Scaling in Ecology and Biodiversity Conservation

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Edited by

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PENSOFT

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Preface

Human actions, motivated by social and economic driving forces, generate various pressures on biodiversity, such as habitat loss and fragmentation, climate change, land use related disturbance patterns, or species invasions that have an impact on biodiversity from the genetic to the ecosystem level. Each of these factors acts at characteristic scales, and the scales of social and economic demands, of environmental pressures, of biodiversity impacts, of scientific analysis, and of governmental responses do not necessarily match. However, management of the living world will be effective only if we understand how problems and solutions change with scale.

SCALES (http://www.scales-project.net), a research project lasting for five years from May 2009 to July 2014, was seeking for ways to build the issue of scale into policy and decision-making and biodiversity management. It has greatly advanced our knowledge of how anthropogenic and natural processes interact across scales and affect biodiversity and it has evaluated in a very practical way how this knowledge can be used to improve the scale-sensitivity and effectiveness of policy instruments for conservation and sustainable use of biodiversity.

During the project we have especially emphasized approaches that utilize existing biodiversity databases as they are the most widely available information in applied biodiversity conservation. We also tried to integrate the most appropriate assessment tools and policy instruments into a coherent framework to support biodiversity conservation across spatial and temporal scales. While the guidelines, practical solutions and special tools are presented as a special web based portal at a central place, the SCALETOOL (http://scales.ckff.si/scaletool/), the scientific outcome is widely spread over the scientific literature in regional and international journals.

With the SCALES book we want to bundle the main results of SCALES in a comprehensive manner and present it in a way that is usable not only for pure scientists but also for people making decisions in administration, management, policy or even business and NGOs; to people who are more interested in the "practical" side of this issue.

Yrjö Haila, Tampere

Acknowledgements

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The scaling of genetic diversity in a changing and fragmented world

Miguel Arenas, Stefano Mona, Audrey Trochet, Anna Sramkova Hanulova, Mathias Currat, Nicolas Ray, Lounes Chikhi, Rita Rasteiro, Dirk S. Schmeller, Laurent Excoffier

Species living in a changing world

Most species do not live in a constant environment over space or time. Their environment is often heterogeneous with a huge variability in resource availability and exposure to pathogens or predators, which may affect the local densities of the species. Moreover, the habitat might be fragmented, preventing free and isotropic migrations between local sub-populations (demes) of a species, making some demes more isolated than others. For example, during the last ice age populations of many species migrated towards refuge areas from which re-colonization originated when conditions improved. However, populations that could not move fast enough or could not adapt to the new environmental conditions faced extinctions. Populations living in these types of dynamic environments are often referred to as metapopulations and modeled as an array of subdivisions (or demes) that exchange migrants with their neighbors. Several studies have focused on the description of their demography, probability of extinction and expected patterns of diversity at different scales. Importantly, all these evolutionary processes may affect genetic diversity, which can affect the chance of populations to persist. In this chapter we provide an overview on the consequences of fragmentation, long-distance dispersal, range contractions and range shifts on genetic diversity. In addition, we describe new methods to detect and quantify underlying evolutionary processes from sampled genetic data.

Spatial and temporal genetic simulation using SPLATCHE2

Computer simulations mimic the processes that occur in the real world and allow us to study which patterns may affect systems. We have developed the program SPLATCHE2 (http://www.splatche.com) (Ray et al. 2010), which performs spatially explicit simulations of genetic data under different environmental scenarios and accounting for recombination, complex migration and long-distance dispersal. As input, the program requires a map (specified by a grid of demes) where the carrying capacity (K) and the migration rate must be user-specified for each deme. Optionally, both K and migration rate can change with time (moreover, a model allowing for different migrations rates in different directions is also implemented). Other important inputs are related with demography (e.g., initial population size and geographic origin, growth rate, total number of generations and a number of demographic models). Then, SPLATCHE2 performs a demographic simulation over the map followed by a coalescent simulation based on user-defined samples (Figure 1). The coalescent simulation just traces the evolutionary history of the sampled genes going backwards in time until their most recent common ancestor. It is followed by a simulation of genetic data (DNA, STRs and SNPs) along the coalescent (gene) genealogy. Although the model makes several assumptions (such as a molecular clock or non-overlapping generations) it is probably one of the most realistic software packages available and has been used in a variety of important publications.

