Supplemental materials for "The relevance of genetic structure in ecotype designation and conservation management"

Supplemental Table S1. Ecotype criteria reported across taxa in a literature review of 112 publications from a Web of Science search for "ecotype AND conservation AND management". Several studies reported multiple criteria for ecotype. One study considered plants and invertebrates, and three (simulation/review) were not specific to any taxon. No records were found for amphibians.

Taxa (n*)	Behaviour	Diet/trophic	Genetic	Habitat use	Phenology	Phenotype	Other†	Reference
		level	differentiation					number§
Birds (4)	0	0	3	0	0	2	1	1-4
Fish (32)	14	4	27	20	5	18	3	5-36
Invertebrates (10)	3	2	0	6	1	4	0	37-46
Mammals (30)	8	9	15	23	0	6	2	47-76
Plants (32)	n/a	0	13	15	4	9	5	45, 77-107
Reptiles (2)	0	0	1	2	0	1	0	108-109
Across taxa (3;	0	0	1	2	0	0	0	110-112
review/simulation)								
Total no. studies	25	15	60	68	10	40	11	112

^{*} Number of studies reviewed, including one study that included both invertebrates and plants.

[†] Pollinator species and anthropogenic ecotypes (plants), production (birds [indigenous African chicken]), parasite fauna, predation level and differences in maturation times (fish), isotope (mammal), and life history (fish and mammals).

[§] Genomic analyses were reported for 20 studies, two for birds (reference number 2-3) and 18 for fish (reference number 5, 8-16, 26-27, 29-31, 33-34, 36).

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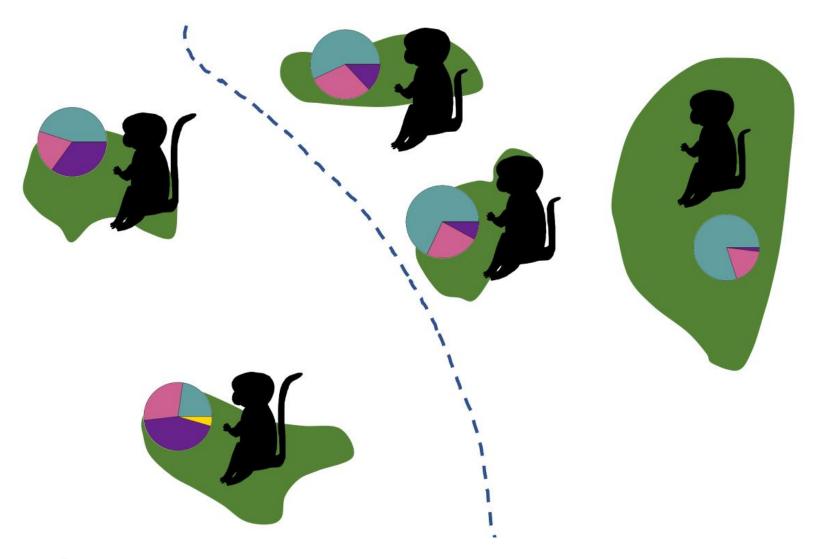


Figure S1. A hypothetical meta-population of a monkey split into two morphs: long-tailed and short-tailed. The dashed line suggests two distinct populations based on ecotype. The pie charts show the genetic structure of each subpopulation. The ecotype distinction and the genetic structure suggest two different histories, with the southern-most population containing unique ancestry (yellow portion of the pie).

Supplemental Note S1. Taxonomy

Careful delineation of taxonomic groups is important because these classifications have long-term implications for conservation efforts (Luo et al., 2018), and such intraspecific units represent important evolutionary potential within a species. Yet confounding – or a lack of – clear criteria to categorise these entities can seriously delay or limit conservation action, also because management agencies sometimes lack the taxonomic expertise to assess conflicting scientific assessments (Haig et al., 2006). Scientists should likewise be mindful of the importance of translating new evidence for genetically defined units into categories that can be considered under local legislation, while communicating the nuances of speciation that is emerging from genomic research (Coates et al., 2018). Defining excessively broad taxonomic units can lead to management actions resulting in outbreeding depression, whereas taxonomic units that are too narrow risk management actions that lead to inbreeding depression (Frankham et al., 2012). Frankham et al. (2012) and Haig et al. (2006) have therefore suggested that taxonomic splitting with the aim of conserving more biodiversity can actually hinder conservation aimed at preserving small populations, resulting in a loss in biodiversity over time (but see Gippoliti & Groves, 2012 for a different view). There are long-held concerns that scientific evidence behind taxonomic distinction should be clear and transparent, to avoid concerns over 'taxonomic inflation', which can affect conservation priorities and actions (Berta & Churchill, 2012). Oftentimes, there are clear links between systematic rankings and priorities for preservation (Stanton et al., 2019), whereby reassignment to a lower status can be deemed unfavourable for conservation (Bowen & Karl 1999; Crandall et al., 2000). Several authors have highlighted that, although taxonomic units should influence conservation strategies, conservation strategies ought not to influence taxonomic decisions (Bowen & Karl, 1999; Haig et al., 2006). Moreover, taxonomic status assessments, like that of other adaptive management, may need periodic re-evaluation to consider new knowledge and technical developments (Ford, 2004; Haig et al., 2006) and the same may be relevant for conservation of intraspecific variability. Multiple lines of evidence should be considered for taxonomic decisions (Stanton et al., 2019), and this approach is also likely to benefit assessments of ecotypes.

