

1 **How to bring genetic diversity to the forefront of conservation policy and management**

2

3 Sean M Hoban, Heidi C Hauffe, Sílvia Pérez-Espona, Giorgio Bertorelle, Katie Frith, Oscar  
4 Gaggiotti, Peter Galbusera, A Rus Hoelzel, Richard Nichols, Craig Primmer, Gernot  
5 Segelbacher, Hans R Siegismund, Marjatta Sihvonen, Critiano Vernesi, Carles Vilà, the  
6 ConGRESS Consortium\*, and Michael W Bruford

7 \*José Godoy, Pim Arntzen, Isa-Rita Russo, Josef Bryja

8

9

## 10 INTRODUCTION

11 The contribution of genetic diversity to the maintenance of species and habitat diversity  
12 (Struebig 2011), and to fundamental ecosystem processes (e.g. pollination, decomposition, soil  
13 fertility; Hughes et al. 2008) is now widely recognized by the conservation community. Genetic  
14 diversity is also appreciated as an essential component of ecosystem resilience and the  
15 capacity for species to adapt in changing and challenging environments (Sgro *et al.*, 2011).  
16 Furthermore, genes from adapted wild populations can contribute desired traits (e.g. drought  
17 tolerance, disease resistance) to cultivated plants and livestock, helping to reduce conventional  
18 inputs (e.g., irrigation, chemical pesticides) and ensure long-term food security. Genetic  
19 resources also contribute billions of dollars to pharmaceutical and biotechnology industries.  
20 However, it is estimated that genetic resources are being depleted by 2-4.5 trillion US  
21 dollars/year globally (ten Brink et al. 2009). The message is clear: if sufficient within-species  
22 genetic diversity is not conserved, the ecological and economic effects will be widespread and  
23 catastrophic.

24 In recognition of the importance of the genetic component of biodiversity, the Convention on  
25 Biological Diversity has for the first time included consideration of genetic diversity with the Aichi  
26 Targets, in the 2010 revised Strategic Plan for Biodiversity (<http://www.cbd.int/sp/>). Specifically,  
27 Target 13 states that, by 2020, (1) “*the genetic diversity of cultivated plants and farmed and*  
28 *domesticated animals and of wild relatives, including other socio-economically as well as*  
29 *culturally valuable species is maintained*”, and (2) “*strategies have been developed and*  
30 *implemented for minimizing genetic erosion and safeguarding their genetic diversity.*” It is a  
31 bold, explicit goal to minimize near-term loss as well as put in place plans to ensure genetic  
32 variation is secure for the future. While the target primarily emphasizes domesticated species,  
33 its wording could and should be interpreted to also require conservation of genetic resources of  
34 any species providing benefits to humans via cultural, provisioning, recreational, or other  
35 ecosystem services, or species that helps ensure the stability or resilience of natural systems  
36 intimately connected to human society. Achieving these objectives will require an array of *in-*  
37 *situ* and *ex-situ* conservation initiatives such as habitat restoration and managing exposure to  
38 selection (Lankau *et al.*, 2011), and achievable targets and indicators for measuring progress.  
39 Genetic tools, which can rapidly obtain various ecological information, will surely serve multiple  
40 Aichi targets (Santamaría & Méndez 2012).

41 Designing, executing and monitoring appropriate actions to preserve and protect genetic  
42 biodiversity will in turn require a stronger foundation of genetic knowledge and capabilities  
43 among all parties, a foundation that is currently weak. Indeed, Frankham (2010) highlighted  
44 insufficient genetic training of decision makers as a major challenge in conservation genetics  
45 today (though knowledge varies extensively among countries). At minimum, decision-makers  
46 should have knowledge regarding the value of genetic biodiversity, basic genetic topics and  
47 concerns, what questions genetic tools can and can't answer, and how to access more  
48 information and form partnerships. Clear, practical and engaging dissemination of well-  
49 established genetic tools and topics, and their applications in conservation biology, is  
50 prerequisite to sound policy and management. Equally, conservation genetics experts and  
51 translational researchers should understand and participate in policy-making processes, and  
52 offer direct support to managers (Osmond *et al.*, 2010), but this connection is rare. Of 1646  
53 articles published in the journal Conservation Genetics since its inception in 2000, 408 (24.8%)  
54 contained the term "management" and a scant 13 (0.8%) mentioned "policy."