Genetic diversity can be scale-dependent as a consequence of environmental or evolutionary heterogeneities, the former ones being potentially driven by climatic changes, whereas the latter can be driven by natural selection. Thus, geographic barriers, geographic provenance, or migration abilities of the species may increase genetic heterogeneity at various scales. Below, we study a variety of complex evolutionary scenarios with scaling genetic diversity by using our simulation evolutionary framework.

Influence of habitat fragmentation on genetic diversity

Previous studies have suggested that environmental heterogeneity can affect genetic diversity, but these effects were not evaluated at different spatial scales. For instance it is unknown if a given climatic change will equally affect (e.g. decrease) genetic diversity within and between populations, which is fundamental information for nature conservation and management studies, such as to predict the influence of climate change on global and local biodiversity. By using the results from extensive simulations, we address here the influence of fragmented habitats at different scales on the species genetic diversity. Using SPLATCHE2, we simulated range expansions where demes were partitioned into groups (patches) by adding barriers to dispersal. We also included scenarios with long-distance dispersal events, where individuals can migrate to non-neighboring demes. Then, samples were collected within demes, patches, regions and at the global landscape level.

Range expansion

Range contraction

A

B

Re-expansion from all Southern Europe

Re-expansion from Iberian Peninsula
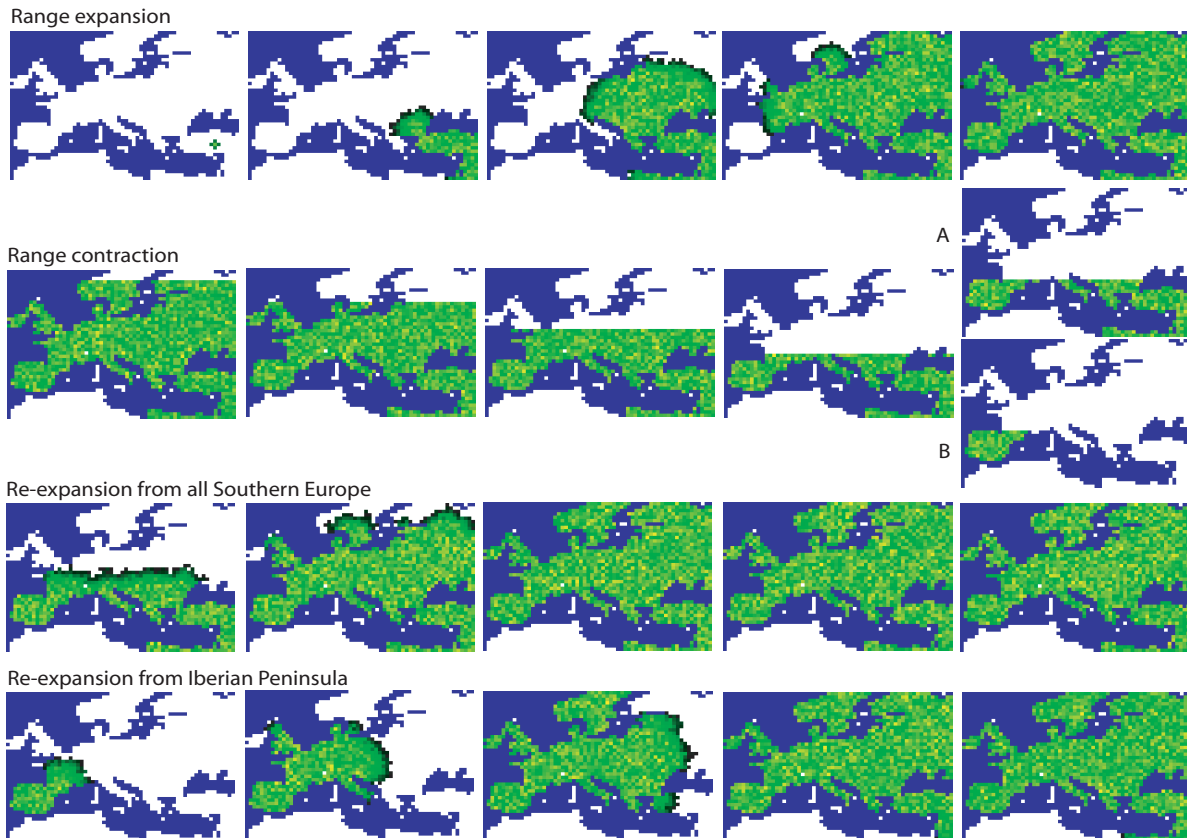
Figure 1. Timeline simulation of complex scenarios of range expansion, range contraction and posterior re-expansion. Each plot corresponds to a snapshot of the program SPLATCHE2. White areas indicate unoccupied demes while green areas represent occupied demes. Snapshots presented at each line differ in 50 generations, see detailed settings in Arenas et al. (2013). At the top, we describe a range expansion over Europe from the Near East. Then, we show a range contraction from the north to the south, which mimic the Last Glacial Maximum period and leads to two situations (as shown on the left of the second row: A: refuge areas cover all southern Europe, and B: there is a single refugium in the Iberian Peninsula. The third and fourth rows show a re-expansion from these two types of refuge areas.

