in heterogeneous landscapes, but optimum switchover shape is little affected by any of the landscape attributes. In most landscapes, it is most profitable to switch gradually rather than abruptly. (3) The success and optimal switching level depend not only on the prey's spatial distribution but also on average prey density while the value of prey items has little effect on the optimal movement parameters.



Figure 6 (from Barton & Hovestadt, 2013). **Upper plot**: Example trajectory of individual following ACS in a clumped landscape. The line shows the movement path, dark dots represent food items, white bullets encounters, and the starting point is marked by a cross. **Middle plot**: The satiety (E_t) of individual at each step of the trajectory shown above. Satiety increases after prey consumption and decreases gradually. **Lower plot**: Changes in the directional persistence of the moving individual (thick line). White bullets mark prey encounters. Gray bars show local food availability (i.e. actual prey density within radius of 25 units around individual position, multiplied by prey item's caloric value, Q). Generally, directional consistency is lower in areas with larger resource density.

We have utilized this ACS approach to investigate the emergence of the widely discussed phenomenon of so called 'Levy flights' (LF) consist of straight-line 'flights' of lengths that follow a power-law scaling; therefore being scale-invariant. LF may be more 'efficient' in bridging large distances but long-distance moves may be rare enough to typically remain unnoticed in empirical studies. The ACS described usually produces paths with periods of tortuous movement interspersed by long straight-line moves but despite apparent similarity, limited previous studies have failed to show ACS trajectories' conformity with LF patterns.

We found that LF patterns indeed emerge over a wide spectrum of ACS model parameters, especially when the transition from intensive (tortuous) to extensive (straight) movement was gradual: the distribution of flight lengths emerging under ACS closely matches the power-law distribution with Levy exponent between 1.2 and 2.5. The phenomenon was robust to modifications in the spatial distribution of resources, and arises with destructive and non-destructive searching. We even find that the most efficient ACS leads to LF with exponents of c. 2.0 – the value claimed to be optimal in LF type of search. ACS strategies may thus be an alternative mechanistic basis for the emergence of LF movement patterns in many species. Further, compared to the purely random Lévy



strategy proposed ACS has a more behaviourally rational basis, as it does not assume foragers that are completely ignorant of their surroundings. These results may also explain why simple CRW approaches obviously underestimate the likelihood of larger distance dispersal events as revealed, for example, by the genetic analyses of butterfly dispersal described above.

5.3 Movement model: "Cognitive movement"

In a completely different approach we have also started a new movement model type that is far more mechanistic in approach than any of the models based on the CRW approach. We develop a model that can account for four fundamental (cognitive) abilities that may exist (to a smaller or larger degree) in most actively moving animals: (1) The ability to perceive the environment within a certain distance and thus target movement directly towards desirable resources (or away from undesired ones). (2) The ability to memorize properties of the environment visited in the past. (3) The ability to infer the likely position of new resources (patches) based on past experience or general knowledge and (4) the ability to anticipate the effects of a movement decision for the possible benefit/costs of future movement options. The model is currently still very general and cannot directly be linked to empirical systems (due to a lack of data needed to parameterize such a model) but we have demonstrated that movement modelled with this approach generates movement trajectories that resemble in many ways those empirically observed (Figure 7): (1) efficient harvesting of resources within resource concentrations, (2) more or less straight line movement between resource aggregations (patches), (3) emergence of 'looping' behaviour where individuals leave a resource patch but return in a loop, and (4) even the emergence of home-ranges without any further model assumptions.



Figure 7; from Fronhofer et al. in press). Examples of movement trajectories (simulated on a hexagonal grid) generated by the "Cognitive movement model" with different model parameters (here modifications of the inference-radius R). We find typical attributes or real movement trajectories like straight-line movement between resource patches, looping, or spiral searching.

5.4 Metapopulation model.

In the course of TenLamas we developed a general metapopulation tool allowing utilizing connectivity matrices (as provided by e.g. WP 2-4) and basic population parameters to simulate the population dynamics of spatially structured populations as well as of genetic attributes. Unlike the classical metapopulation models, it is individual-based, thus accounting for variability and stochasticity within population. Also, it allows for simulating and predicting of population genetic dynamics, with individuals carrying genetic markers patterned after microsatellite sequences. The implementation provides great flexibility as to population model type (including both deterministic



and stochastic dynamics), individual life-histories, and mutation types. Connectivity (dispersal) matrices and population structure are provided as an input, the output being the population state at the end of the simulation. The output has a form identical to that of the input data, which makes it possible to analyse the simulation results with population genetic software also applied to empirical data (e.g. calculate relatedness measures such as F_{st}).

