

On applications of landscape genetics

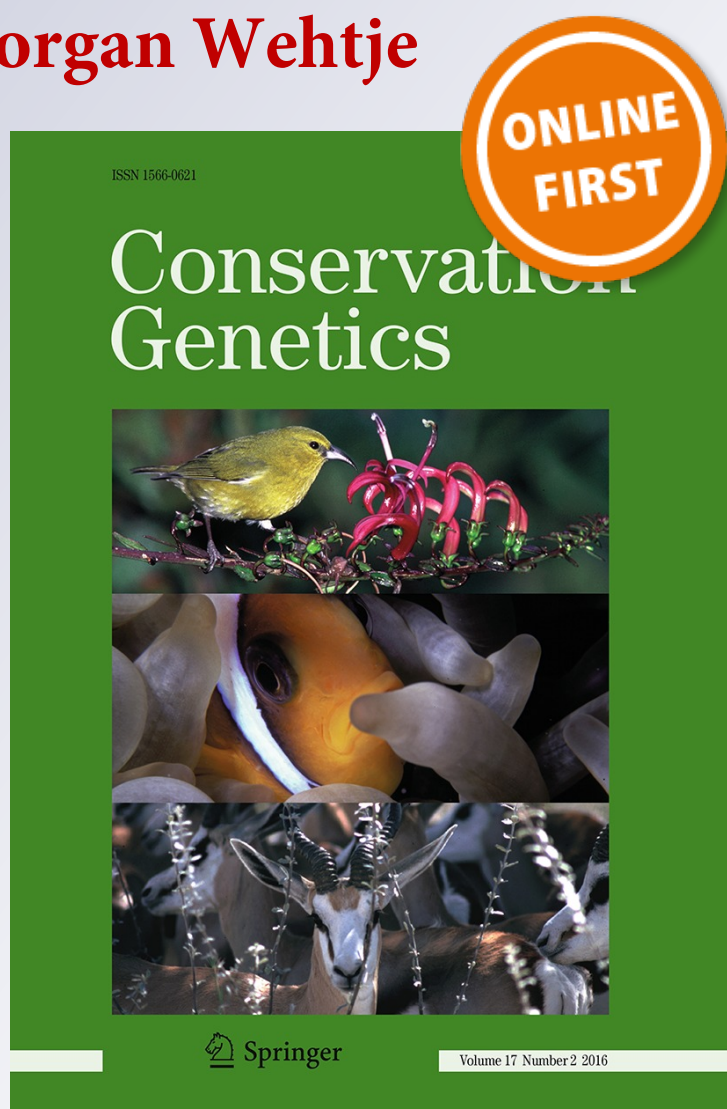
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On applications of landscape genetics

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Abstract Recent assertions in the literature (e.g., Keller et al. 2015) suggest that landscape genetic research has been infrequently applied by practitioners. We were interested to test this assertion, which is difficult to assess, since applications may not be detectable through searches of peer-reviewed literature. Producing publications may not be a goal of practitioners. We developed a method to search the internet for evidence of research applications and evaluated 25 different research fields in the natural sciences. We found that fields with more publications also had more applications, but the field of landscape genetics was less applied than expected based on the number of peer-reviewed publications—only about 4 % of landscape genetics articles were applied. In fact, all research fields in genetics or evolutionary biology were under-applied compared to ‘whole organism’, ecological research fields. This result suggests the lack of applications in landscape genetics may be due to a systemic under-application of genetics research, perhaps related to a lack of understanding of genetics by practitioners. We did find some evidence of landscape genetic applications however, which we sorted into 5 categories: (1) identification of evolutionarily significant units for conservation, (2)

managing pathogens and invasive species, (3) natural heritage systems planning, (4) assessing population status, and (5) restoration of populations.

Keywords Application · Gray literature · Landscape genetics · Peer review · Policy · Practitioner · Web scraping

Introduction

Landscape genetics combines landscape ecology and population genetics to address questions about the spatial ecology of populations. Manel et al. (2003) defined the field as having two key steps, which are “the detection of genetic discontinuities and the correlation of these discontinuities with landscape and environmental features such as barriers”. The first peer-reviewed articles to use the phrase “landscape genetics” were published in the early 2000s (e.g., Saenz-Romero et al. 2001; Morris et al. 2002; Costello et al. 2002; Manel et al. 2003), and since that time, the discipline has grown in concert with the increasing availability of genetic data and the development of analytical methods.