As expected, we found that strong levels of fragmentation result in a severe loss of genetic diversity in the population at a global scale, but we also found that the detection of this decreased diversity requires sampling at different scales (Mona et al. 2014). Moreover, we varied fragmentation intensity at specific time points and we found that local genetic diversity and population differentiation were markedly affected by ancient fragmentation, and much less by recent events (Mona et al. 2014). Our results explain why recent habitat fragmentation does not always lead to detectable signatures in the genetic structure of populations. Conversely, if habitat fragmentation is removed, it also takes a long time to recover lost diversity by natural processes, suggesting that long-term conservation measures (e.g., by restoring gene flow) should be implemented to locally restore previously lost genetic diversity (Mona et al. 2014). We also found that species with long-distance dispersal abilities can, however, mi-grate across the barriers. As a consequence, their diversity is less influenced by the fragmented landscape.

Influence of range contractions and range shifts on genetic diversity

Range contractions and range shifts may occur as a consequence of temporal climatic fluctuations, depending on the geographical structure of the landscape, the duration of the climatic changes, or the species' dispersal abilities. Under such environmental changes, a common response of species is migration towards more suitable regions. Many studies have analyzed the migration behaviour and spatial distribution of range-contraction and -shifting species; nevertheless, less attention has been paid to the influence of such processes on genetic diversity. We simulated DNA sequence data in populations suffering diverse range shifts and contractions over a landscape constituted by a grid of demes (Arenas et al. 2012). Simulated scenarios of range shifts and range contractions varied according to dispersal abilities and migration patterns. For example fast range contractions (e.g., as a consequence of rapid climate change) may lead to the extinction of populations that do not move. We analyzed genetic diversity of the simulated data. Contrary to our expectations, we found that fast contractions preserve higher levels of diversity and induced lower levels of genetic differentiation among refuge areas than slow contractions towards refuge areas. Thus slow contractions have the highest negative impact on final levels of diversity. We obtain rather different results when the range of species is shifting rather than expanding: fast range shifts lead to lower levels of diversity than slow range shifts. Interestingly, we found that species actively migrating to-

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Box 1. Effect of range contractions on current European molecular diversity

The genetic signal of range contractions can be also observed in genetic gradients estimated by principal component analysis (PCA), a method for analyzing patterns of similarity between multiple samples. Initial studies that represented genetic relationships among human populations with PCA revealed the presence of a southeast–northwest (SE-NW) gradient of genetic variation in current European populations, which was interpreted as being the result of a diffusion process of early Neolithic farmers during their expansion from the Middle East. However, this interpretation has been widely questioned, as PCA gradients may occur even when there is no expansion, and because the first PC axis is often orthogonal to the expansion axis (i.e. the main axis of change in levels of genetic diversity is perpendicular to the expansion direction). However, the effect of more complex evolutionary scenarios on PCA, such as those including both range expansions and contractions, had not been investigated.

In a recent study, we (Arenas et al. 2013) performed simulations of range contractions that might have occurred during the last glacial maximum period to better understand the formation of genetic gradients across Europe. In particular, we have simulated range contractions of human Paleolithic populations and admixture between Paleolithic and Neolithic populations over Europe (see Figure 1). The simulations were performed for diverse levels of admixture and under two range contraction scenarios where the refuge areas were either over all southern Europe or only in the Iberian Peninsula (see Figure 1). We observed that the first PC (PC1) gradients were orthogonal to the expansion, but only when the expansion was recent (Neolithic). More ancient (Paleolithic) expansions altered the orientation of the PC1 gradient due to 1) a spatial homogenization of genetic diversity over time, and 2) the exact location of the Last Glacial Maximum (LGM) refugia. Overall we found that PC1 gradients consistently follow a SE-NW orientation if there is a large Paleolithic contribution to the current European gene pool, and if the main refuge area during the last ice age was in the Iberian Peninsula. Our study suggests that the observation of a SE-NW PC1 gradient is compatible with the view that range contractions have affected observed patterns of genetic diversity, and suggest that the genetic contribution of Neolithic populations to the current European gene pool may have been limited (Figure 2). Although this study was focused on humans, this framework could be applied to other species that might have experimented with range contractions as a consequence of environmental changes.