55 Several recent initiatives (the United States Fish & Wildlife Service Genetic Monitoring for  
56 Managers [http://alaska.fws.gov/gem/mainPage\\_1.htm](http://alaska.fws.gov/gem/mainPage_1.htm), the Knowledge Exchange Project  
57 <http://www.shef.ac.uk/aps/research/ke>, and the Conservation Genetic Resources for Effective  
58 Species Survival Project, ConGRESS, <http://www.congressgenetics.eu>) address the challenge  
59 to facilitate application of knowledge from past and present conservation genetic research.  
60 These initiatives recognize that for many situations we already have sufficient genetic data to  
61 make specific recommendations, that much important knowledge has not been made accessible  
62 beyond the scientific community, and as a consequence, decisions and policies are not based  
63 on the best available information. Better interpretation, presentation, and integration are  
64 needed (knowledge mobilization), but this cannot be accomplished by a review article or book  
65 written with only the scientific community in mind. To reach policy makers and managers,  
66 material must be interactive, attractive, participatory, and in non-technical language. These  
67 efforts use multiple vehicles to share information including simple, narrative explanations of  
68 fundamental genetic processes; accessible definitions for technical vocabulary; suggestions as  
69 to when conservation genetics may and may not be useful for conservation problems (including  
70 case studies); practical tools for making decisions using genetic data; and most importantly,  
71 forums and contact-lists to encourage partnerships between researchers and non-researchers.  
72 Such partnerships are envisioned as flexible networks that embrace the views and needs of

73 local stakeholders and decision makers, and promote bidirectional learning (Smith *et al.*, 2009).  
74 These features distinguish several emergent biodiversity networks: the US Fish & Wildlife  
75 Conservation Genetics Community of Practice  
76 (<http://www.fws.gov/ConservationGeneticsCOP/>), the European Union Biodiversity Knowledge  
77 Network (<http://www.biodiversityknowledge.eu/>), and the European Wildlife Network  
78 (<http://europeanwildlife.net/>). The goals of such communities are to establish communication  
79 links, broaden perspectives, facilitate information exchange and training, ensure that diverse  
80 interests are represented, and identify and bridge knowledge gaps. In doing so, these initiatives  
81 facilitate Aichi Target 16, a mandate that genetic resources benefits can be accessed and fairly  
82 shared by all, and Target 19, which mandates broad sharing and application of biodiversity  
83 knowledge.

84 A challenge that such efforts face is that knowledge-sharing and capacity-building must be  
85 focused and efficient in synthesizing and simplifying knowledge in a way that non-academic  
86 parties can absorb and use (Osmond *et al.*, 2010). Generally, policy makers and managers are  
87 not and do not want to be geneticists. In general, they are unable to intensively read the  
88 scientific literature (Laurance *et al.*, 2012), due to scientific terminology, time constraints, and  
89 difficulties in finding and accessing appropriate publications. Thus in spite of a wealth of data  
90 generation from geneticists, much important data is dispersed, inaccessible or misunderstood.  
91 Within Europe, a further challenge is varying needs and priorities among many nations, which  
92 makes efforts to find common ground especially important.

### 93 **SURVEY**

94 Given current policy-drivers and emerging opportunities and challenges for the use of genetics  
95 in conservation, an assessment of the current state of applied conservation genetics is timely.  
96 Focal questions include: What is the current level of knowledge, capabilities, and interests of  
97 managers, and what actions are being performed? What are key topics and concerns to which  
98 conservation geneticists should focus to make scientific results usable, and possibly direct  
99 future research? To assess genetic knowledge and application in European biodiversity  
100 conservation, ConGRESS distributed a simple questionnaire during 2010 and 2011, receiving  
101 131 responses from ten nations (Belgium, Spain, Finland, France, Germany, Italy, Netherlands,  
102 Portugal, Sweden, UK), covering governmental and non-governmental organizations, with a  
103 range of experience and education. This was not a systematic survey, and may suffer some

104 bias in the returns. We use survey results to discuss some current directions, challenges and  
105 opportunities for the European conservation genetics community.

