Integrating Population Genetics with Landscape Ecology to Infer Spatio-temporal Processes

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Abstract

The last decade has seen the rise of the research fields of DNA analysis and population or ecological genetics. They have the potential to allow the revision of landscape ecological concepts such as habitat connectivity or fragmentation. In this chapter, we first ask how population genetics can support and extend landscape ecological research from analysing patterns to understanding processes, and we introduce the concepts of neutral and adaptive genetic diversity. We further outline relevant population genetic applications, provide corresponding examples and discuss the benefits and limitations of molecular techniques by referring to the topics of migration, dispersal and gene flow at various spatial and temporal scales. The discussion highlights migration patterns of species in the postglacial landscape, the assessment of historical dispersal and gene flow among populations, a description of how the current movement of plant propagules can be measured and a brief reassessment of the metapopulation concept and of what would be required to provide unequivocal empirical data on metapopulations. Despite the evident usefulness of molecular methods in landscape ecological research and the spatial context inherent to both landscape ecology and population genetics, the two fields have hitherto virtually stayed apart. Thus, we claim that the emerging field of landscape genetics, a marriage of population genetics with landscape ecology, should be given research priority, both theoretically and empirically. We expect a significant contribution of this field to basic and applied topics such as fragmentation and the management of natural ecosystems.

Keywords: adaptive genetic variation, connectivity, gene flow, landscape genetics, metapopulation, neutral genetic variation, population genetics

Population Genetics as "A Bridge Over Troubled Water" in Landscape Ecology?

Landscape ecology is a rapidly evolving and flourishing field of ecological research (Li and Wu 2004). The qualitative and quantitative description of landscapes is a key issue in applying ecological knowledge to current environmental and socio-cultural problems (Turner *et al.* 2001). From a biological point of view, it has long been recognised that the landscape influences the ecological and evolutionary processes that took, take or will place in it. Terrestrial habitat patches embedded in a landscape matrix can theoretically be treated as "islands in the sea" according to the classical island biogeography model of MacArthur and Wilson (1967). However, the real world often does not function along the rules of theoretical models with spatial idealisations and multiple assumptions (Baquette 2004). The matrix of the landscape may dramatically alter the way the system behaves. For instance, dispersal corridors may locally interrupt the fundamental relationship of decreasing movement of individuals (or genes) with increasing distance among habitat patches. Two remote islands connected by "a bridge" will show higher exchange than two close islands separated by "troubled water". Connectivity as a "bridge over troubled water" could well act independent of pure spatial distance, depending on the quality of a landscape (Levin 1992). Hence, the evaluation of landscape structure is essential (Turner *et al.* 2001), especially in problem-orientated fields such as conservation biology or restoration ecology.

The above mentioned landscape structure is often described with spatial, temporal and ecological indices (Bolliger *et al.* 2007). Landscape indices that have been extensively used are, e.g., "connectivity", "contagion" or "fractal dimension" (Turner *et al.* 2001). In order to adequately determine landscape structure, more than one index is usually needed, since "connectivity" is only partly defined by "proximity" as illustrated above. However, do values of landscape indices really reflect an underlying ecological (or evolutionary) process? Li and Wu (2004) recently stated that the relationship between pattern and process has rarely been shown in landscape ecological research. Often, a close relationship is simply assumed but not proven. Spatial pattern analysis in landscape ecology would be of limited use if it could not help in explaining or predicting processes. This dilemma led Li and Wu (2004) to doubt the relevance of landscape indices (Bolliger *et al.* 2007).

How can the ecological meaning of landscape indices be verified? As we will show below, population (Hartl and Clark 1997) or ecological genetics (Lowe *et al.* 2004) offer powerful tools to investigate ecological processes. By studying an appropriate gene (or locus) and by using an appropriate sampling design, population genetics can generate data on ecological processes acting at various spatial and temporal scales (from single habitat patches to whole continents and from years to decades or even millennia; Lowe *et al.* 2004). Genetic data may thus give credit to landscape indices.

Using Neutral Genetic Diversity to Infer Landscape Processes

Genetic diversity is a major facet of biodiversity (Rio Convention; www.biodiv.org/convention/articles.asp). It is essential for the short- and long-term evolution of species and for their potential to react to environmental change (Lande and Shannon 1996). Thus, genetic investigations are often incorporated in conservation projects and practical management plans of endangered species. But is all the genetic diversity that we measure of such high importance?