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wards refuge areas can actually bring additional diversity to these areas, but only if the range contraction is rapid. When contractions or shifts are slow, we found that active migrations towards refuge areas could lead to a more pronounced loss of diversity than if migration was similar in all spatial directions (Arenas et al. 2012). These results suggest that species with different generation times and different migration abilities should be differently affected by environment change.

Inference of fragmentation levels from genetic data gathered at different scales over the species range

Populations living in a heterogeneous environment usually show a large variance in local population densities and migration rates, and generally present less local genetic diversity and higher levels of population differentiation than populations of similar size living in a constant and uniform environment. This is because genetic diversity is more rapidly lost in small demes than it is gained in large demes, leading to higher rates of local genetic drift.

Patterns of genetic diversity have been used to assess many properties of a population, but no attempt has been made to estimate the degree of environmental heterogeneity directly from patterns of diversity at different scales. It would therefore be useful to be able to infer the degree of environmental heterogeneity directly from genetic data, especially for sparse and cryptic species, or for species for which the exact definition of the population is difficult to assess.

We have simulated environmental heterogeneity using SPLATCHE2 where local deme carrying capacities (K) can vary in space according to a Gamma distribution with mean $\bar{K}$ and shape parameter α. The Gamma distribution is often used to describe various levels of heterogeneity of a given biological parameter (e.g. mu-

tation rate, migration rate, population size, etc). The important thing to note here is that small values of α (typically α < 1) are indicative of strong environmental heterogeneity, where a few demes have very high population densities and most others have very low densities (even being zero, which correspond to uninhabitable regions). Therefore, because habitat fragmentation usually creates uninhabitable regions, it is also associated to high levels of environmental heterogeneity. On the other hand, large values of α (typically α >5) imply little environmental heterogeneity, such that most demes have a very similar carrying capacity. Previous studies have shown that both local genetic diversity and levels of population differentiation would strongly depend on α, suggesting that patterns of genetic diversity at different scales could be used to infer α, and therefore, indirectly, the level of environmental heterogeneity.

We used an analytical method based on the Approximate Bayesian Computation approach (a statistical inference method allowing one

to estimate parameters in complex models by computer simulation) to infer the shape parameter of a Gamma distribution directly from patterns of genetic diversity of several samples taken from a population having gone through a recent range expansion. Our results show that the degree of environmental heterogeneity (α) can be very well estimated if all other parameters of the model are known (Figure 3). When all other parameters need to be co-estimated, the estimation of α becomes difficult, and we can mainly distinguish small from large α values (Figure 4). In other words, we only have power to distinguish very heterogeneous environments from more homogeneous ones, but little prospect to get accurate estimations of α.