In the course of TenLamas we further addressed a series of issues related to the application of the metapopulation concept in general and to the evolution of dispersal within spatially structured populations. Of special interest in terms of conservation strategy is the meta-population concept. In the large body of literature that has accumulated, the term "metapopulation" is often used in a very broad sense; most of the time it simply implies spatial heterogeneity. A number of reviews have recently addressed this problem and have pointed out that, despite the large and still growing popularity of the metapopulation concept, there are only very few empirical examples that conform with the strict classical metapopulation (CM) definition.

In order to understand this discrepancy between theory and observation, we used individual-based modeling that allows us to pinpoint the environmental conditions and the life-history attributes required for the emergence of a CM structure. We find that classical CM dynamics are restricted to a specific parameter range at the border between spatially structured but completely occupied and globally extinct populations (summarized in Figure 6). Considering general life-history attributes, our simulations suggest that CMs are more likely to occur in arthropod species than in (large) vertebrates.

Since the specific type of spatial population structure determines conservation concepts, our findings have important implications for conservation biology. Our model suggests that most spatially structured populations should be panmictic, patchy, or of the mainland–island type, which makes the usefulness of efforts spent on increasing connectivity (e.g., corridors) questionable. The observation of true CM dynamics may indicate, however, that the focal metapopulation is likely on the brink of extinction and in need of (drastic) conservation measures.



Environmental stochasticity, σ

Figure 7 (from Fronhofer et al. Ecology 93: 1967-1978). Schematic representation of the influence of dispersal mortality (\mathbb{Z}) and environmental stochasticity (\mathbb{Z}) on patch occupancy, turnover [O and T, panel (a)] and genetic structuring [F_{ST} , panel (b)]. As becomes clear from our results, occupancy and turnover react similarly to dispersal mortality and environmental stochasticity. Classical metapopulation dynamics can only be found in a well-defined band in parameter space characterized by intermediate occupancy, relevant turnover, and spatial structure; genetic structuring emerges, however, in a wider spectrum of the parameter space.

6. Synthesis

One of the most significant outcomes of TenLamas has been the development of two modelling packages (SMS and RandomWalker) as well as fist steps towards more sophisticated modelling of cognitive decision processes involved in movement. The latter approach takes up concepts that have



been developed recently in the movement ecology literature and applies them to dispersal and connectivity. This potentially fills a fundamental knowledge gap and enables spatial conservation management to begin to benefit from our considerable ecological knowledge related to the movement behaviour of animals on complex landscapes. Our aim within the project has not, however, been to demonstrate that conservation management should always utilise more complex movement models such as those we have developed. Indeed, it would be extremely pleasing if we were to have found that, for all species tested, a structural connectivity measure or a simple functional measure (i.e. LCP) performed as well as more complex individual-based models. Our message is currently a mixed one. For the butterflies, we find that a structural measure is as good as either the simple or complex functional measure. But for the natterjack toad and Cabanni's greenbill, an individual-based model (SMS) substantially outperforms the other metrics. So the question remains: how do we determine how much information is needed to specify connectivity robustly for a species; a hypothesis to propose here is that such models will proof especially useful where dispersal occurs in heterogeneous landscapes and/or landscapes that contain spatially small but functionally massive obstacles to movement. In order to provide a general answer to this question we need to test the methods on a substantially larger number of species and across a larger range of landscapes. Then, we may gain some rules of thumb, whereby for species with certain characteristics we can say with some degree of confidence that a structural estimate suffices.