Landscape genetics has been championed as a useful tool for many conservation applications, given the insight that can be gained about population structure and contemporary movement and gene flow patterns (Manel et al. 2003; Segelbacher et al. 2010). Indeed, it has been a discipline permeated by applied research questions from the outset. Therefore, it is useful to ask whether landscape genetic research is actually being applied in practice. Although some authors have taken the position that ‘few landscape genetics studies have been used by practitioners’ (e.g., Keller et al. 2015), we had the impression from closely working with practitioners that this was not the case, and that landscape genetic findings are being widely applied in a variety of ways. Applications can be

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difficult to review however, because, as Keller et al. (2015) noted, many applications are described in gray literature, rather than being published in peer-reviewed journals, and are therefore not available in typical academic databases. As such, we considered it difficult to rigorously evaluate applications of landscape genetics. Our objectives were to develop a method for evaluating the frequency of research applications, and to apply this method to review real-world applications of landscape genetics research.

Evaluating the frequency of research applications

We considered that the frequency with which the research of any particular field is applied can only be evaluated in comparison to other, similar fields. Therefore, one needs to

evaluate the extent of applications in a number of fields simultaneously. To accomplish this, we selected 25 different research fields in the natural sciences, and searched Web of Science for the number of unique, peer-reviewed journal articles published in each field (Table 1). We then sought to determine whether each of these fields was more or less represented by applications than might be expected.

The number of applications arising from any particular research field is difficult to quantify, since it involves summarizing a nearly infinite, hard-to-define pool of possible sources (e.g., gray literature). We considered that the best way to approach this problem was to develop an index of applications that approximated the true value. Since we suspected that governments would be a major source of applications of landscape genetics and other research fields in the natural sciences, we sought to review government use of research. We

Table 1 The number of peer-reviewed journal articles published in various research fields, and the year of origin of the field

Research field	Number of studies ^a	Year ^b	Proportion applied ^c
Capture-mark-recapture	813	1950	0.07
Community ecology	2662	1922	0.06
Conservation biology	3106	1936	0.15
Disease ecology	479	1938	0.13
Ecosystem management	2759	1953	0.15
Ecosystem services	7902	1930	0.09
Epigenetics	14,017	1892	0.03
Ethnoecology	122	1942	0.17
Evolutionary biology	3026	1866	0.05
Genomics	35,781	1844	0.05
Island biogeography	1060	1944	0.09
Landscape ecology	2332	1954	0.14
Landscape genetics	879	1984	0.04
Metapopulation	5482	1965	0.09
Molecular biology	28,892	1932	0.05
Molecular epidemiology	10,880	1955	0.05
Natural history	57,158	1800	0.06
Phylogeography	10,302	1958	0.03
Population genetics	14,306	1868	0.05
Predator–prey theory	57	1969	0.33
Primatology	324	1902	0.06
Radio telemetry	1755	1925	0.11
Remote sensing	45,623	1938	0.09
Restoration ecology	695	1962	0.11
Wildlife management	2144	1890	0.15

^a The number of studies was estimated through a Web of Science search conducted in November 2015. Quotes were placed around the field name, as in “Island biogeography”

^b Year of origin for each field was estimated using Google’s Ngram Viewer, which searched the corpus of English literature for occurrences of the research field name. We considered the first occurrence to be the year of origin. Due to limitations of the Ngram viewer, we did not search prior to 1800, and therefore, we underestimated the age of the field “Natural history”, which we arbitrarily assigned our earliest value of 1800. This had no substantive effect on our subsequent results

^c Estimated as proportion of titles published in each research field that were cited in a search of national or sub-national government web sites

developed a web-scraping algorithm to search government web sites for the titles of peer-reviewed research articles arising from our Web of Science search of the different fields in the natural sciences. We were able to search all web sites with “.gov”, “.gouv”, or “.gc” in the URL, allowing us to review the public web sites from 161 different national governments along with numerous additional sub-national governments (see Appendix 1 in supplementary material for detailed methods). We limited our search to PDF documents, so that if a title showed up in any PDF document it was identified. This would have occurred for example, if the title was cited in a report that was posted in PDF format to a government web site. We used the number of Web of Science article titles from each research field appearing on government web sites as our index of applications.

