Chapter 1

INTRODUCTION TO LANDSCAPE GENETICS – CONCEPTS, METHODS, APPLICATIONS

Niko Balkenhol,[1] *Samuel A. Cushman,*[2] *Andrew Storfer,*[3] *and Lisette P. Waits*[4]

[1]*Department of Wildlife Sciences, University of Göttingen, Germany*
[2]*Forest and Woodlands Ecosystems Program, Rocky Mountain Research Station, United States Forest Service, USA*
[3]*School of Biological Sciences, Washington State University, USA*
[4]*Fish and Wildlife Sciences, University of Idaho, USA*

1.1 INTRODUCTION

Genetic variation is considered the most basic level of biological diversity and a prerequisite for the variability of species, populations, and ecosystems (Primack 2014). Diversity at the genetic level is also crucial for the fitness and survival of individuals, the viability of populations, and the ability of species to adapt to environmental change (Allendorf et al. 2012; Frankham et al. 2010). Thus, conserving genetic diversity is important in itself, and researchers in many disciplines, including ecology, evolution, and conservation, are interested in understanding the factors that shape patterns of genetic variation in nature. The foundations for understanding genetic diversity were laid more than 100 years ago (e.g., Hardy 1908; Weinberg 1908; Wright 1917), at which time time, laboratory techniques did not yet allow the actual quantification of genes or DNA (deoxyribonucleic acid, see Chapter 3). Consequently, much of the early work of population geneticists was theoretical and conceptual. This changed after the discovery of the structure of DNA in 1953 by Francis Crick, James Watson, and Maurice Wilkins, and even more so after the development of PCR (polymerase chain reaction) by Kary Mullis in 1983. PCR made it possible to obtain large quantities of DNA even from minuscule samples, and the technique revolutionized many research disciplines, including medicine, forensics, genetic engineering, and population genetics.

Due to these technological advancements, genetic data also became more readily available to ecologists and conservationists, who increasingly realized the tremendous

Landscape Genetics: Concepts, Methods, Applications, First Edition. Edited by Niko Balkenhol, Samuel A. Cushman, Andrew T. Storfer, and Lisette P. Waits.

impact of human activities on biological diversity. In the 1970s and 1980s, genetic factors were recognized to be of fundamental importance for successful conservation strategies (e.g., Frankel 1970, 1974) and genetic diversity was explicitly considered in two of the earliest books on conservation biology (Soulé & Wilcox 1980; Frankel & Soulé 1981). Furthermore, human-caused loss and fragmentation of habitats were determined to be major drivers (e.g., Wilcove et al. 1986) and the ability to move among remaining habitat patches was identified as a key for the long-term conservation of populations and species in fragmented landscapes (e.g., Levins 1969; Hanski 1998). The consequences of changing environments also became a central topic of landscape ecology, which emerged as a scientific discipline in the 1980s (e.g., Naveh & Lieberman 1984; Forman & Godron 1986). Given these almost simultaneous developments in several research areas, it is not surprising that scientists began to combine concepts and methods from population genetics and landscape ecology to assess the influence of environmental heterogeneity on gene flow and genetic diversity (e.g., Pamilo 1988; Merriam et al. 1989; Manicacci et al. 1992; Gaines et al. 1997). Nevertheless, "landscape genetics" did not exist as a research area until it was formally defined in a seminal paper by Manel et al. (2003). This paper stimulated a tremendous interest in the scientific community, so that many novel methods for analyzing landscape genetic data were introduced (e.g., Guillot et al. 2005; Murphy et al. 2008) and the number of published landscape genetic studies grew quickly (reviewed in Holderegger & Wagner 2006; Storfer et al. 2010). Just ten years after its first formal definition, landscape genetics had already contributed substantially to research in ecology, evolution, and conservation (see Manel & Holderegger 2013). Currently, landscape genetics still presents itself as a highly dynamic and rapidly advancing field. New methods are frequently suggested and novel research questions are identified as a result of both conceptual and technological improvements. The rapid growth of landscape genetics is both exciting and motivating, but it is also accompanied by tremendous challenges.

In this introductory chapter, we highlight some of these challenges and explain the rationale for this book and its particular structure. Before doing so, we provide a definition of what we feel constitutes landscape genetics. Furthermore, we provide a simple conceptual framework for landscape genetic analyses, which can be particularly useful for the novice landscape geneticist.