Another very important outcome of TenLamas has been the clear demonstration that spatial genetic data can be used to arbitrate between different movement models. We have achieved this for five species now (more than we expected to be able to) and now that the method is established, it should be relatively straightforward and fast to do it for more species. A potentially very useful, if challenging, next step will be to utilise the genetic data, not as a test of the models, but as a source of data for fitting the model parameters. To the best of our knowledge this has not yet been carried out for an individual-based movement model. However, the tools that we have developed are ideal for this purpose. In subsequent work, we envisage collecting genetic data for a range of species on a given landscape to infer both the movement parameters as well as the cost values. Then we can utilise our individual-based model to test, *in silico*, the performance of alternative management strategies for multi-species and seek to optimise the design of a network across an assemblage. This is a major outstanding challenge, but is one that we are now in a much stronger position to address.

A tempting conclusion may thus be to estimate connectivity using (increasingly cheap and sophisticated) genetic methods instead of carrying out very challenging and detailed movement/dispersal studies. A common drawback of the use of the genetic methods is that we cannot be sure whether these measures reflect actual connectivity, especially if landscapes change rapidly, just because genetic measures of population structures tend to reflect dispersal of the past. This is certainly true for measures based on FST that integrate dispersal over multiple generations. However, recent advances in analytical methods of allelic frequencies (re-sampling algorithms of multi-locus gentotypes) give access to the number of individuals that disperse among populations over the last few generation (see Baguette et al. 2013 for a review). Nonetheless, without any mechanistic understanding of dispersal between habitat patches we cannot easily foresee how changes in landscape attributes would modify connectivity in the future. So we firmly believe that the use of genetic methods should be complemented by mechanistic models like those developed in the frame of TenLamas.

Finally, members of TenLamas contributed strongly as a consortium to two synthesis papers and a book composed during the funding period. In one paper we review the many aspects of dispersal costs emerging during emigration, transition and settlement in a second paper we review and advance methods for modelling movement. The book is a synthesis of dispersal theory and application, in which members of TenLamas and their staffs co-authored 11 chapters.

List of scientific publications



Published book:

Clobert, J., Baguette, M., Benton, T.G. & Bullock J.M.J. (2012). *Dispersal Ecology and Evolution*. Oxford University Press, Oxford.

Published chapters:

1. Baguette, M., Legrand, D., Fréville, H., Van Dyck, H. and S. Ducatez (2012). Evolutionary ecology of dispersal in fragmented landscapes. In Clobert, J., Baguette, M., Benton, T.G. & Bullock J.M.J. eds. *Dispersal Ecology and Evolution*. Oxford University Press, Oxford.

2. Clobert, J., Massot, M. and J.F. Le Galliard (2012). Multi-determinism in natal dispersal: the common lizard as a model system. In Clobert, J., Baguette, M., Benton, T.G. & Bullock J.M.J. eds. *Dispersal Ecology and Evolution*. Oxford University Press, Oxford.

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1. Baguette, M., J. Clobert and N. Schtickzelle (2011). Metapopulation dynamics of the bog fritillary butterfly: experimental changes in habitat quality induced negative density-dependent dispersal. *Ecography* 34:170-176.

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Deliverable name	Lead partner (country)	Date delivered	Comments
WP1 getting data	Clobert (F), Baguette (F)	08/2009	
WP2 structural connectivity estimates	Baguette (F), Clobert (F)	12/2010	Completed on time for the butterflies. Delayed for the lizard due to the need of digitalizing the land cover map of the landscape at the highest possible resolution.
WP3 Results of behavioural experiments	Clobert (F), Baguette (F)	01/12/2011	Published: Butterflies - Turlure et al. 2011 Lizards - Zajitschek et al. 25012a, 2012b.
WP4 Genetic data	Baguette (F) Clobert (F)	06/2012	Delayed for the butterflies: (1) change in data collection strategy, need of designing more powerful microsatellite markers for butterflies, (2) two maternal leaves of the postdoc in charge. On time for the lizard.
WP5 User-friendly software MOVE	Travis (UK), Hovestadt (D)		SMS published: Palmer et al. 2012. Random walk simulator:
WP6 Results of LCPs	Baguette (F) Clobert (F),	12/2011	Completed for the butterflies. Completed for the lizards
WP7 Connectivity toolbox	Hovestadt (D), Travis (UK)		Theoretical syntheses on dispersal: Bonte et al. 2012, Clobert et al. 2012 Review on dispersal, connectivity and ecological networks in Baguette et al. 2013 New methods to predict dispersal from life history traits: Stevens et al. 2012, 2013 Suite of movement models (Palmet et al. 2011, Barton et al. in prep) and integrative metapopulation model (Barton et al. in press).
WP8 Final report	All	02/2013	Delayed due to the continuation of the work.