Concluding remarks

In this chapter we described the strong influences that habitat fragmentation and dispersal heterogeneity can have on genetic diversity, at different geographical and temporal scales. To this purpose, we mainly used the SPLATCHE framework to perform spatially explicit simulations of genetic diversity under complex demographic models, also allowing for temporal heterogeneity. We found that fragmented habitats often have a significant loss of genetic diversity relative to homogeneous habitats. This effect was reduced in species with long distance dispersal abilities. Similarly, range contractions led to a loss of genetic diversity, in particular when the contraction was slow. Note that the rate of environmental change needs to be considered relative to the generation time of the species involved, and the generation time of species needs to be taken into account when considering genetic diversity after climatic changes. Species with shorter generation times should suffer from more diversity loss after a range contraction than long-lived species (Arenas et al. 2012). We note however, that such species may also adapt more quickly to new environments. Fast range shifts, on the contrary, reduced genetic diversity more than slow range shifts where more individuals can track favorable
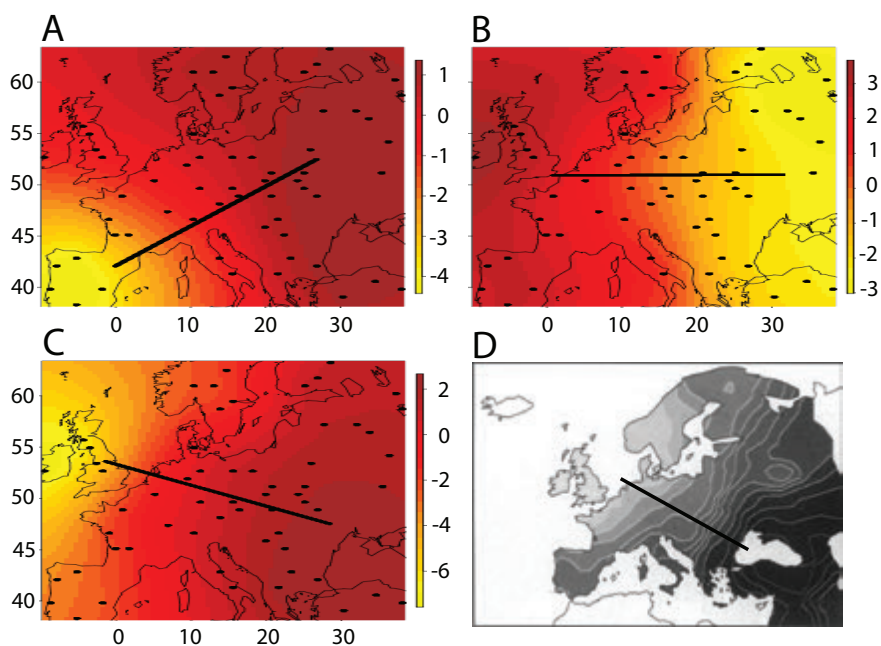
Figure 2. Influence of range contraction on Principal Component (PC) maps. We show the results of Principal Component Analysis (PCA) on Single Nucleotide Polymorphism (SNP) data in the case of a Neolithic range expansions from Middle East resulting in a final population that shows 80% with the pre-existing Paleolithic population: (A) Illustrative example of PCA derived from a range expansion. The PC1 gradient has a SW-NE orientation. (B) Illustrative example of PCA derived from range expansion followed by a range contraction towards all of southern Europe, and subsequent re-expansion. The PC1 gradient has an E-W orientation. (C) Illustrative example of PCA derived from range expansion followed by a range contraction towards the Iberian Peninsula only, and subsequent re-expansion from this refugium. The PC1 gradient has an NW-SE orientation. (D) Original PC1 map inferred from Piazza et al. (1995) [© 1995 National Academy of Sciences, USA] with a superimposed line connecting positive and negative PC1 centroids. The PC1 gradient shown in (C), which is the most similar to real data (D), was also found in scenarios with a larger Paleolithic contribution and either pure range expansions or range expansions with range contraction towards the Iberian Peninsula (see Arenas et al. 2013 for further details).
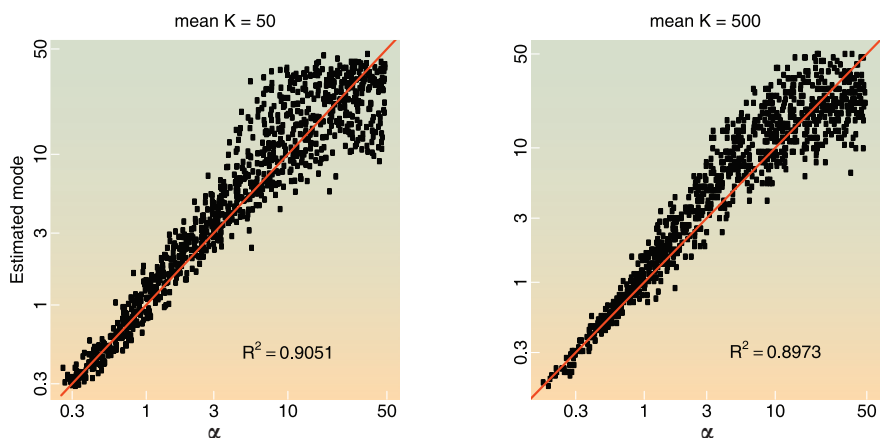
Figure 3. ABC estimation of our index of environmental heterogeneity (α) from genetic diversity simulated in species with small and large carrying capacity (K) when all other parameters of the model are known. The true value of α is shown on the x-axis and its estimation (as the mode of its posterior distribution resulting from an ABC analysis) is shown on the y-axis.