1.2 DEFINING LANDSCAPE GENETICS

Most readers of this book will already know that landscape genetics combines landscape ecology and population genetics. This is certainly correct, but is also not very specific or precise. To better understand landscape genetics, it is worthwhile to define the field more clearly. Three commonly used definitions of landscape genetics are shown in Table 1.1.

In the original definition of Manel et al. (2003) the focus was on "microrevolutionary processes", which can be measured using genetic data. Thus, the

Table 1.1 Overview of definitions of landscape genetics.

Reference	Definition of landscape genetics*	Analytical consequence
Manel et al. (2003), page 189	[Landscape genetics . . .] aims to provide information about the interaction between landscape features and **microevolutionary processes, such as gene flow, genetic drift and selection.**	Need to quantify mircoevolutionary processes
Holderegger and Wagner (2006), page 793	[. . .] landscape genetics endorses those studies that combine population genetic data, adaptive or neutral, with data on **landscape composition and configuration, including matrix quality.**	Need to quantify landscape heterogeneity
Storfer et al. (2007), page 131	[. . .] research that **explicitly quantifies the effects** of landscape composition, configuration and [or] matrix quality on gene flow and [or] spatial variation.	Need to explicitly test for landscape-genetic relationships

* Bold emphases are ours.

emphasis of this definition lies on the population genetic aspects of landscape genetics, but was not very specific about the 'landscape features' to be included in the analyses. The definition was extended by Holderegger and Wagner (2006) who clarified that landscape heterogeneity can be measured in terms of landscape composition, configuration and/or matrix quality (see Chapter 2 for explanations of these terms). Holderegger and Wagner (2006) also noted that landscape genetics can be conducted using different types of genetic data and that appropriate analyses and correct inferences depend strongly on whether the data is adaptive (i.e., under selection) or not (i.e., neutral; see also Holderegger et al. 2006). Finally, Storfer et al. (2007) highlighted that landscape genetics needs to quantitatively link landscape and genetic data to explicitly test for landscape-genetic relationships. This aspect is particularly important, because it allows landscape genetics to move beyond descriptive studies that visually assess spatially coinciding patterns in genetic and landscape data, towards quantitative models that make it possible to predict the genetic consequences of environmental change (e.g., Jay et al. 2012, Wasserman et al. 2012).

Putting these three definitions together, we can define landscape genetics as *research that combines population genetics, landscape ecology, and spatial analytical techniques to explicitly quantify the effects of landscape composition, configuration, and matrix quality on microevolutionary processes, such as gene flow, drift, and selection, using neutral and adaptive genetic data.*

1.3 THE THREE ANALYTICAL STEPS OF LANDSCAPE GENETICS

The definitions provided above lead to a simple conceptual framework for landscape genetic data analysis. Specifically, three general steps are necessary to reach the goals of landscape genetics (see last column in Table 1.1). First, we have to measure genetic variation so that we can quantify the miroevolutionary processes we are interested in. This step relies heavily on population genetic approaches and involves the description of the genetic composition of individuals or populations sampled across space – see Chapters 3, 7, and 9 for details.

Second, we have to quantify landscape heterogeneity so that we can capture the composition, configuration, and/or matrix quality of the study landscape – see Chapters 2 and 8. Third, we have to statistically link landscape heterogeneity and genetic variation, so that we can explicitly and quantitatively test for landscape–genetic relationships (Chapters 5 and 10).

Note that the order of steps one and two is not crucial and could be reversed. For example, in this book the chapter on landscape ecology (Chapter 2) precedes the chapter on population genetics (Chapter 3) because we felt that it is often more sensible to first think about the landscape and its characteristics and next think about the genetic processes occurring in that landscape for a particular study species. In reality, the two steps will ideally be considered simultaneously, as only this will lead to optimal study design and strong inferences (Chapter 4).

Obviously, this three-step framework simplifies actual landscape genetics studies, because many decisions have to be made during all steps, because analytical choices in one step will affect options for another step, and because some methods actually combine multiple steps within a single analysis. Thus, finding optimal combinations of methods for all three steps and for the specific research questions, study landscape and species is not trivial and is unlikely to be covered by a single, cookbook-style recipe. Nevertheless, viewing landscape genetics in terms of the three basic analytical steps can help tremendously when designing a landscape genetic study and when trying to navigate through the thick jungle of landscape genetic methods. Thus, we encourage readers to keep this simple framework in mind when working through the other chapters of this book.