106 The first question assessed the current reach of conservation genetics, relative to its potential.  
107 We found that almost half of respondents (42%) had never participated in, used data from or  
108 commissioned a genetic study. However, nearly all respondents (94%) would use genetic  
109 information if they perceived that it was available to them. We can infer that, in spite of only  
110 moderate incorporation or consideration of genetic data up to now, there is a high level of  
111 interest in, and recognition of, its potential utility in conservation decision-making. Therefore,  
112 while genetics has only very recently been a primary consideration in policy at the European  
113 and global level, individual practitioners are aware of its importance and anticipate using  
114 genetics if tools, funding, and partnerships are made available.

115 Respondents who had implemented or commissioned a conservation genetics project, were  
116 asked to specify the study topic. Three main topics were identified (c. 40% of responses): 1)  
117 identifying units for conservation (15%), 2) monitoring individuals and populations over time  
118 (11%, including invasive species), and 3) species identification and clarification (13%). The  
119 popularity of these topics may relate to their relevance to EU policy directives, among other  
120 reasons. The first two are applications that can strongly contribute to selection and  
121 maintenance of Natura 2000 sites, the European network of nature conservation areas  
122 (<http://ec.europa.eu/environment/nature/natura2000/>) which conservation managers have been  
123 involved in identifying. The second and third are relevant to protecting and monitoring particular  
124 species as specified under Articles 11, 12 and 13 of the Habitats Directive  
125 (<http://ec.europa.eu/environment/nature/legislation/habitatsdirective/>). Species identification  
126 also contributes to policing actions, such as enforcing CITES (the Convention on International  
127 Trade in Endangered Species, <http://www.cites.org/>). Thus there appears to be a good match  
128 between the current most common uses of genetics in management and relevant directives,  
129 implying that these topics can be directly used in the current policy arena. Another likely reason  
130 for the popularity of these topics is that they have a large empirical and theoretical body of work,  
131 and increasingly powerful and practical molecular and statistical tools for clarifying species  
132 boundaries; monitoring and assessing genetic biodiversity with ancient samples, environmental  
133 DNA, and DNA barcoding; and prioritizing populations for protection.

134 The next most common topics reported by respondents who had applied genetics to their  
135 conservation projects were those of quantifying population size (6%), measuring inbreeding  
136 (4%), connectivity (7%), and hybridization (5%). Such questions focus on population  
137 vulnerability, and response to recent environmental changes. A substantial interest in these  
138 topics suggests that practitioners understand that genetics concerns affect population and  
139 species' viability, and this in turn may reflect recognition of the importance of long-term  
140 population viability for determining 'favorable conservation status' (FCS), a central concept in  
141 the biodiversity legislation of the European Union (Laikre *et al.*, 2009). Viability and connectivity  
142 are topics that managers and policy makers may be already familiar with, so they represent  
143 easy "entry points" for networking.

144 Several less frequently reported topics included assignment/parentage (4%) and local  
145 adaptation (1%), indicating that some practitioners are already aware of and using specific and  
146 technical applications, sometimes including recent molecular advances. This awareness may  
147 provide collaboration opportunities; practitioners that are already experienced in genetics could  
148 be key partners in recruiting and teaching others. Some managers and policy makers will be  
149 more familiar with conservation genetics as a tool rather than a concern, while others may have  
150 the opposite experience. This provides a potential opportunity to show that powerful genetic  
151 tools can reveal a wide variety of ecological information (Frankham 2010). For less common  
152 topics and tools it may be especially important to use case studies to illustrate the importance of  
153 the issue and the solutions that genetic tools provide.

154 The second question concerned potential future uses of genetics. Responses largely  
155 overlapped with current uses, with similar emphasis on identifying conservation units,  
156 monitoring, and species identification but a greater emphasis on assessing habitat connectivity.  
157 A challenge here is to maintain and enhance awareness of emerging tools (e.g., ancient and  
158 environmental DNA, genomics, simulation software), and demonstrate applications and case  
159 studies, while simultaneously avoiding information-overload. It is also important to reiterate that  
160 general measurements of genetic diversity (e.g. differentiation levels) are a first step in other  
161 applications (e.g., population assignment, forensics, certification), emphasizing the need to  
162 adequately organize, archive and share samples and data for future projects. Another emerging  
163 use of genetics is to establish baseline genetic diversity measures against which future  
164 comparisons can be made to demonstrate decline or recovery (Jackson *et al.* 2011).