We observed a positive relationship between the number of peer-reviewed articles from research fields indexed on Web of Science, and the number of titles from these articles found on government web sites (Fig. 1; $R^2 = 0.90$). The strong relationship suggests that generally, more peer-reviewed publications are associated with more applications.

The number of applications might also be influenced by the age of the field, such that newer fields have fewer applications. We used Google's Ngram Viewer (<http://books.google.com/ngrams>) to determine the age of each research field, which we estimated by the year the phrase first appeared in the corpus of English books (Table 1). There was a negative relationship between the number of applications of research fields and the estimated year of origin of the field ($F = 6.12$; $df = 1, 23$; $P = 0.021$; slope [SE] = -0.007 [0.003]; intercept [SE] = 14.40 [5.38]; $R^2 = 0.21$). Variation explained by age

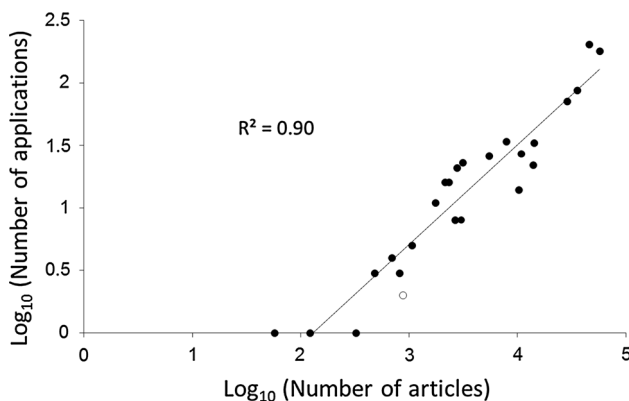


Fig. 1 An ordinary least-squares regression comparing the number of peer-reviewed articles in 25 different research fields in the natural sciences to the number of applications of that research ($F = 213$; $df = 1, 23$; $P < 0.0001$; slope [SE] = 0.80 [0.05]; intercept [SE] = -1.69 [0.19]). Variables are on a \log_{10} scale. The number of articles was estimated from a Web of Science search carried out in November 2015. Applications were estimated as the number of titles from each research field that were located in a search of the web pages of different national or sub-national governments, also carried out during November 2015. The *open symbol* is landscape genetics

of field was redundant with number of articles however (Appendix 2 in supplementary material), as there was also a negative relationship between number of articles and age of field ($F = 7.36$; $df = 1, 23$; $P = 0.012$; slope [SE] = -0.009 [0.0003]; intercept [SE] = 20.49 [6.27]; $R^2 = 0.24$). Therefore, we retained only number of articles for further analysis.

We used residuals from the linear regression between the number of Web of Science articles and the number of applications to determine whether research fields were applied more or less often than expected (Fig. 2). Landscape genetics had a negative residual, confirming that, as suggested by Keller et al. (2015), landscape genetics has been applied less than might be expected.

Reviewing applications of landscape genetics research

Although we found that landscape genetics had relatively few applications, we note that there were still a number of titles that appeared to be applied. Our Web of Science search for “landscape genetics” revealed 879 journal articles, and we detected 37 of these titles in our search of government web sites (4 %). We reviewed the uses of each of these 37 titles, in order to (1) validate our index of applications, and (2) learn more about the ways that landscape genetics has been applied. We found that 22 of the titles had been used in 56 different applications (Appendix 3 supplementary material). Some papers were not used at all, but were associated with government sites for spurious reasons, whereas several papers were used more than once. There was a taxonomic bias in applied papers. We found that while 32 % of applications involved mammals, there was only 1 plant application, and there were no applications involving birds (Appendix 3 supplementary material). From this selection of papers, we identified 5 different categories of landscape genetic applications: (1) identification of evolutionarily significant units for conservation, (2) managing pathogens and invasive species, (3) natural heritage systems planning, (4) assessing population status, and (5) restoration of populations (Table 2; Fig. 3). We describe and give examples of each category below. Some of the examples we provide for each category were uncovered by our web-scraping search, whereas other examples were found through additional literature review.