1.4 THE INTERDISCIPLINARY CHALLENGE OF LANDSCAPE GENETICS

Regardless of what definition of landscape genetics is used, they all highlight the fact that the field combines multiple, usually autonomous disciplines. Consequently, landscape genetics is often described as "interdisciplinary". However, the simple combination of various research approaches, concepts, and theories does not necessarily constitute true interdisciplinarity. Specifically, the level of integration across the various disciplines involved determines whether a scientific field is multidisciplinary, interdisciplinary, or transdisciplinary (e.g., Morse et al. 2007). A multidisciplinary field involves various disciplines that address a research topic collaboratively, but still rely on their traditional disciplinary approaches and paradigms.

Thus, answers to the research question are often found within involved disciplines and overall conclusions are drawn by comparing and combining results obtained from the different research approaches.

In an interdisciplinary field, the research should be much more coordinated among the different disciplines. This coordination involves the standardization of vocabulary, mutually defined research questions and study design, and the synchronization of conceptual frameworks used in each discipline. Addressing a topic through interdisciplinary research should lead to knowledge that impacts all of the involved disciplines. Thus, research that creates new disciplinary knowledge by simply addressing a question through an unusual analytical approach "borrowed" from some other discipline is not really interdisciplinary.

Finally, in a transdisciplinary field, disciplinary boundaries no longer exist, as research approaches from formerly distinct disciplines are fully integrated into a single conceptual framework. This framework involves all aspects of research, from problem definition and study design to actual data analysis and interpretation of results. Importantly, transdisciplinary research should lead to new ways of thinking about a problem and thus to the development of novel theories and research areas.

In our opinion, not all current landscape genetic research is truly interdisciplinary. While we are beginning to develop analytical and conceptual frameworks specifically for landscape genetics (e.g., Wagner & Fortin 2013; Chapter 5), many landscape genetics methods are still borrowed from other disciplines and usually focus on a single analytical step at a time. Various barriers to truly interdisciplinary research exist, with two of the most substantial ones being (a) the difficulties of effectively communicating across different disciplines and (b) the lack of experts that have received enough training across involved disciplines to close communicative gaps and overcome disciplinary boundaries. This is definitely also the case for landscape genetics.

Currently, very few researchers possess the background knowledge and skills to be experts in all of the subjects involved in landscape genetics. Most scientists to date have received disciplinary training and are either experts in landscape ecology, or population genetics, or spatial data analysis, but not in all three areas. This kind of complementary expertise may not even be available within a single university, and very few academic curricula include a comprehensive combination of population genetics, landscape ecology, and spatial quantitative data analysis (Wagner et al. 2012). Thus, for many students, the only options thus far for learning about the different components of landscape genetics is either to attend a landscape genetics seminar (see Wagner et al. 2012), or to read the many, often very brief and rather technical, published papers on landscape genetics. In our experience, the latter is often not very efficient, because of the rapid developments in the field and because papers are usually targeted towards a specific audience for which a certain level of preexisting knowledge on the topic can safely be assumed. For example, it is not necessary to explain the term "genotype" in a genetics journal or to explain the term "spatial grain" in a landscape ecological journal. However, for the beginning landscape geneticist, unknown technical terms, methods, and concepts used in landscape genetic publications often add up to a substantial mass of ambiguity or even confusion. Furthermore, readers without adequate background knowledge might be able to redo the analysis presented in a certain paper, but it will be unlikely that they will be able to critically evaluate the study and make significant contributions to the advancement of the field. Hence, short-term progress in landscape genetics depends on collaborations among disciplinary experts that know enough about all aspects of landscape genetics to effectively communicate with each other, evaluate published studies, and identify existing limitations and possible improvements (Cushman 2014). Similarly, the long-term future of the field depends on providing sufficient training opportunities for the next generation of landscape geneticists.

1.4.1 The two scopes of landscape genetic research

In addition to these challenges,which are quite typical for any interdisciplinary field, landscape genetics is also based on approaches that can be used for quite different purposes. Specifically, we currently see at least two major research avenues that are followed in landscape genetics. On the one hand, there are those studies that are interested in understanding how landscape characteristics affect microevolutionary processes. These studies follow the original idea of landscape genetics as defined by Manel et al. (2003) and are interested in genetic variation itself. Researchers following this avenue often have a background in genetics or evolutionary biology and are currently especially interested in using genomic approaches in landscape genetics (see Chapter 9).