There are two basic types of genetic diversity, namely neutral and adaptive genetic diversity (Holderegger *et al.* in press). Genetic diversity values obtained from most molecular genetic markers currently analysed in laboratories represent neutral genetic variation (Pearman 2001), because the corresponding genes are not subject to natural selection. Which

gene variants or alleles an individual carries, does thus not affect its fitness. The corresponding genetic variation is, in effect, selectively neutral (Reed and Frankham 2001). Unfortunately, the identification of genes subject to natural selection, such as genes that influence juvenile survival, growth rates or disease resistance, needs labour-, time- and cost-intensive experiments under controlled environmental conditions (quantitative genetics; Latta 2003). The corresponding genetic variation is adaptive or selective. In the future, the new field of ecological genomics might open a way to directly investigate adaptive genes in the laboratory using molecular techniques (Jackson *et al.* 2002; Luikart *et al.* 2003).

If most measurements of genetic diversity based on the analysis of molecular markers are selectively neutral, what are then their meaning and practical benefit? Is there a correlation between the diversity of neutral genes and the diversity of genes upon which natural selection acts that would allow us to draw conclusions on the evolutionary potential (adaptability) of populations? This question is not of purely academic interest but central to conservation biology and the management of natural living resources, because neutral molecular genetic variation is often taken as a surrogate for the variation of adaptive genes (Pearman 2001; Reed and Frankham 2001).

Unfortunately, there seems to be no such direct correlation as shown by several recent reviews on animals and plants (Reed and Frankham 2001; Merilä and Crnokrak 2001; McKay and Latta 2002; Latta 2003; Holderegger *et al.* 2006). Thus, neutral genetic variation does not provide direct evidence for adaptation or the evolutionary potential of populations or species. Why should such a relationship between neutral and adaptive genetic variation have been expected anyway? Genetic variation and genetic differentiation (i.e. the dissimilarity among populations; Lowe *et al.* 2004) is not only caused by local adaptation, which would affect the selectively active genes, but also by population processes such as random sampling effects (genetic drift and bottlenecks; Hartl and Clark 1997), migration, dispersal and gene flow among populations, changes in population size, population fragmentation or mating behaviour (Frankham *et al.* 2002). All these processes act upon neutral genes in essentially the same way as they act on adaptive genes, but since selection does not interfere with neutral genetic variation, the latter truly reflects the action of these processes free of distortion. Neutral genetic markers are therefore excellent tools to study ecological processes such as dispersal and gene flow (see below), but the naive use of neutral genetic diversity as an indicator of biodiversity at the population level is questionable (Pearman 2001; Holderegger *et al.* in press; for a discussion of value systems see Buchecker *et al.* 2007 and Duelli *et al.* 2007).

Different Places, Different Times, Different Processes

Once upon a time: postglacial migration

Biogeographic patterns perfectly serve to show how molecular genetic methods allow the investigation of historical processes acting over thousands of years and on large spatial scales. Here, our example deals with the postglacial migration of species during the last 15 000 years. Molecular biogeography, i.e. phylogeography, has seen a tremendous rise during the last decade (Avise 2002). Phylogeography allows determining the evolutionary relationships between extant populations. Hence, postglacial (re-)immigration pathways can be inferred from genetic variation (Taberlet *et al.* 1998).