Identification of evolutionarily significant units for conservation

Landscape genetics studies are used in the identification of evolutionarily significant units (or ESUs) for conservation planning. ESUs are populations at or below the species-level

Fig. 2 Residuals from an ordinary least-squares regression between the number of peer-reviewed articles in different research fields from the natural sciences, and the number of research applications from each field. The number of articles was estimated from a Web of Science search carried out in November 2015. Applications were estimated as the number of titles from each research field that were located in a search of the web pages of different national or sub-national governments, also carried out during November 2015. Variables were \log_{10} -transformed prior to regression. Negative residuals indicate fewer applications than expected based on the number of articles, whereas positive residuals imply the opposite

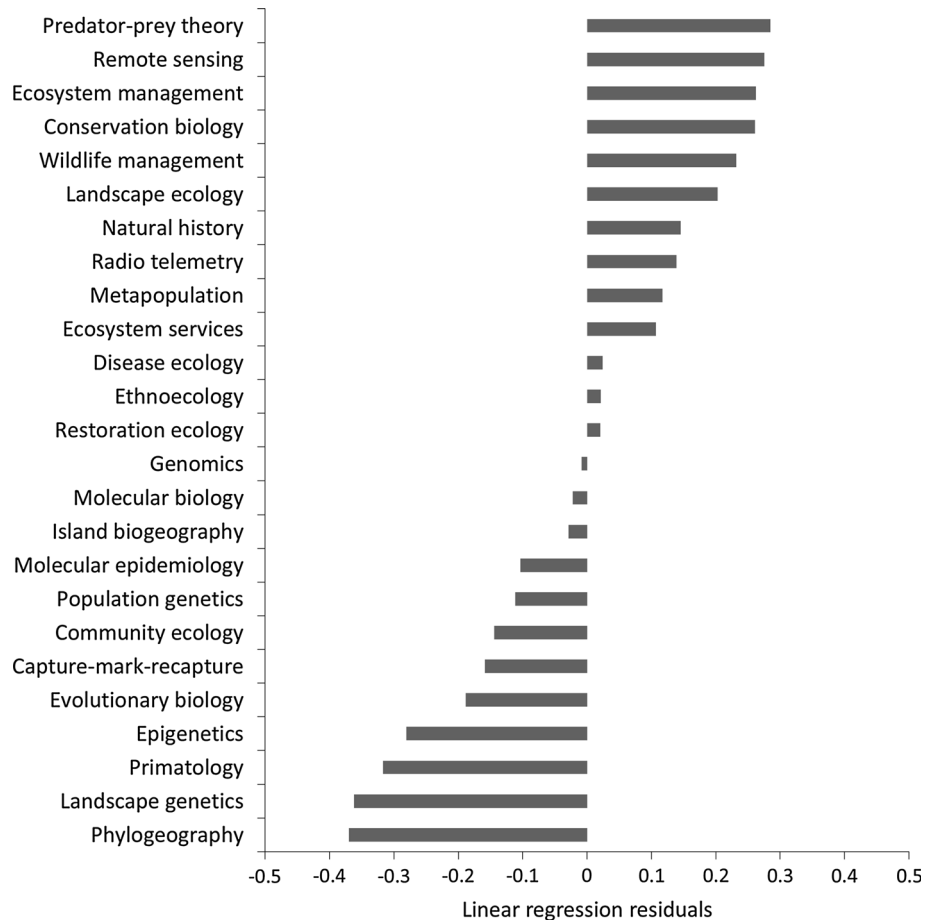


Table 2 Five different kinds of landscape genetic applications to real-world problems