165 **DIRECTIONS**

166 We now discuss some overall challenges and opportunities regarding genetic tools,  
167 partnerships, and applications.

168 *Genetic tools*

169 One challenge in connecting conservation genetic tools and topics to management and policy is  
170 to explain the power and utility of highly technical tools, while simultaneously promoting and  
171 ensuring proper use. What can be done? First, it is important to clearly delineate what genetics  
172 tools and techniques can and cannot do for conservation management, to avoid making  
173 promises beyond our capabilities, while highlighting instances of good practice. In addition,  
174 scientists can organize training workshops for those without experience in genetics who wish to  
175 begin genetic-based studies (Anthony *et al.*, 2012). Next, case studies can be used to help  
176 practitioners understand the process of applying a genetic tool to a management objective  
177 (*sensu* Weeks *et al.* 2011). Then geneticists can promote proper use by sharing cautions and  
178 suggestions, such as the NCEAS/NESCent Working Group on Genetic Monitoring sampling  
179 guidelines (Jackson *et al.* 2011). To do so, it is important to delineate appropriate sampling  
180 schemes and other requirements to obtain relevant data, such as by evaluating tools and  
181 techniques with simulations and empirical data (Hoban *et al.*, 2012). As Frankham cautions,  
182 “*the burgeoning development of methods has outstripped the quality control processes.*”

183 At the same time, conservation geneticists should recognize the activities, needs, and pressures  
184 of practitioners, which may not match our perceived priorities. What is academically exciting  
185 (e.g., cutting-edge technology) will not always have high practicality or necessity. Further, the  
186 role of the conservation geneticist and the manager of natural resources are different.  
187 Conservation geneticists may aim to understand population dynamics and risks, but managers  
188 will make and implement decisions, balancing various practical concerns. In explaining and  
189 recommending genetic methods, scientists might consider focusing on study avenues that have  
190 a high benefit/cost ratio.

191 *Partnerships*

192 We suggest closer and more constant collaborations with local managers, from sourcing  
193 research questions to interpreting results to clearly translating results into specific applications

194 (Knight *et al.*, 2008). Geneticists can also help in reviewing project proposals and reports, and  
195 evaluating post-project success. These consultancies would be relatively simple for genetics  
196 experts, would save public spending on projects by ensuring optimal design and interpretation,  
197 and would build trust and partnerships between academics and practitioners (possibly leading to  
198 collaborations that are mutually beneficial). Each collaborator or stakeholder maintains his/her  
199 expertise while learning and profiting from the other (complementary expertise, shared samples  
200 and funds, publicity). Networking is needed not only between scientists and managers, but also  
201 among in-situ and ex-situ conservationists for integrated species management (Lacy, 2012).  
202 One requirement to achieve fruitful partnerships is more flexible timelines and a wider variety of  
203 funding mechanisms to match these kinds of investigations (weeks or months to genotype  
204 samples for a poaching investigation, many years for monitoring).

205 As participation in conservation genetics broadens, a concomitant challenge will be to explain  
206 basic genetic concepts (e.g., mutation, connectivity) in a simple, memorable manner without  
207 complex vocabulary (e.g. the coalescent, Bayesian). In addition, conservation geneticists must  
208 accept and confront the fact that disagreements exist about some central conservation genetics  
209 topics within the community (Pertoldi *et al.*, 2007), e.g.: the best options for managing  
210 hybridization, if and when to use translocations, criteria for selecting protected sites,  
211 evolutionary significant units, and what defines a species. Disagreements within the research  
212 community about the role of genetics, the solutions it provides, and confidence in the tools are  
213 important discussions to advance the field, but scientific debate traditionally makes non-  
214 specialists and policy-makers wary or uncomfortable. A key challenge is to emphasize the  
215 issues where there is near universal agreement and the tools that have been validated in many  
216 cases, while working towards resolving existing disagreements to avoid confusion among policy  
217 and management professionals (Frankham, 2010).