Cells contain organelles which possess their own DNA. Unlike genes from the cell nucleus, genes of these organelles are mostly uniparentally inherited, i.e. solely by the mother or the father. This is the case for mitochondria in both animals and plants and for chloroplasts in plants (Avise 2002; Holderegger *et al.* in press). In most plant species, chloroplasts are
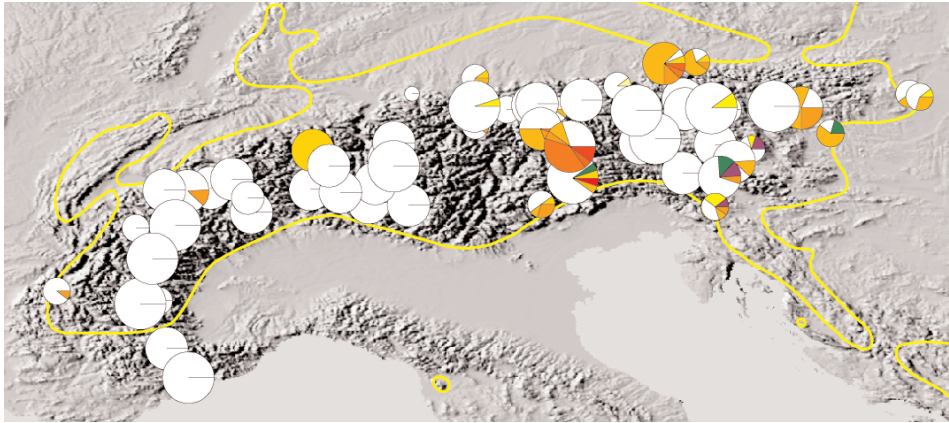
Fig. 1. Evidence of a founder effect in the western part of the Alpine range of Norway Spruce *(Picea abies)*. The relative frequencies of different mitochondrial DNA types *(nad*1 intron 2 sequence genotypes) are given by different colours, and sizes of circles are proportional to sample size per site. (Figure taken from Gugerli *et al.* (2001) with permission by Blackwell Science.)

inherited from the mother (maternally inherited), and the spatial distribution of chloroplast genotypes thus reflects seed dispersal. One can also distinguish dispersal by seed from gene flow by pollen if both nuclear genes and chloroplast and/or mitochondrial genes are investigated (for methods see Ennos 1994 and Lowe *et al.* 2004). This illustrates the elegance of molecular genetics with its large set of different genetic markers, each of which is potentially appropriate for a different question.

By making use of uniparentally inherited organelle markers (gene sequence variants from mitochondrial DNA), Gugerli *et al.* (2001) studied the postglacial re-colonisation of Central Europe by Norway Spruce *(Picea abies)*. The results suggest that Norway Spruce re-immigrated from eastern European glacial refugia. Northern and western Alpine populations were predominantly founded by immigrants originating from the Carpathian Mountains, while the Southern Alps appear to have been mainly colonised by individuals arriving from the Balkan Peninsula. Furthermore, Norway Spruce experienced a severe founder effect (i.e. colonisation by only a few colonising individuals; Frankham *et al.* 2002) during the postglacial re-colonisation of the Alps, which has led to a lower genetic diversity in the western than in the eastern Alps (Fig. 1). These phylogeographic findings are in good agreement with fossil pollen records (Lang 1994). The example shows that (1) molecular genetics can provide an empirical test of a given hypothesis by using an independent data source (here DNA markers versus fossil pollen) and (2) additional details about a dynamic process (here the origin and migration pathways of colonising individuals) can be inferred.

Intensive phylogeographic research has now been carried out, and reviews are provided, e.g., by Taberlet *et al.* (1998) and Hewitt (2004), as well as Petit *et al.* (2003) concentrating on European woody species and Schönswetter *et al.* (2005) recapitulating the glacial history of alpine plants. However, phylogeographic research has mainly dealt with single species. Ongoing research now aims at correlating multi-species phylogeographic patterns (i.e. comparative phylogeography; Taberlet *et al.* 1998) with several ecological parameters at large geographic scales. The latter is a typical subject of landscape ecological research. A corresponding example is the INTRABIODIV project on habitat, plant species and gene diversity in the European Alps and the Carpathians (http://intrabiodiv.vitamib.com).

Once just before: historical gene flow

Genetic differentiation among populations, e.g., expressed as F_{ST} (Frankham *et al.* 2002), is one of the most often calculated population genetic parameters. It ranges between 0 (no differentiation at all) and 1 (complete differentiation). Theoretically, high gene flow among populations should lead to genetic homogenisation of populations, while genetic isolation should cause pronounced genetic differentiation of populations. Based on this simple reasoning, the genetic differentiation of populations (under Wright's island model; Conner and Hartl 2004) can be used to indirectly infer the amount of past migration or gene flow among populations, *Nm,* using the equation $F_{ST} = 1/(4Nm + 1)$ (Frankham *et al.* 2002).