Category of application	Example	Source
1. Identification of evolutionarily significant units for conservation	Identifying designatable units in Canada and distinct population segments in the USA	United States Fish and Wildlife Service and National Oceanic and Atmospheric Administration (1996); Schwartz et al. (2009); COSEWIC (2011); Ethier et al. (2012); Mee et al. (2015)
2. Managing pathogen and invasive spread	Identifying barriers to spread of chronic wasting disease and rabies	Blanchong et al. (2008); Cullingham et al. (2009); DeYoung et al. (2009); Root et al. (2009); United States Department of Agriculture (2010); Cullingham et al. (2011); Walsh and Samuel (2012)
3. Natural heritage systems planning	Connecting Indian tiger populations; maintaining connectivity of bighorn sheep populations	Epps et al. (2007); Sharma et al. (2013); Gubbi et al. (2015); United States Department of the Interior (2015)
4. Assessing population status	Harvest management of wildlife species, such as black bears and grizzly bears; stock assessments of marine species	Ontario Ministry of Natural Resources (2009); B.C. Ministry of Forests, Lands and Natural Resource Operations (2012); Hunter et al. (2012); Proctor et al. (2012); Spies (2012); Howe et al. (2013); A'mar and Palsson (2014); United States Fish and Wildlife Service (2014)
5. Restoration of populations	Identifying insularity, barriers, and opportunities for genetic rescue	Hagerty and Tracy (2010); United States Department of the Interior (2013)

that are considered distinct for the purposes of conservation. In Canadian and American endangered species legislation, these are referred to as designatable units (DU) and distinct populations segments (DPS), respectively. In both cases,

genetic distinctiveness is cited as a factor that can be used to classify a population as a DU or a DPS (United States Fish and Wildlife Service and National Oceanic and Atmospheric Administration 1996; Green 2005; COSEWIC 2013).

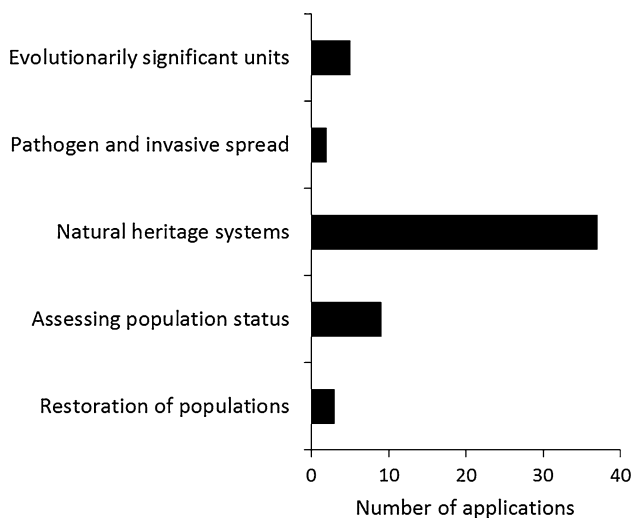


Fig. 3 Five different categories of landscape genetic applications, based on a search for peer-reviewed research articles on the web pages of national or sub-national governments. We found 22 different papers that were used in 56 different applications

It is standard for species-at-risk status reports in Canada to include a section on DUs, which usually includes references to population and landscape genetics studies on the species if available. For example, in the 2012 status report on American badger (*Taxidea taxus*), the decision was made to split the previously recognized *T. t. jeffersonii* DU into western and eastern populations on either side of British Columbia's Selkirk Mountains, based on evidence that the mountains restricted gene flow (Ethier et al. 2012). Evidence from landscape genetics studies was also used extensively in the restructuring of DUs for caribou (*Rangifer tarandus*; COSEWIC 2011 and references therein) and is currently being used to clarify DUs for lake whitefish (*Coregonus* spp.) and prioritize these DUs for conservation (Mee et al. 2015). In the United States, the work of Schwartz et al. (2009) on the landscape genetics of the wolverine (*Gulo gulo*) was cited in the decision to recommend listing the wolverine in the contiguous United States as a DPS separate from Canadian and Alaskan wolverines (United States Fish and Wildlife Service 2010). Reasons for this decision included restricted gene flow caused by a lack of suitable habitat, creating a distinct break between Canadian and American populations, and the genetic distinctiveness of wolverines in the contiguous United States.