### 218 *Applications*

219 Scientists must also have courage to offer strong, science-based advice, even if it is imperfect.  
220 Lankau et al (2011) and Weeks et al. (2011) are two examples of management-directed  
221 syntheses of current knowledge combined with practical recommendations. The first provides  
222 practical suggestions to incorporate evolutionary thinking in policy and management strategy,  
223 especially to enhance and accelerate adaptation to climate change. The second provides a  
224 review of evidence regarding translocations, a decision tree to help guide when to apply it, and



225 a set of translocation case studies. They both stress that while desired outcomes may not be  
226 assured, the chance of a good outcome can be facilitated with appropriate guidance and tools.  
227 Conservation genetic scientists should also examine the potential management and policy  
228 implications of their work, especially before beginning a particular study, in order to produce  
229 knowledge and understanding that will truly be applied to the issue or species in question.  
230 Howes et al. (2009) propose a decision key to assist evaluation of the “conservation merit of  
231 genetics research questions,” and demonstrate its use with several case studies.

232 The main challenge is to spread available knowledge *now*. This requires increased  
233 understanding by the conservation geneticist community of the policy-making process, socio-  
234 economic issues, and awareness of management resource limitations. If we want the  
235 conservation community to consider and incorporate genetics, we as geneticists must  
236 appreciate the practical concerns- political, social, and economic. Those members of the  
237 conservation genetics community who are able can take initiative to provide consultation  
238 services for decision makers, or become directly involved in policy discussions, which may be  
239 especially effective at local levels (Smith *et al.*, 2009). Scientific input is also needed at the EU  
240 level- Santamaría & Méndez (2012) highlight numerous policies in which genetic aspects could  
241 be considered (e.g., the Sustainable Hunting Initiative, reformation of the EU Fisheries Policy).  
242 These publicly available proposals are an opportunity to introduce genetic aspects and highlight  
243 case studies closely linked to human society (e.g., forensics, zoos, urban species, iconic wild  
244 species). As individual action is challenging, another solution is that scientific societies (e.g.,  
245 Society for Conservation Biology) are increasingly involved in policy discussions, position  
246 statements, and funding policy training.

247 Another instrument for engagement is the systematic review, which identifies and synthesizes  
248 all available knowledge relating to a particular research question (examples at  
249 <http://www.environmentalevidence.org/>). Communities like ConGRESS, and larger interface  
250 organizations (e.g., <http://www.spiral-project.eu/>), are also central. Scientists rarely become  
251 policy experts but can work and interact with lawyers, political scientists, economists and  
252 decision makers (Smith *et al.*, 2009). Also, biologists who are just beginning post-graduate  
253 education may enroll in emerging transdisciplinary programs that immerse students in policy,  
254 communication, formal logic, ethics/philosophy, and science. Lastly, as academic labs are  
255 constrained by funding organization priorities (high impact publications, novel results) and  
256 timelines, it is also imperative to create and fund applied conservation genetics laboratories

257 (governmental or non-governmental) whose mandate is to gather, translate and disseminate  
258 genetic information about key species and ecosystems. Examples of such efforts include the  
259 Molecular Ecology team of the US National Marine Fisheries Service  
260 (<http://swfsc.noaa.gov/textblock.aspx?Division=FED&id=902>), the Institute of Forest Genetics of  
261 the US Forest Service (<http://www.fs.fed.us/psw/locations/placerville/>), the Wildgenes  
262 Laboratory of the Royal Zoological Society of Scotland ([http://www.rzss.org.uk/research/applied-](http://www.rzss.org.uk/research/applied-conservation-genetics)  
263 [conservation-genetics](http://www.rzss.org.uk/research/applied-conservation-genetics)), and the Canadian Forest Gene Conservation Association  
264 (<http://www.fgca.net>).

265 In conclusion, policy makers and managers already possess some awareness of the relevance  
266 of genetic concepts and tools in many areas of conservation. Conservation geneticists can  
267 become more aware of the policy and management implications of their work by: identifying key  
268 genetic issues, considering conservation applications while formulating research questions,  
269 forming partnerships in planning and executing projects, and clearly defining the contribution  
270 that we expect genetics to make and its connections to other data and issues. An especially  
271 open and necessary research direction is to better evaluate the economic and ecological value  
272 of genetic resources and define exactly the services that genetic diversity provides to society  
273 and the planet (ten Brink et al. 2009), including but certainly not limited to monetary valuation.  
274 Of course, integration of genetic benefits into environmental decision-making will require much  
275 more extensive theoretical research and empirical quantification of the role of genetics in  
276 ecosystem stability, as relatively few examples exist (Cardinale *et al.*, 2012). We may bemoan  
277 the fact that genetic information and tools are underused and underappreciated, but they will  
278 remain so until we clearly demonstrate their practical application.