An example is provided by a molecular investigation (genetic fingerprinting with random amplified polymorphic DNAs, RAPDs) of populations of English Yew *(Taxus baccata)* in Switzerland by Hilfiker *et al.* (2004a). This marker type, mainly from the nuclear genome of the plants, is distributed to the next generation both by seed and pollen. In this study, *Nm*-values between population pairs of this conifer were calculated based on their pairwise genetic differentiation *(F_{ST})* and subsequently correlated with the geographic distances between them (Fig. 2). Swiss populations were connected by substantial past gene flow through pollen and/or seed, which decreased with increasing geographic distance (a pattern called "isolation by distance"; Lowe *et al.* 2004). However, Hilfiker *et al.* (2004b) found that the average genetic differentiation of small populations was higher than that of large populations, indicating that English Yew could well suffer from the negative population genetic consequences of small population size such as lower genetic variation or genetic drift (i.e. stochastic changes of the genetic composition of a population; Frankham *et al.* 2002). This example illustrates that the genetic structure of populations is a function of inter-population differences, but that the local random sampling effect of genetic drift within populations determines their genetic diversity.
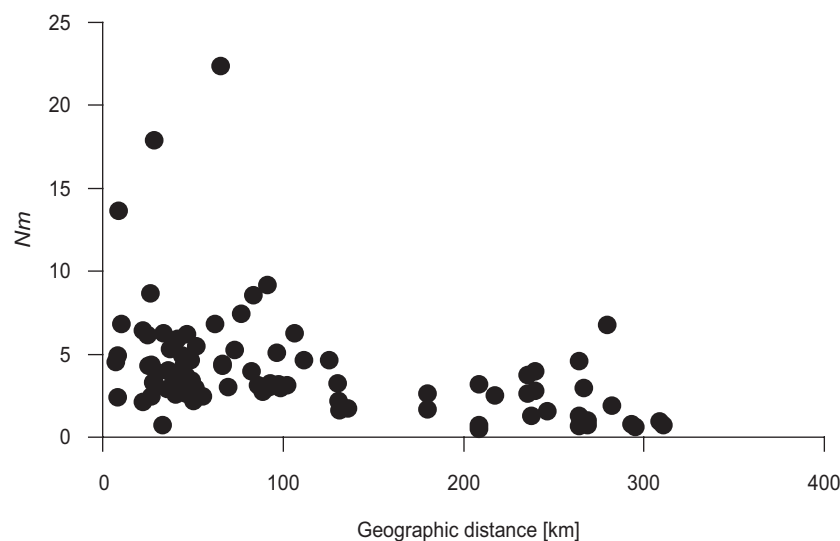

Fig. 2. Historical gene flow of English Yew *(Taxus baccata)* in Switzerland as estimated by *Nm*-values. The *Nm*-values are based on random amplified polymorphic DNAs (RAPDs). The data show decreasing gene flow with increasing geographic distance (Mantel test: $r_m = -0{,}166$, $P < 0{,}05$).

There are two important points to be stressed. (1) The calculation of *Nm*-values of gene flow does not take into account the spatial arrangement of populations. Hence, it is spatially not explicit and disregards any landscape feature. (2) The gene flow estimates presented in the example on English Yew (Fig. 2) are mainly a measure of past processes in the history of populations (Whitlock and McCauley 1999). They are based on population differentiation, which is a result of several processes acting in space *and* time. *Nm*-values are integrals over a certain, but usually unknown time period. This is an important fact, because *Nm*-values refer to historical patterns and do not necessarily reflect current processes. For instance, a molecular-genetic analysis of adults in the remaining populations of a long-lived tree species that recently experienced a substantial decrease in abundance due to habitat fragmentation might still indicate outcrossing and frequent gene exchange among populations. In reality, the populations may currently be characterised by inbreeding and almost complete genetic isolation in the recently fragmented landscape. However, it is the current processes that are most relevant for population persistence and of interest for conservation biologists (Frankham *et al.* 2002).

The present picture: current dispersal and gene flow

Population and ecological geneticists use two principal methodological approaches to refer to current migration and gene flow patterns: (1) progeny analysis (Smouse and Sork 2004) and (2) assignment tests (Manel *et al.* 2005).