Managing pathogen and invasive spread

Landscape genetics is also used to measure how landscape structure affects the rate and direction of spread of pathogens and invasive species. Researchers have found

relationships between landscape properties and spatial risk of disease spread (Blanchong et al. 2008; Cullingham et al. 2009; Kelly et al. 2010; Cullingham et al. 2011) and species invasion (Estoup and Guillemaud 2010; Estoup et al. 2010), using genetics to assess movement. Applications of landscape genetics have included the management of chronic wasting disease (CWD) in cervids (Blanchong et al. 2008; Cullingham et al. 2011). For example, the surveillance strategy for CWD in the state of Wisconsin, USA, is based on CWD spatial risk inferred from white-tailed deer (*Odocoileus virginianus*) genetics and habitat barrier analysis (Walsh and Samuel 2012). In addition, the United States federal government suggests that surveillance strategies for CWD should account for the relationship between landscape features and the movement and behaviour of cervids, which can be achieved using landscape genetic methods (Walsh and Samuel 2012). Similarly, landscape genetics has been applied in the management of the spread of rabies (Cullingham et al. 2009; DeYoung et al. 2009; Johnson et al. 2009; Root et al. 2009; United States Department of Agriculture 2010). The US government has used genetics to identify physical barriers that prevent rabies spread (Johnson et al. 2009) and identified movement behaviors that can be used to improve baiting strategies for their oral rabies vaccination program (Root et al. 2009).

Natural heritage systems planning

Landscape planning often aims to establish connected populations or ecosystems, which are thought to be more resilient than unconnected systems (Mumby and Hastings 2008). Landscape genetics is a useful technique for evaluating connectivity, due to its ability to measure contemporary gene flow (Manel et al. 2003), and genetic techniques have been used many times for this purpose (e.g., McRae and Beier 2007; Schwartz et al. 2009). In one example, landscape genetics was applied to evaluate a natural heritage system in India. Degraded corridors between protected areas were shown to have reduced gene flow for tigers, *Panthera tigris* (Sharma et al. 2013), but an expanded network of protected areas was created to increase connectivity for tiger populations (Gubbi et al. 2015). In another case, landscape genetics has provided important insight for the maintenance of habitat connectivity of the Desert Bighorn sheep, *Ovis canadensis*. For example, the U.S. Bureau of Land Management has used inference about gene flow from Epps et al. (2007) as part of the rationale for amending the planned development of a solar project, to mitigate effects on sheep connectivity (United States Department of the Interior 2015).

Assessing population status

Traditional population genetic measures have long been used to characterize the structure of populations in relation to landscape features. For example, measures such as allelic richness may be affected by landscape conditions (e.g., Koen et al. 2014). Recently, landscape genetics studies have also been used in various kinds of population assessments, including stock assessments of the Pacific cod (*Gadus macrocephalus*) and the Antillean subspecies of the manatee (*Trichechus manatus*) (Spies 2012; Howe et al. 2013; United States Fish and Wildlife Service 2014; A'mar and Palsson 2014).

Over the past decade improvements in genetic sampling and analysis techniques have established the use of genetic markers as a valid identification unit in genetic capture-mark-recapture analyses. In Ontario, Canada, for example, genetic tagging, spatially explicit capture-recapture, and a landscape stratification were used to develop a provincial population estimate for black bears (*Ursus americanus*) (Howe et al. 2013) which has been used as a cornerstone of the provincial bear management plan (Ontario Ministry of Natural Resources 2009). Similar methods have been used for estimating bear abundance in other jurisdictions, including British Columbia, Canada (BC Ministry of Forests, Lands and Natural Resources Operations 2012; Proctor et al. 2012).