Table of deliverables

List all staff and students supported by or affiliated with this project

- Student Name: Emanuel Fronhofer
 Major/Degree field: Diploma student, ecology
- 3. Major Professor: Poethke/Hovestadt
- 4. Degree (Ph.D., M.S., M.A., B.S., B.A., etc): PhD
- 5. Dissertation/Thesis title: "Evolving dispersal in a landscape context"



5. Dissemination of results and knowledge transfer

Participation in scientific events; posters and presentations

Michel Baguette:

- invited seminar, 5th "Ecology & Behaviour" Meeting, Lyon, Apr 2009
- invited seminar, Univ. Louvain, Oct 2012
- invited seminar, Univ. Lyon, Nov 2012

Thomas Hovestadt

- invited lecture, Univ. Louvain, Jan 2012
- invited lecture, Linnean Society London, Oct 2011
- Oral presentation, German Ecological Society, Sept 2011
- Oral presentation EEF conference, Sept 2011
- Oral presentation, German Ecological Society, Sept 2010

Justin Travis

- Invited lecture, 'Everything disperses to Miami' Miami, Dec 2012.
- Invited lecture, 'Dispersal and connectivity', Montreal, Jan 2013

- Talk on 'Eco-evolutionary dynamics of range shifts' at European Congress of Conservation Biology, Sept 2012

Camille Turlure

- Talk 'Estimating landscape connectivity for two specialist butterfly species, International Symposium on Future of Butterflies in Europe III Wageningen March 2012

- Invited seminar 'Integrating habitat quality and functional connectivity in Population Viability Analysis. Case study with two butterfly species', School of Life Sciences seminars, Arizona State University, Tempe, Nov 2012

Steve Palmer:

- Talk on, 'Estimating movement and connectivity using the stochastic movement simulator (SMS)', Sept 2012 [NB demand for this talk was so high that >20 people were not allowed in!]

Aurélie Coulon

- Presentation 1st French congress of ecology, Montpellier, Sept 2010

Interactions and joint activities

The initial board of stakeholders has not really participated to the project, apart from Kevin Watts (Program Leader, Landscape Ecology, Forest Research, UK) who participated actively to two meetings in November 2009 and December 2010. Justin Travis developed a working relationship with Kevin Watts that has resulted in a joint research proposal (k£350) being funded by the UK's Natural Environment Research Council . This project will utilise and extend the methods developed in TenLamas in the context of UK forest landscapes.

But we got very positive interactions with the SPN (Service du Patrimoine Naturel, *Natural Heritage Service*) in France, which is in charge of the deployment of the French Ecological Network (the so-called *Trame verte et Bleue*). Géraldine Rogeon from the SPN was associated to the project from our mid-term review (Aberdeen, dec. 2010) onwards. Rogeon advertised the TenLamas project in Italy, Switzerland and Germany. In 2010 Michel Baguette was nominated at the Scientific Council of the SPN and becomes a referent for connectivity issues. He participated to the writing of two orientations document aiming at proposing test procedures of the efficiency of the French Ecological Network (Sordello, R., Rogeon, G., Touroult, J. 2011. *Contribution à la réflexion sur le suivi et l'évaluation de la Trame verte et bleue. Enjeux nationaux de biodiversité : propositions sur les espèces et les habitats*. Convention MNHN/MEDDTL fiche 3i; Sordello, R., Absalem, J., Dubus, V. 2012 *Trame verte et bleue. Suivi et Évaluation. Quelle faisabilité d'utiliser l'outil génétique?* Rapport SPN 2012-38). In 2012, Baguette becomes also member of an ad hoc committee of the French Ministery of Ecology, which is in charge of the development of the French Ecological Network. He is associated Final report template for BiodivERsA funded projects Annex B to reporting requirements and guidelines



with two research projects initiated by the MEDDTL (*French Ministry of Ecology and Environment*) aiming at testing how genetic-based landscape connectivity could assist decision taking in real situations (project TRANS-FER, $k \in 374$ and project LEVANA, $k \in 167$).