In a progeny analysis of the scattered, insect-pollinated Wild Service Tree *(Sorbus torminalis)* in Switzerland by Hoebee *et al.* (WSL, Birmensdorf, unpubl. data), the positions of all adult individuals within a population were mapped and their genotypes determined using highly resolving genetic markers (microsatellites; Frankham *et al.* 2002). These trees represented all potential mates within the sampled area. Open pollinated seeds from several mother trees were then sampled, and the progenies (offspring) also submitted to genetic analysis. From the combined data set, it was possible to determine the fathers that sired the seeds of a given mother tree and to directly calculate current gene flow by pollen (Sork *et al.* 1999). As an example of the results of such a progeny analysis, Figure 3 shows that (1) many fathers, scattered over the ca. 20 ha area, sired the seeds of a chosen mother tree, (2) pollen was transported by insects over several hundred metres and (3) about 30% of the pollen entered the population from outside, i.e. none of the trees within the study population was identified as father. Hence, the amount 30% refers to gene immigration by pollen into the population. Similar results were obtained by Oddou-Muratorio *et al.* (2003, 2004) for a French population of the Wild Service Tree. A review of current gene flow in forest trees is provided by Smouse and Sork (2004).

In another example, Godoy and Jordano (2001) conducted a genetic study of the St. Lucy Cherry *(Prunus mahaleb)*, in which they made use of the fact that not only the genes of the offspring are transported in the seed of plants, but that the seed coat consists of maternal tissue and, thus, carries the genotype of the mother plant. Therefore, the authors trapped bird-dispersed seeds and allocated them to the genotype of their respective mother using a molecular-genetic method (microsatellites). In this way, these authors determined contemporary seed dispersal. In particular, they could also evaluate the potential for long-distance dispersal (as defined as dispersal among populations), which is otherwise difficult to estimate (Ouburg *et al.* 1999). Godoy and Jordano (2001) identified almost 18% of the sampled seeds as long-distance immigrants – an unexpectedly high value. The information gained from such a genetic analysis clearly exceeds that of traditional seed trapping experiments. In the latter, the exact location of the seed sources can often not be identified.
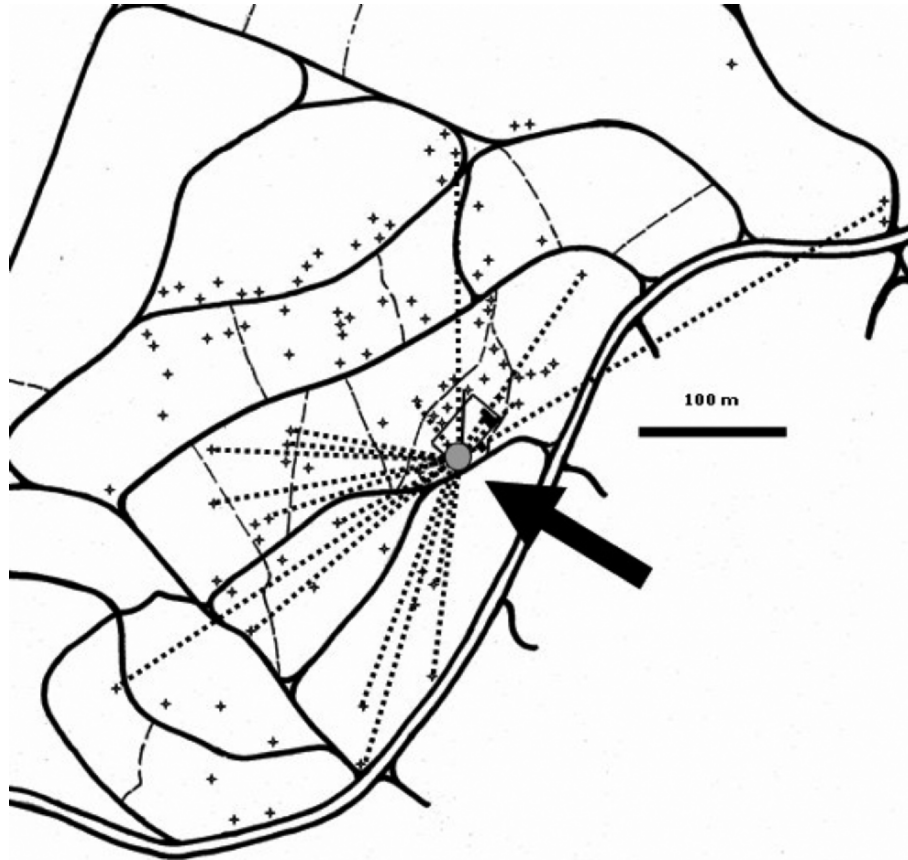
Fig. 3. Contemporary gene flow by pollen in a Swiss population of the Wild Service Tree *(Sorbus torminalis)* as revealed by genetic progeny analysis using microsatellite markers. The grey circle refers to a focal mother tree whose progeny was investigated, crosses refer to adult *S. torminalis* trees, broken black lines connect the mother with the fathers that sired the progeny, and the solid black arrow refers to 30% pollen immigration from outside the investigated population.