On the other hand, there are those studies that are not interested in genetic variation or microevolution in itself, but rather use genetic data to infer underlying ecological processes, such as dispersal or disease transmission. Researchers following this research avenue are usually trained in ecology, and increasingly try to combine landscape genetics with other field methods, such as mark-recapture or telemetry (e.g., Cushman & Lewis 2010).

These different scopes of research further complicate the interdisciplinary nature of landscape genetics, simply because someone interested in evolutionary questions will emphasize different data types and methods compared to someone investigating ecological questions. Clearly, ecological and evolutionary processes and resulting population dynamics and biodiversity patterns are often strongly intertwined (e.g., Hairston et al. 2005, Palkovas & Hendry 2010), and landscape genetics has tremendous potential for untangling the relative roles of ecology and evolution in shaping biological patterns (e.g., Wang et al. 2013). However, it will be difficult to realize this potential if researchers interested in evolution neglect the data and methods provided by ecologists or if ecologists shy away from using the novel data and tools developed by geneticists. Thus, to realize the potential of landscape genetics for eco-evolutionary research, we need to maintain and strengthen the communication and collaboration among different disciplines, and ideally provide a reference baseline as a starting point for future developments in the field.

Overall, learning about, applying, and improving landscape genetics remains a challenging task because of the multiple, highly diverse disciplines involved in the field and because of the different research foci in the field.

1.5 STRUCTURE OF THIS BOOK – CONCEPTS, METHODS, APPLICATIONS

With this book, we aim to facilitate the first steps of learning about landscape genetics. We envisage the book as a guide for anybody wanting to learn about the field, as a tool for facilitating interdisciplinary communication and collaboration, and as a primer for disciplinary experts wanting to teach classes on landscape genetics at their home institutions. Ultimately, we also hope that the book with serve as a baseline for critical discussions about landscape genetics and become a starting point for future advancements.

To reach these goals, we structured chapters in this book into three interrelated parts, each reflecting a slightly different purpose. Chapters in the first part deal with *Concepts* in a broad sense. These chapters serve as an introduction to the three major steps involved in landscape genetics research and are intended for readers with little or no experience in landscape genetics. These textbook-style chapters obviously include introductions to landscape ecology (Chapter 2) and population genetics (Chapter 3), as the two most fundamental disciplines involved in landscape genetics. In addition, this first section includes a chapter on the basics of landscape genetic study design (Chapter 4) and on the spatial analytical approaches for statistically linking landscape and genetic data (Chapter 5). While these latter two chapters are again quite fundamental, they include aspects we hope will be interesting and novel even for more experienced landscape geneticists.

Chapters in the second part of the book deal with *Methods* and are more in-depth treatments of certain topics that we currently deem particularly important. These chapters are intended for the advanced reader who is interested in the technical details of specific analytical approaches. This second part includes a chapter on landscape genetic simulation modeling (Chapter 6), because simulations hold tremendous potential for advancing landscape genetic methods and theory development. Genetic assignment and clustering methods are among the most commonly used approaches for quantifying genetic structure (analytical step 1) and are therefore covered separately in Chapter 7. Similarly, resistance surfaces are often used to quantify landscape heterogeneity in landscape genetic studies (analytical step 2), so they are treated in detail in Chapter 8. Chapter 9 then deals with genomic approaches that are increasingly used to generate large quantities of genetic data. These approaches are highly valuable for (adaptive) landscape genetics, especially because they can separte the patterns and processes of neutral markers genetic data from markers under selection. Chapter 10 introduces graph theory and network approaches, as these are increasingly used in both landscape genetics and genomics.

The third part of the book contains chapters that summarize *Applications* of landscape genetics in different systems. This section includes a chapter on landscape influences on plant population genetics (Chapter 11), a chapter on landscape genetic applications for understanding connectivity in terrestrial animals (Chapter 12), and a chapter on landscape genetic approaches for aquatic systems (Chapter 13).

Finally, in Chapter 14, we highlight some of the conclusions contained in the preceding chapters, identify emerging challenges and offer suggestions for future research and development needs in landscape genetics. Throughout the book, bold italics indicate terms that are described in the Glossary.