environments. Indeed species with low migration rates and going through fast range shifts can easily become extinct (Arenas et al. 2012). In addition, we found signatures of range contractions on diversity by using PCA. In this case, a re-expansion after a range contraction introduces spatial genetic diversity gradients that depend on the location of refuge areas (Arenas et al. 2013). We also described a procedure to detect the level of habitat fragmentation from observed patterns of genetic diversity. Finally, we

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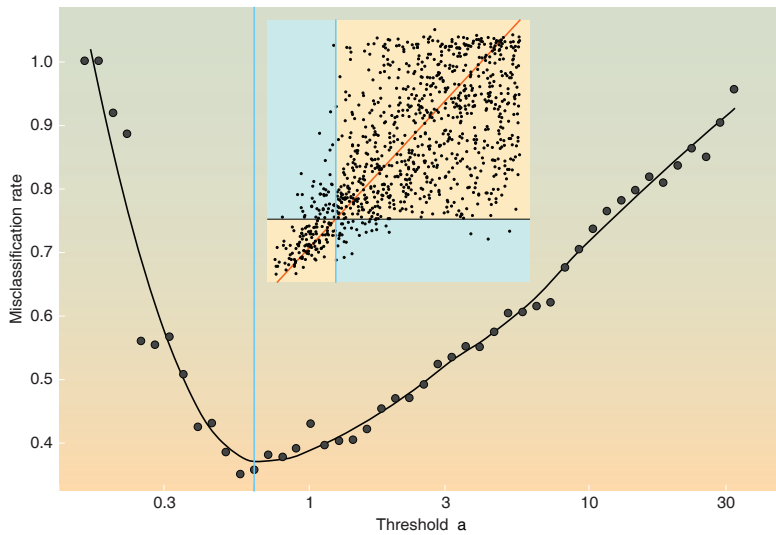
Figure 4. Optimal distinction between small and large α values when all parameters of the range expansion model need to be co-estimated with the environmental heterogeneity. The plot shows the estimated proportion of times where α was incorrectly estimated as below or above a threshold (a given true value). This incorrect assignment is minimized for α=0.63 (blue line), showing a maximal power to distinguish between values of α above and below this value. Here, the misclassification rate is inferred from an analysis of the plot of true (x-axis) vs. estimated (y-axis) α values shown in the central insert. Misclassification rate is obtained as the sum of the proportion of points in the blue regions relative to those in the orange regions on the left and right hand side of the blue line.

Box 2. Sex-biased dispersal

Population genetic structure is influenced by migration patterns. This includes sex-biased dispersal, likely impacting life-history evolution, population genetic structure and metapopulation functioning. In population genetics, sex-biased dispersal may not only reflect a difference in the number of dispersing individuals of one sex in relation to the opposite sex, but also the unequal reproductive success of dispersers. Fine-scale genetic structure and adaptation to local environments might therefore be promoted by sex-biased dispersal. Sex-biased dispersal can be identified and quantified by e.g. comparing the genetic differentiation of females to that of males. The sex with the highest dispersal frequency would have a lower genetic differentiation among different subpopulations (i.e. as measured by the genetic parameter F_{ST}). Similarly, sex-biased dispersal could be measured by comparing the level of genetic structure inferred from nuclear markers (inherited by both parents) to that indicated by mitochondrial DNA (as children inherit their mitochondria from their mothers) or Y chromosome (which male children inherit from their fathers). If the level of genetic differentiation inferred from mtDNA is higher than that inferred from nuclear markers, male-biased dispersal may be assumed. Simulations, undertaken with a different program inspired by SPLATCHE2 (Rasteiro et al. 2012), clearly show that different patterns of genetic differentiation can be detected under three scenarios, 1) bilocality (no sex-biased dispersal), 2) matrilocality (male-biased dispersal), and 3) patrilocality (female-biased dispersal, Figure 5). Y-chromosome genetic diversity is very low, especially in the patrilocality scenario for which only one Y-haplotype often remains after 1000 simulated generations. Note that the same effect was not seen in simulated mtDNA, probably due to differences in mutation rates and types of markers (Rasteiro et al. 2012). Indeed, the authors showed that the simple difference in mutation rates between the two types of sex-related genetic systems is sufficient to create an asymmetry that could be mistaken for differences in migration rates, even under bilocality scenarios.