The second, widely used approach to infer contemporary migration and gene flow is the application of assignment tests (Rannala and Mountain 1997; Manel *et al.* 2005). Based on its genotype, an individual is probabilistically assigned to the population with which it has the greatest genetic similarity. If it is not assigned to the population from which it had been sampled, it is presumed to be a recent migrant (Frankham *et al.* 2002). Assignment tests require relatively strong genetic differentiation of populations to assign an immigrant individual to a distinct population with high probability, which can be a drawback in empirical studies.

Other methods to infer current gene flow exist. One is the TWOGENER approach, which does not require complete sampling of adult populations (Smouse and Sork 2004; Sork *et al.* 2005). It should also be stressed that for many organisms with minute diaspores such as fungi or lichens, molecular techniques are currently the only methods available that provide reliable estimates of propagule dispersal at the species level (Walser *et al.* 2001).

From the examples given above, it is evident that genetic methods can be used to get real-world estimates of migration, dispersal and gene flow at the landscape level. They may therefore be used to evaluate the ecological relevance of landscape indices of fragmentation or, otherwise, connectivity (Li and Wu 2004). Given the possibility to infer both historical and current patterns of gene flow, population and ecological genetics also offer the possibility to link changes in population connectivity with landscape changes in time (Bürgi *et al*. 2007). For instance, the isolating effect of motorways on wild animals could be estimated by (1) investigating the historical gene flow among populations that are nowadays separated by motorways and (2) by comparing historical gene flow with current gene flow among populations on both sides of the motorways. Corresponding research is conducted on Bobcat *(Lynx rufus)* and Coyote *(Canis latrans)* in California (Riley *et al*. 2004) and on Roe Deer *(Capreolus capreolus)* in Central Europe (Coulon *et al*. 2004; Hindenlang *et al*.; WSL, Birmensdorf, unpubl. data). However, in contrast to what is sometimes suggested by practitioners, population genetics cannot provide absolute measurements of population isolation (Whitlock and McCauley 1999).

Whatever will be: metapopulations

Strictly speaking, a metapopulation can be defined as a group of local populations, partly occupying a set of suitable local habitat patches, showing a turnover of local extinction and re-colonisation in each generation (Baquette 2004). The inclusion of "in each generation" in this definition is important, because it sets the time frame of metapopulation dynamics. By applying this strict definition, real metapopulation dynamics have only been proven for a hand-full of animal species of mainly short generation times such as several butterflies and some amphibians and passerines (Hanski 1998; Baquette 2004). The scientific debate on whether plant species show classical metapopulation dynamics is still continuing (Freckleton and Watkinson 2002; Ehrlén and Eriksson 2003). This is not surprising given the overlapping generation times and the long life span of many plant species (e.g., beyond 100 years for tree species). In plants, metapopulation dynamics have often been indirectly inferred from the genetic structure of populations, in cases where regional processes were shown to overrule local ones (Oddou-Muratorio *et al*. 2001; Hilfiker *et al*. 2004a). However, this genetic inference better fits to a relaxed definition of metapopulations as a group of local populations connected by gene flow (Freckleton and Watkinson 2002). Given the lack of sufficient empirical evidence, the strict metapopulation concept for plants is far from being generally accepted.