1.5.1 Limitations and potential of this book

The structure of the book, with the combination of introductory-level chapters and quite advanced discussions of certain topics, is rather unusual. However, we believe that this structure reflects the actual situation of contemporary landscape genetics. On the one hand, we still lack a single source of information that covers all of the required basics for interested beginners. On the other hand, certain – mostly analytical – aspects of landscape genetics have advanced rapidlly and are already too complex to be dealt with in a basic manner. Closing the void between the basics and advanced applications in a single book is obviously very challenging. We are aware of the limitations of this book and have no doubt that for many disciplinary experts, the basic chapters will not be as detailed or as all-embracing as they could be. For example, much more could be said about landscape ecology and about population genetics, respectively. As pointed out above, the intention of the book is not to replace the excellent textbooks on these disciplines (e.g., Allendorf et al. 2012; Turner et al. 2010) but rather to provide beginners with first introductions to the respective topics. These introductions will obviously not convert readers into experts, but they should enable beginners to (a) gain a sufficient overview of the disciplines involved and provide a starting point for further explorations; (b) better understand and critically evaluate published landscape genetic studies; and (c) more effectively communicate about landscape genetic research with experts from different disciplines.

Similarly, the advanced chapters provide more details on certain methods and are mostly intended for readers interested in actually applying these methods. The goal of these chapters is to provide guidance to identify common pitfalls and the most crucial assumptions, advantages, and limitations of different approaches. Finally, the three application chapters illustrate that landscape genetic methods can be used in a variety of circumstances and for different research questions. However, these three chapters are not intended to provide syntheses or even comprehensive reviews of the current state-of-the-art in landscape genetics. The field is already too diverse to allow for full reviews of all studies falling under the grand umbrella of landscape genetics. At the same time, the field may be too nascent for extensive syntheses. Nevertheless, the three application chapters should generate many ideas and motivate readers to apply or improve landscape genetic approaches for their own research.

Overall, we realize that the book is limited. Readers who desire a single source that covers all of the aspects involved in landscape genetics in a basic, yet detailed and application-relevant manner, will likely be disappointed. We hope that the book will nevertheless provide a useful overview and first starting point for learning about landscape genetics.

How successful this book will be in reaching its goals will largely depend on its readers, on their willingness to move towards truly interdisciplinary research, and on their motivation for advancing landscape genetics beyond its current state. Hence, we look forward to the feedback and discussion this book will generate and its impact on the future development of landscape genetics toward an inter- or even transdisciplinary field.

REFERENCES

Allendorf, F. W., Luikart, G.H., & Aitken, S.N. (2012) *Conservation and the Genetics of Populations*. Wiley-Blackwell, Oxford.

Cushman, S. A. (2014). Grand challenges in evolutionary and population genetics: the importance of integrating epigenetics, genomics, modeling, and experimentation. *Frontiers in Genetics*, **5**, 197.

Cushman, S. A. & Lewis, J. S. (2010) Movement behavior explains genetic differentiation in American black bears. *Landscape Ecology* **25**, 1613–25.

Forman, R.T.T. & Godron, M. (1986) *Landscape Ecology*. John Wiley and Sons, Inc., New York.

Frankel, O.H. (1970) Sir William Macleay memorial lecture 1970: variation – the essence of life. *Proceedings of the Linnean Society of New South Wales* **95**, 158–69.

Frankel, O.H. (1974) Genetic conservation: our evolutionary responsibility. *Genetics* **78**, 53–65.

Frankel, O.H. & Soulé, M.E (1981) *Conservation and Evolution*. New York: Cambridge University Press, New York.

Frankham, R., Ballou, J.D., & Briscoe, D.A. (2010) *Introduction to Conservation Genetics*. Cambridge University Press, New York.

Gaines, M.S., Diffendorfer, J.E., Tamarin, R.H., & Whittam, T.S. (1997) The effects of habitat fragmentation on the genetic structure of small mammal population. *Journal of Heredity* **88**, 294–304.

Guillot, G., Mortier, F., & Estoup, A. (2005) Geneland: a program for landscape genetics. *Molecular Ecology Notes* **5**, 712–15.

Hairston, N.G., Ellner, S.P., Geber, M.A., Yoshida, T., & Fox, J.A., (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters* **8**, 1114–27.

Hanski, I. (1998) Metapopulation dynamics. *Nature* **396**, 41–9.

Hardy, G.H. (1908) Mendelian proportions in a mixed population. *Science* **28**, 49–50.

Holderegger, R. & Wagner, H.H. (2006) A brief guide to landscape genetics. *Landscape Ecology* **21**, 793–6.

Holderegger, R., Kamm, U., & Gugerli, F. (2006) Adaptive vs. neutral genetic diversity: implications for landscape genetics. *Landscape Ecology* **21**, 797–807.