279

## 280 REFERENCES

- 281 Anthony NM, Mickala P, Abernethy KA, Atteke C, Bruford MW, Dallmeier F, *et al.* (2012).  
 282 Biodiversity and conservation genetics research in Central Africa: new approaches and  
 283 avenues for international collaboration. *Conservation Genetics Resources* 4: 523–525.
- 284 ten Brink P, Berghöfer A, Schröter-Schlaack C, Sukhdev P, Vakrou A, White S, *et al.* (2009).  
 285 TEEB–The economics of ecosystems and biodiversity for national and international policy  
 286 makers.
- 287 Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, *et al.* (2012). Biodiversity  
 288 loss and its impact on humanity. *Nature* 486: 59–67.
- 289 Frankham R (2010). Challenges and opportunities of genetic approaches to biological  
 290 conservation. *Biological Conservation* 143: 1919–1927.
- 291 Hoban S, Bertorelle G, Gaggiotti OE (2012). Computer simulations: tools for population and  
 292 evolutionary genetics. *Nature Reviews Genetics* 73: 2–14.
- 293 Howes BJ, Pither R, Prior KA (2009). Conservation implications should guide the application of  
 294 conservation genetics research. *Endangered Species Research* 8: 193–199.
- 295 Hughes AR, Brian DI, Marc TJJ, Nora U, Mark V (2008). Ecological consequences of genetic  
 296 diversity. *Ecology Letters* 11: 609–623.
- 297 Jackson J a., Laikre L, Baker CS, Kendall KC (2011). Guidelines for collecting and maintaining  
 298 archives for genetic monitoring. *Conservation Genetics Resources* 4: 527–536.
- 299 Knight AT, Cowling RM, Rouget M, Balmford A, Lombard AT, Campbell BM (2008). Knowing  
 300 but not doing: Selecting priority conservation areas and the research–implementation gap.  
 301 *Conservation Biology* 22: 610–617.
- 302 Lacy RC (2012). Achieving true sustainability of zoo populations. *Zoo Biology* 13: 1–13.
- 303 Laikre L, Nilsson T, Primmer CR, Ryman N, Allendorf FW (2009). Importance of genetics in the  
 304 interpretation of Favourable Conservation Status. *Conservation Biology* 23: 1378–81.
- 305 Lankau R, Jørgensen PS, Harris DJ, Sih A (2011). Incorporating evolutionary principles into  
 306 environmental management and policy. *Evolutionary Applications* 4: 315–325.
- 307 Laurance WF, Koster H, Grooten M, Anderson AB, Zuidema PA, Zwick S, *et al.* (2012). Making  
 308 conservation research more relevant for conservation practitioners. *Biological Conservation*  
 309 153: 164–168.
- 310 Osmond DL, Nadkarni NM, Driscoll CT, Andrews E, Gold AJ, Allred SRB, *et al.* (2010). The role  
 311 of interface organizations in science communication and understanding. *Frontiers in*  
 312 *Ecology and the Environment* 8: 306–313.

- 313 Pertoldi C, Bijlsma R, Loeschcke V (2007). Conservation genetics in a globally changing  
314 environment: present problems, paradoxes and future challenges. *Biodiversity and*  
315 *Conservation* 16: 4147–4163.
- 316 Santamaria L, Mèndez PF (2012). Evolution in biodiversity policy—current gaps and future  
317 needs. *Evolutionary Applications* 5: 202–218.
- 318 Sgro CM, Lowe AJ, Hoffmann AA (2011). Building evolutionary resilience for conserving  
319 biodiversity under climate change. *Evolutionary Applications* 4: 326–337.
- 320 Smith RJ, Verissimo D, Leader-Williams N, Cowling RM, Knight AT (2009). Let the locals lead.  
321 *Nature* 462: 280–281.
- 322 Struebig MJ (2011). Parallel declines in species and genetic diversity in tropical forest  
323 fragments. *Ecology Letters* 14: 582–590.
- 324 Weeks AR, Sgro CM, Young AG, Frankham R, Mitchell NJ, Miller KA, *et al.* (2011). Assessing  
325 the benefits and risks of translocations in changing environments: a genetic perspective.  
326 *Evolutionary Applications* 4: 709–725.
- 327