Restoration of populations

Population reintroduction and translocation programs have also used landscape genetic information. According to the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) guidelines, the “rescue” of a declining population or species involves the “immigration of gametes or individuals that have a high probability of reproducing successfully, such that extirpation or decline of a population, or some other DU, can be mitigated” (COSEWIC 2010). Such rescue effects often take the form of a “genetic rescue”, where the low genetic diversity and poor fitness of a population or subspecies can be mitigated and even increased by the introduction of unrelated and genetically diverse individuals (Tallmon et al. 2004). Efforts for genetic rescue also often involve some degree of landscape consideration. For example, individuals inhabiting ecologically similar habitats (or populations with which gene flow once occurred) are often chosen for translocations into at risk populations in order to maintain locally adapted traits and avoid maladaptation (e.g., the Florida panther Pimm et al. 2006). In a more recent example, landscape genetic information about distinctiveness and barriers to gene flow for the Mojave desert tortoise, *Gopherus*

agassizii (Hagerty and Tracy 2010), has been used in the development of translocation plans for the species (United States Department of the Interior 2013). Thus, the use of landscape genetic research has been successfully integrated into conservation management, and even allowed for the restoration of declining populations or species at risk.

Discussion

We were interested to investigate applications of landscape genetics because our perception differed from recent suggestions that research in the field ‘has not been used by practitioners’ (Keller et al. 2015), and we considered that there was a lack of data to evaluate this idea. We did find in our review that landscape genetics was used less often than expected based on the number of publications in the field. To increase the rate of application of landscape genetics by practitioners, Keller et al. (2015) mostly focused on technical suggestions, such as improvements to data analysis. Our analysis showed however, that all genetic research fields were less applied than expected (Fig. 2), suggesting that technical aspects of implementing landscape genetics do not underlie the limited applications. Instead, we speculate that there is a systemic reason why research in genetics and evolutionary biology are poorly applied compared to more ‘whole-organism’, ecological fields. Thus, our findings may also help to explain the relatively low translation of genomics to conservation practice highlighted by Shafer et al. (2015). They argued that scientific and policy-practitioner communities operate in different spheres, and that a gap exists between these spheres. Our results suggest that the gap is bigger for genetics research fields than other fields in the natural sciences. It may be that practitioners do not have the expertise or understanding to take best advantage of available research tools and data, in which case it may be incumbent on geneticists to demonstrate the practical application of their research (Hoban et al. 2013). Shafer et al. (2015) point out however, that the gap between science and policy may be maintained through a lack of career incentives and financial resources that limit the ability of scientists to engage fully in applied research. This does not explain the bias in applications across research fields however, which suggests that increased emphasis on communication of research tools and findings by geneticists appears warranted.

Genetics research may also be more easily applied where a direct link can be made between research findings and a policy or management action (e.g., Baskerville 1997). Ravetz (1987) referred to this as usable knowledge. For example, the concept of an evolutionarily significant unit is enshrined in endangered species legislation in Canada as a DU, which is explicitly defined with respect to genetic distinctiveness. Therefore, landscape genetics may

often be a suitable tactic to gather information for many endangered species assessments according to the Canadian legislation (e.g., Mee et al. 2015). For landscape genetics to be used in conservation policy and management, studies must be designed such that they address policy and management knowledge gaps or hypotheses, reducing uncertainty, and contributing to the policy cycle (Baskerville 1997; Folke et al. 2004).

Despite the lower than expected number of applications, we do not want to overlook that we found a number of landscape genetic applications in our review, so research from the field is being applied, if at a slow rate. We were able to sort the landscape genetic applications into 5 categories (Table 2), of which those related to establishing natural heritage systems were the most frequently applied. These were generally studies of landscape connectivity. We considered DNA forensics (e.g., Wasser et al. 2008) as a possible 6th category but did not observe any applications of this field in our review of the gray literature.

Conclusions

We developed a method to search for applications of research on government web sites, and used this review to evaluate the frequency of applications of different research fields in the natural sciences. Overall, we found that landscape genetics, like other genetics fields, was applied less than expected based on the number of peer-reviewed publications in the field. Given that all genetics fields were under-applied, we suggest that the effect may be due to a systemic issue in application of genetics research, rather than being due to a shortcoming of landscape genetics in particular. The gap in applications may be due to lack of understanding by practitioners of the relevance of genetics research. In other cases, it may be that the research is designed in such a way that it has low policy or management relevance.

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