Jay F., Manel S., Alvarez N., Durand, E.Y., Thuiller, W., Holderegger, R., Taberlet, P., & Francois, O. (2012) Forecasting changes in population genetic structure of Alpine plants in response to global warming. *Molecular Ecology* **21**, 2353–68.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**, 237–40.

Manel, S. & Holderegger, R. (2013) Ten years of landscape genetics. *Trends in Ecology and Evolution* **28**, 614–21.

Manel, S., Schwartz, M.K., Luikart, G., & Taberlet, P. (2003) Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology and Evolution* **18**, 189–97.

Manicacci, D., Olivieri, I., Perrot, V., Atlan, A., Gouyon, P.H., Prosperi, J.M., & Couvet, D. (1992) Landscape ecology: population genetics at the metapopulation level. *Landscape Ecology* **6**, 147–59.

Merriam, G., Kozakiewicz, M., Tsuchiya, E., & Hawley, K. (1989) Barriers as boundaries for metapopulations and demes of *Peromyscus leucopus* in farm landscapes. *Landscape Ecology* **2**, 227–35.

Morse, W.C., Nielsen-Pincus, M., Force, J., & Wulfhorst, J. (2007) Bridges and barriers to developing and conducting interdisciplinary graduate-student team research. *Ecology and Society* **12**, 8. [online] URL: http://www.ecologyandsociety.org/vol12/iss2/art8/.

Murphy, M.A., Evans, J.S., Cushman, S.A., & Storfer, A. (2008) Representing genetic variation as continuous surfaces: an approach for identifying spatial dependency in landscape genetic studies. *Ecography* **31**, 685–97.

Naveh, Z. & Lieberman, A.S. (1984) *Landscape Ecology – Theory and Application*. Springer, New York.

Palkovacs, E.P. & A.P. Hendry (2010) Eco-evolutionary dynamics: intertwining ecological and evolutionary processes in contemporary time. *F1000 Biology Reports* **2**, 1.

Pamilo, P. (1988) Genetic variation in heterogeneous environments. *Annales Zoologici Fennici* **25**, 99–106.

Primack, R.B. (2014) *Essentials of Conservation Biology*. Sinauer Associates, Inc., Sunderland.

Soulé, M.E. & Wilcox, B. (1980) *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer Associates, Inc., Sunderland.

Storfer, A., Murphy, M.A., Evans, J.S., Goldberg, C.S., Robinson, S., Spear, S.F., Dezzani, R., Delmelle, E., Vierling, L., & Waits, L.P. (2007) Putting the "landscape" in landscape genetics. *Heredity* **98**, 128–42.

Storfer, A., Murphy, M.A., Spear, S. F., Holderegger, R., & Waits, L.P. (2010) Landscape genetics: Where are we now? *Molecular Ecology* **19**, 3496–514.

Turner, M.G., Gardner, R.H., & O'Neill, R.V. (2010) *Landscape Ecology in Theory and Practice: Pattern and Process*. Springer, New York.

Wagner, H.H. & Fortin, M.-J. (2013) A conceptual framework for the spatial analysis of landscape genetic data. *Conservation Genetics* **14**, 253–61.

Wagner, H., Murphy, M., Holderegger, R., & Waits, L. (2012) Developing an interdisciplinary, distributed graduate course for 21st century scientists. *BioScience* **62**, 182–8.

Wang, I. J., Glor, R.E., & Losos, J.B. (2013) Quantifying the roles of ecology and geography in spatial genetic divergence. *Ecology Letters* **16**, 175–82.

Wasserman, T.N., Cushman, S.A., Shirk, A.S., Landguth, E.L., & Littell, J.S. (2012) Simulating the effects of climate change on population connectivity of American marten (*Martes americana*) in the northern Rocky Mountains, USA. *Landscape Ecology* **27**, 211–25.

Weinberg, W. (1908) Über den Nachweis der Vererbung beim Menschen. *Jahreshauptversammlung des Vereins für Vaterländische Naturkdunde in Württemberg* **64**, 369–82.

Wilcove, D.S., McLellan, C.H., & Dobson, A.P. (1986) Habitat fragmentation in the temperate zone. In: Soulé, M.E. (ed.), *Conservation Biology: Science of Scarcity and Diversity*. Sinauer Associates, Inc., Sunderland.

Wright, S. (1917) Color inheritance in mammals. *Journal of Heredity* **8**, 224–35.