A short summary on the present state of the art in metapopulation research including metapopulation genetics could be: there is much theory, simulation and modelling, but little empirical data. What would be needed to prove that a group of populations shows metapopulation dynamics in a strict sense? (1) The suitable habitat of a species must coincide with a network of empty and occupied patches, and the local populations are located in discrete areas. This requires complete field surveys and sound analyses of habitat quality. It is not an easy task to show that a habitat patch is principally suitable but not occupied. In plants, one could achieve this task with seeding and/or transplantation experiments. (2) There must be extinction and re-colonisation events in each generation (Baquette 2004). This calls for long-term demographic data sets that are usually not available and almost impossible to be generated for long-lived species. For instance, metapopulation dynamics of a long-lived tree species could be expected to act within a time frame of several hundred years. Here, the typical solution is to take habitat history as a surrogate of population history using landscape historical methods (Landergott *et al*. 2001; Lindborg and Eriksson 2004;

Bürgi *et al.* 2007). (3) Local population dynamics need to be asynchronous (Baquette 2004) in order to verify that the system under study is not driven by a generally acting intrinsic or extrinsic ecological factor or process other than regional population dynamics. Again, detailed long-term demographic data would be required. (4) Dispersal among local populations has to be shown in each generation. By definition, local populations within metapopulations have to be loosely connected or partially isolated (Frankham *et al.* 2002). To show dispersal (and gene flow by pollen in plants), population genetics comes into play again.

An example is provided by a genetic investigation of an assumed metapopulation of the Water Clover Fern, *Marsilea strigosa,* in a French pond system (Vitalis *et al.* 2002). The classical metapopulation concept assumes that (re-)colonisation of an unoccupied patch takes place by founders form a random sample of all occupied habitat patches in the system. By using microsatellite markers, Vitalis *et al.* (2002) found near-patch recolonisation to be dominant. This leads to a distinct structuring of the genotypes within the assumed pond metapopulation. It thus takes a long time for a gene-variant (allele) to spread over the metapopulation. This rather small-scale dispersal pattern, in contradiction to the classical metapopulation theory, would have been impossible to detect without genetic methods. An overview of population genetics in metapopulation research is provided by Hanski and Gaggiotti (2004).

As Baquette (2004) points out, the metapopulation concept has had a huge conceptual effect on the thinking of both empirical and theoretical ecologists, because it has reorientated their perspectives of the importance of spatial patterns and migration or gene flow among populations. But, perhaps, the importance of the concept lies more in its heuristic value than in practical applications.

Que Sera: An Outlook

A glance at textbooks on landscape ecology shows that issues of population and ecological genetics (including conservation genetics) are either not treated at all (e.g., Turner *et al.* 2001) or treated only in a general way (e.g., Forman 1995). On the other hand, the same could be said about textbooks on population genetics with respect to landscape ecological issues (e. g., Frankham *et al.* 2002). However, the two fields are not as disparate as one might assume at first glance. They often have the same aim, but use different methods or concepts. Most population genetic concepts are at least spatially implicit, and spatial statistics such as autocorrelation analyses are standard methods in population genetics. Investigations of the evolution of species in space and time increasingly apply statistical or modelling approaches from landscape ecology, e.g., kriging (Hoffmann *et al.* 2003). It therefore seems a timely task to incorporate population genetics into landscape ecological studies and vice versa (Holderegger *et al.* in press). Both fields would benefit from this integration. So far, population genetic studies have often investigated single populations below or sets of populations at larger spatial scales beyond a landscape. Spatially explicit genetic investigations at the scale of real landscapes have meanwhile become necessary.

The integration of population genetics and landscape ecology has recently been named landscape genetics by Manel *et al.* (2003; for an extension to landscape genomics see Luikart *et al.* 2003). The field promises to bring population and ecological genetics closer to real-world problems. This asks for a spatially and often also temporarily explicit approach. Landscape ecology can provide the theoretical framework to interpret corresponding spatio-temporal genetic data. Literally, the comparison of isolines exhibiting a spatially explicit measure of habitat fragmentation with "genetic contour lines" based on the genetic differentiation of populations would allow a verification of the effects of dispersal barriers

and/or dispersal corridors. On the other hand, molecular investigations provide independent tests for basic assumptions of landscape ecology (see above). Genetic studies can also be used to infer how historical processes have affected species diversity (Lindborg and Eriksson 2004). An example that integrates habitat quality and population demography in the field, landscape assessment by GIS and testing for historical (from museum specimen) and present population isolation using molecular genetics is given for Capercaillie *(Tetragalus urogallus)* in Suter *et al.* (2007). As shown by this example on an endangered bird species, landscape genetic research needs the collective knowledge of scientists from different fields such as landscape ecology, ecological modelling, biodiversity and population genetics: landscape genetics is cross-disciplinary by definition.

Acknowledgements

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