Aurélie Coulon and M. Baguette supervise jointly the PhD of Théo Flavenot, who investigates the effects of quarries on landscape connectivity. T. Flavenot uses a landscape genetic approach on two toad species with contrasted ecological constraints. This project is funded by the ANRT and quarry professionals. Regular (twice a year) meetings with quarry professionals are organized, which ensure a transfer of knowledge from science into stakeholders, and vice-versa. In this context, Coulon and Flavenot participated to an informal meeting between stakeholders (quarry professionals, road professionals, ecological engineers, SPN) and scientists on the use of genetics to assess the effects of industrial activities on connectivity.

Interaction with other Biodiversa projects

CLIMIT, another BiodivERsa project was addressing questions concerning the impact of climate change on interacting insect metapopulations (specifically host ants and myrmecophiles). Dispersal is actually a crucial property for dealing with climate impact and thus was a central issue in that project too. Especially partner 2 (Hovestadt) directly cooperated with members of this project, participating at each of CLIMIT's projects meetings. The cooperation led to insights that will help to improve metapopulation management of insects, specifically butterflies and thus augments findings generated within TenLamas. Specific achievements of this collaboration include specification of dispersal properties of *Maculinea* butterflies (published in *J. Anim. Ecology*), guidelines for habitat management for butterflies (published in *J. Ins. Cons.*) and actually a series of papers addressing large-scale issues concerning species' range shifts (published in *Ecology* and *Ecography*). A further topic in this collaboration was a better understanding how inter-specific interactions may affect (the evolution of) dispersal decisions and habitat specialization (publ. in *J. Evol. Biol* and *Ecol. Model.*) and the emergence of diversity patterns (publ. in *Am. Nat.*)

Information / technology transfer

- A start-up enterprise (TerOïko) was initiated in 2012 by a former PhD student of Clobert. TerOïko aims at proposing solutions of ecological engineering to public communities, administrations, private companies and general public. Landscape management is one of the key issue of TerOïko, and the connectivity framework developed in TenLamas has been incorporated into its diagnosis tools, including the Stochastic Movement Simulator designed by Palmer et al. (2012).

- As mentioned before, the findings that genetic connectivity outperforms movement connectivity have been transferred to the designer of the French ecological network, which led to its application in real situations.

Outreach to the general public

- Baguette and postdocs conceived a short film (ca. 20 min.) on TenLamas, which was realized by a professional cineaste. The film is still unreleased, but will be released very soon, upon the publication of the final results of the project.

Baguette & Clobert wrote a chapter in a general public textbook
 Baguette, M., Clobert, J., Schtickzelle, N. & V. Stevens
 Populations locales, dispersion et métapopulations
 In Sciences de la Conservation. Ed by Gauthier-Clerc M., Mesleard F. & J. Blondel



De Boeck Université, Bruxelles (2013).

- Baguette wrote a chapter in a general public textbook

Baguette, M & B. Locatelli Biodiversité et aires protégées In Adaptation et changements climatiques. Ed. by JF Soussana QUAE, Paris (in press).

Education projects

- Baguette, Coulon, Hovestadt and Clobert taught a course (4 ECTS) on "evolutionary ecology in heterogeneous and changing landscapes" at the Doctoral School of the National Museum of Natural History (MNHN, Paris) in 2011 and 2012, in which they addressed connectivity, dispersal issues and the TenLamas project.

- Baguette taught 1 ECTS on individual dispersal, landscape connectivity and ecological networks in a course on applied demography (Master in Biology) at the Univ. Paul Sabatier in Toulouse

- Baguette and Clobert are invited to teach 1 ECTS each on dispersal, metapopulation dynamics and landscape connectivity at the thematic school on Ecological Networks organized by the CNRS in September 2013 in Dinar.

- Hovestadt taught course on developing spatially explicit (movement) models including ecological and evolutionary aspects at the University of Würzburg.

- Travis jointly ran a workshop on 'Dispersal and Connectivity' for European PhD students that took place at UFZ Leipzig. This course included general discussion of issues related to dispersal and connectivity as well as specific training in emerging methods, including SMS.