Accounting for sex-biased migration in population and conservation genetics studies is of great importance as significant differences in sex-biased dispersal have been demonstrated among different taxonomic groups. Dispersal of mammals, reptiles and fishes were more frequently male-biased whereas dispersal in birds was more frequently female-biased (Figure 6). Therefore, knowledge on sex-biased dispersal may prove essential to develop and assess habitat management and landscape planning strategies for different species.

In many species, population decline has been linked directly to loss and fragmentation of habitats and indirectly to reduced inter-patch dispersal. Concerns about habitat fragmentation and landscape structure are usually based on the ability of wildlife to disperse between the blocks of habitat types that they require. Our simulations showed that patterns of sex-biased dispersal can have important consequences on some genetic markers and conversely they should inform us on the importance of sex-biased dispersal in natural systems that are difficult to study. Some studies have suggested that the different sexes may have a differing impact on demographic connectivity at different scales, the less dispersing sex more on local scales, while the more and farther dispersing sex on larger scales. Another consequence of sex-biased dispersal is that the rate of natural recolonization of locally extinct populations may be slower as it requires that both sexes disperse. Sex-biased dispersal may also act as a buffer against reduction of genetic variability due to high genetic drift in populations with small effective size (Schmeller and Merila 2007). Ultimately, explorations of the implication of unequal effective population size, migration rate and non-random individual dispersal will be necessary for synthesizing ecological and genetic theory on dispersal and population structure.
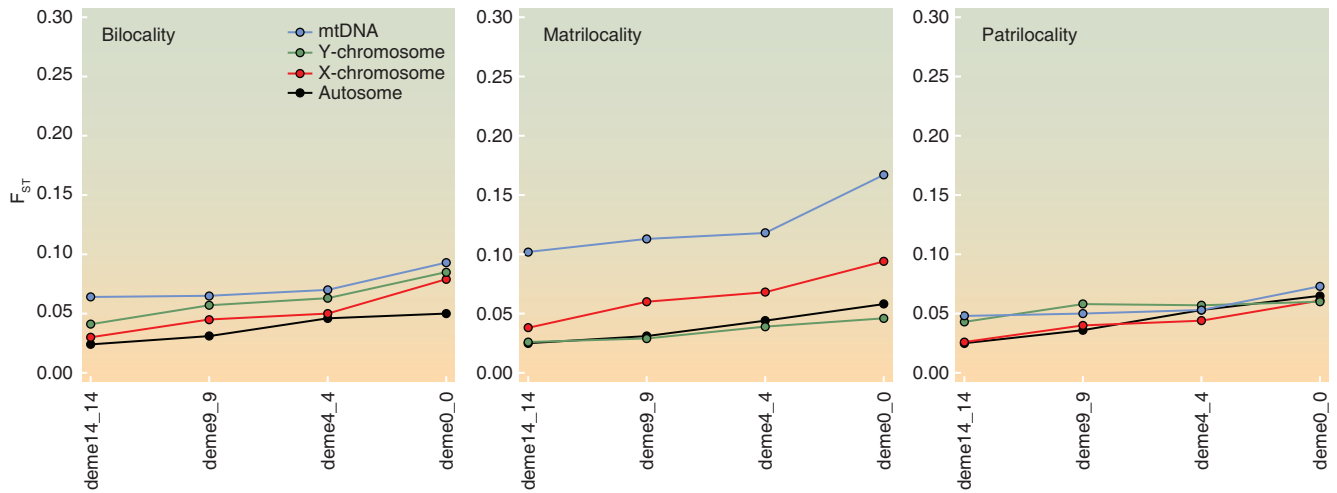
Figure 5. Genetic differentiation patterns under sex-biased migration patterns. Simulations were performed using a forward simulation program similar to SPLATCHE2. A square environment of 400 demes (20×20) was simulated under three scenarios, 1) bilocality (no sex-biased dispersal), 2) matrilocality (male-biased dispersal), and 3) patrilocality (female-biased dispersal). For each scenario we simulated independent autosomal loci, Y and X chromosome and mtDNA sequences. For each scenario and genetic marker type we computed a measure of genetic differentiation between demes at increasing distances. For simplicity only demes from the diagonal were used and compared to the same deme located in one of the corners (deme 19,19). As the panels show, sex-biased migration has a strong impact on the overall level of genetic differentiation, and on the differences between markers. The results also show that mtDNA and Y chromosome markers do not necessarily play symmetrical roles in the patrilocality and matrilocality scenarios because they differ also in mutations rates, as noticed by Rasteiro et al. (2012).

performed simulations incorporating sex-biased migration and found that such a bias could highly impact genetic data, which can therefore be used to infer sex-biased dispersal in species that are difficult to study in the field.