- Palmer has developed a practical course that guides students / users through the steps involved in linking GIS layers with SMS. This has been successfully trialled recently with a Masters class of 24 students.

6. Uses and impacts

List of products intended for policy makers or other policy and management stakeholders derived from this project

- Stochastic Movement Simulator: a new algorithm aiming at predicting individual movements according to context-dependent movement rules (Palmer et al. 2011).

- Edition of a book relating dispersal theory to environmental changes (Clobert et al. 2012)

- Review of the relationships between individual dispersal, landscape connectivity and ecological networks, with an emphasis on genetic connectivity (Baguette et al. 2013).

- ibmpm: an open-source R library for individual-based metapopulation simulations, with genetic structure dynamics (Bartoń K., 2012) (version 0.1, available online at http://ibmpm.r-forge.r-project.org/)



Impact statement

To our opinion, the main impact of TenLamas is the growing insight both from the scientific community and from the stakeholders that landscape connectivity is not a magic, inherent property of the landscape, but rather a complex issue resulting from the interactions between landscape properties and individual, population and species features.

Follow up activities and plans for further exploitation of the results

TenLamas was clearly a successful and very exciting project, in some area progressing even further than planned in others lacking behind schedule – mostly due to delays caused by several maternal leaves. As any such project, TenLamas raised as many new questions as it may have solved, e.g. with respect to the behavioural rules underlying movement. Another equivalent funding that would allow for a methodologically (and technically) more advanced tracking of movement or the experimental manipulation of the environment to find cues relevant for movement decisions would certainly advance our ability to truly understand movement.

7. Data Management and timeline for open access

- Data collected in the frame of the project are available on request.
- Software code or tools developed within TenLamas were made available as open-source products as listed above.

Résumé en français

Pour contrer les effets délétères de l'isolement des populations locales (vortex d'extinction) et donc accroître la viabilité des métapopulations, les stratégies de conservation se concentrent explicitement sur l'amélioration de la connectivité des paysages et la mise en place de réseaux écologiques qui devraient permettre aux organismes de se déplacer entre les habitats et les populations locales. Toutefois, la fonctionnalité de ces réseaux a rarement été testée. La fonctionnalité d'un réseau sera en grande partie déterminée par son effet net sur la mobilité des organismes cibles, qui dépend à son tour des caractéristiques du paysage et des caractéristiques écologiques de l'organisme cible, en particulier les règles selon lesquelles il prend ses décisions de mouvement. Le projet TenLamas vise d'une part à comparer des modèles alternatifs d'évaluation de la valeur et de la fonctionnalité des réseaux écologiques et d'autre part à la comparaison de différents scénarios de gestion du paysage. Du plus simple au plus complexe, les estimateurs de connectivité évalués sont: (1) les paramètres de synthèse de la connectivité structurelle qui sont fonction de la présence et de la distribution de parcelles d'habitat dans le paysage, de la surface ou de la longueur des corridors d'habitat ou d'habitats en pas japonais, (2) des algorithmes généraux de chemins de moindre coût et (3) l'utilisation de modèles de simulation détaillées des comportements individuels (génération des trajectoires les plus probables). Dans TenLamas nous avons évalué simultanément la précision relative de ces estimations de connectivité pour les espèces modèles sélectionnées (papillons, lézards, crapauds et oiseaux) dans des paysages test, en fonction du niveau de précision requis dans la description du paysage et du comportement de l'organisme.



L'un des résultats les plus significatifs de TenLamas a été le développement de deux logiciels de modélisation (SMS et RandomWalker) ainsi que les prémisses vers une modélisation plus sophistiquée des processus de décision cognitives en mouvement qui prenne en compte les concepts qui ont été développés récemment dans la littérature de l'écologie de mouvement et appliqués à la dispersion et à la connectivité. Cette étape comble une importante lacune de connaissances et permet une gestion de la conservation spatiale qui commence à profiter du savoir écologique considérable lié au comportement de déplacement des animaux dans des paysages complexes. Notre objectif dans le projet n'a pas été de démontrer que la gestion de la conservation devrait toujours utiliser des modèles de mouvements plus complexes, tels que ceux que nous avons développés. En effet, il aurait été extrêmement agréable si nous avions constaté que, pour toutes les espèces testées, une mesure de la connectivité structurelle ou une mesure simple et fonctionnelle (comme les chemins de moindre coût) fonctionnait aussi bien qu'un modèle basé sur l'individu. Notre message est cependant de promouvoir la mixité de systèmes. Pour les papillons, nous constatons qu'une mesure structurelle est aussi bonne qu'une mesure fonctionnelle simple ou complexe. Mais pour le crapaud calamite et le Bulbul de Cabanis, un modèle basé sur l'individu (SMS) surpasse nettement les autres options. Alors la question demeure: comment pouvons-nous déterminer la quantité d'informations nécessaire pour évaluer de manière robuste la connectivité pour une espèce. Pour identifier quelle solution convient à quel type d'espèce, il nous faudrait tester les méthodes sur un nombre sensiblement plus élevé d'espèces et à travers une variété de paysages.

Un autre résultat important de TenLamas a été la démonstration que les données de génétique du paysage peuvent être utilisées pour tester et comparer les différents modèles de mouvement. Nous avons atteint cet objectif pour cinq espèces (plus que ce que nous espérions atteindre) et maintenant que la méthode est établie, il devrait être facile de l'appliquer à d'autres espèces. Une étape future sera d'utiliser les données génétiques non comme un test des modèles mais comme une source de données pour ajuster les paramètres du modèle. A notre connaissance, ce type d'approche n'a pas encore été réalisé pour un modèle de mouvement basé-individu, et les outils que nous avons développés ici sont idéaux à cet effet. Dans des travaux ultérieurs, nous envisageons la collecte de données génétiques pour une gamme d'espèces sur un paysage donné, afin d'en déduire les paramètres de mouvement ainsi que les valeurs du coût associé aux différents éléments qui composent les paysages hétérogènes. Ensuite, nous pourrons utiliser notre modèle basé-individu pour tester in silico la performance des stratégies alternatives de gestion multi-espèces et chercher à optimiser la conception d'un réseau qui convienne à l'ensemble. Il s'agit d'un défi majeur, mais nous sommes maintenant dans une position beaucoup plus forte pour y faire face.

Une autre question clé qui a émergé au cours de TenLamas est l'idée qu'il devrait être possible de prévoir des distances de dispersion à partir des traits d'histoire de vie. Une première analyse sur les papillons européens a en effet montré de solides relations entre les traits d'histoire de vie et les différentes estimations de dispersion (taux d'émigration, flux de gènes, distances de dispersion) (Stevens et al. 2012). L'étape suivante a été la démonstration de la robustesse des prédictions de distance de dispersion basée sur ces suites de caractères (Stevens et al. Evol. Appl., Sous presse). Comme la distance de dispersion est le paramètre manquant dans la plupart des analyses de viabilité de populations, cette procédure a une forte applicabilité dans la planification de la conservation. Les partenaires 1 et 3 collaborent avec des collègues finlandais dans un projet visant à prédire les



changements dans l'aire de répartition de papillons, en incorporant de telles prévisions de distances de dispersion dans le modèle de RangeShifter.

Une conclusion tentante des résultats de TenLamas serait qu'estimer la connectivité en utilisant des méthodes génétiques (de plus en plus chères et sophistiquées) est plus efficace que la réalisation d'études de mouvement /dispersion détaillées. Un inconvénient de l'utilisation des méthodes génétiques est que ces mesures peuvent ne pas refléter la connectivité réelle si les paysages changent rapidement, simplement parce que les estimations génétiques de la structure de la population peuvent refléter la dispersion passée. C'est certainement vrai pour les mesures fondées sur la F_{ST} qui intègrent la dispersion sur plusieurs générations. Cependant, les progrès récents dans les méthodes d'analyse des fréquences alléliques donnent accès au nombre de dispersants entre populations au cours de la dernière génération (voir Baguette et al. 2013 pour une revue). Cependant, sans aucune compréhension des mécanismes de dispersion entre les parcelles d'habitat nous ne pouvons pas facilement prévoir comment les changements dans la structure et la configuration du paysage modifieraient la connectivité à l'avenir. Donc, nous croyons fermement que l'utilisation de méthodes génétiques doit être complétée par des modèles mécanistes de mouvement.