The fact that habitat fragmentation, dispersal patterns, and range movements strongly alter genetic diversity of species implies that they need to be considered for biodiversity conservation strategies.

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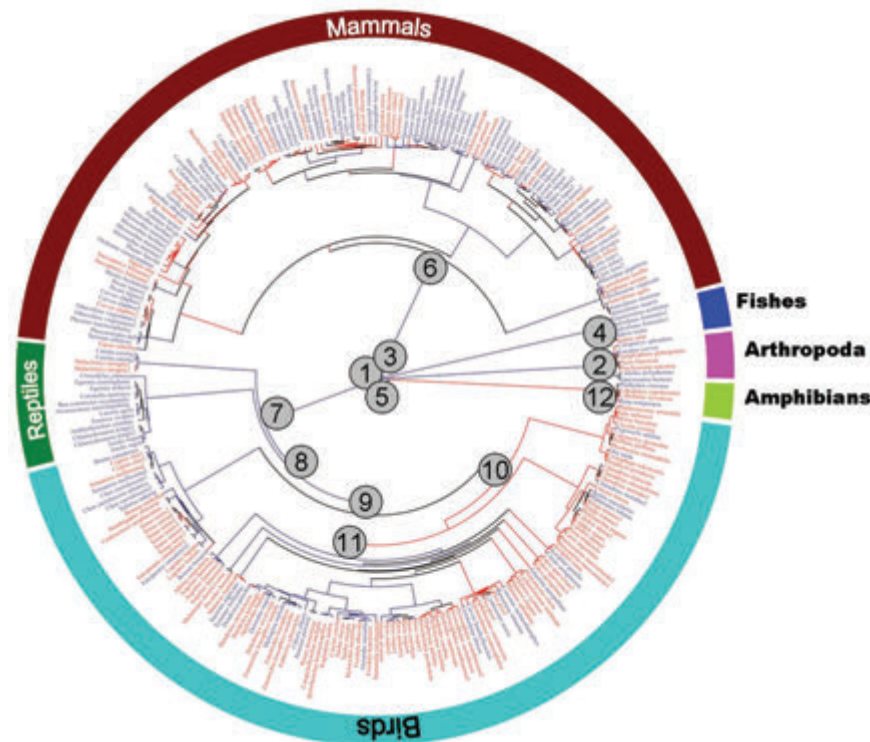
Figure 6. Phylogenetic tree of the ancestral character states reconstruction of sex-biased dispersal based on a parsimonious method on the 216 species (275 populations from publications) used. Branches and tips are coloured in blue for a male biased dispersal state and in red for a female biased dispersal state. In grey, branches for which the reconstruction method did not allow one to choose between a male or a female bias. Numbers on nodes correspond to: 1. Bilateria, 2. Arthropoda, 3. Osteichthyes, 4. Fishes, 5. Tetrapoda, 6. Mammals, 7. Amniota, 8. Sauria, 9. Neognathae, 10. Neonaves, 11. Birds, 12. Batrachia.

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This book is the first of its kind to describe the challenges that arise in studying and conserving biodiversity across different scales. Taking a scale-conscious view of the drivers of change, biodiversity patterns and processes themselves, and policy actions aimed at management and protection, it describes a wide range of practical methods and recommendations to improve conservation at continental and global scales.

Drivers of change are considered at different spatial scales, including the likely effects on biodiversity under land use and climate change. Ecological patterns and processes are examined and modelled at different levels of biological organization, from genetics, through individual dispersal and population viability, to community structure and selected ecosystem services. Trade-offs and tensions between different conservation goals are explored, and promising new methods for the study of scaling effects are digested from the scientific literature. Different governance and policy tools are evaluated and recommendations given. Finally, case studies from both Europe and Taiwan illustrate many of the scaling issues with a focus on networks of protected areas and their connectivity.

The book is addressed to a wide range of readers. Scientists will find readable summaries of analyses, methods and case studies. Conservationists and policy makers will find recommendations and ideas for management, biodiversity governance, and decision-making. Lecturers will find good examples to illustrate the challenges that arise from considering multiple scales in ecology and biodiversity conservation. Moreover, everyone concerned with conservation will find ideas in this book to help in the urgent task of protecting biological diversity through study, insight and action at all kinds of scales: spatial, temporal, administrative and ecological.