Supplemental Note S2. Caribou (Rangifer tarandus) ecotypes

The influence of sporadic gene flow among reported caribou ecotypes remains unresolved (Courtois et al., 2003) and may be affected by various factors including evolutionary history, effective population size, and habitat connectivity (Courtois et al., 2003; Klütsch et al., 2016; Serrouya et al., 2012; Yannic et al., 2017). The terminology used to describe caribou ecotypes is often unclear (COSEWIC, 2011), and from a practical management perspective, low confidence in individual caribou assignment to specific ecotypes have limited its application in law enforcement (Bourret et al., 2020). Microsatellite studies have recently reported conservation units identified by genetic and geographical structure (Jenkins et al. 2018), and a wide-scale investigation across eastern Canada by Klütsch et al. (2016) found overall broad agreement between genetic structure and boreal vs. eastern migratory ecotypes. Moreover, new results from genome-wide analyses indicate parallel evolution of similar ecotypes from separate evolutionary lineages and suggest that the designation of caribou conservation units merits further revision (Taylor et al., 2020). Findings for this highly mobile species with circumpolar distribution have so far been focused mainly on neutral genetic markers (Yannic et al., 2017) which have been the available resources for genetic analyses, but see Cavedon et al. (2019), Kharzinova et al. (2016), Shafer et al. (2016), Taylor et al. (2019, 2020), and Weldenegodguad et al. (2020) for new genomic findings and broader discussions around their interpretation. Even so, studies at various spatial scales have revealed discrepancies between differentiation based on (putatively) neutral genetic markers and ecological units (see illustration in Supplemental Figure S1) and highlight the need for further research on adaptive genetic

differentiation (Taylor et al., 2020; Yannic et al., 2016, 2017). Hence, the case of *Rangifer tarandus* (including North American caribou and Eurasian reindeer) illustrates how new genomic results can help illuminate the spatiotemporal distribution of adaptive (functional) genetic variation within a species (Box 1 Part B) and, over time, inform conservation units that integrate emerging knowledge of ecological and evolutionary genetics. Future study of functional genetic variation could provide key information on natural selection and adaptation, which is increasingly important for long-term persistence in environments rapidly altered by climate change (Sgrò et al., 2011; Yannic et al., 2017), and data on such variation may also help delineate caribou designatable units and ecotypes (COSEWIC, 2011).

Supplemental Note S3. Analytical considerations

Spatial structure and assumptions of genetic equilibrium conditions. Improved understanding of contemporary gene flow and genetic structure can provide important real-time information for conservation management of different ecotypes (Dahle et al., 2018). Contemporary gene flow may be investigated looking at carefully designed marker panels (high minor allele frequency (MAF), unlinked loci) and sampling (homogeneous and high density) optimized for assessing relatedness across the landscape that does not require assumptions based on equilibrium populations (Norman et al., 2017). Here, the degree of "landscape relatedness" will provide a spatial measure of the extent of relatedness among individuals on the landscape. However, whereas standard measures in population genetics will only integrate those movements that cause meaningful population effects (Cushman et al., 2006), landscape relatedness estimates do not assume that animals with low levels of relatedness to individuals sampled nearby have dispersed. Selection can occur in the presence of gene flow (Fitzpatrick et al., 2015), which has the potential to confound our interpretations. Various

complementary methods can therefore be used to highlight different spatiotemporal processes that matter for monitoring genetic diversity and landscape connectivity.

A key issue for future genetic analyses will be to harness the information from analyses with different markers, sampling areas, time spans, and objectives to extract as much information as possible on the influence of various spatiotemporal processes (de Groot et al., 2016). At the individual level, dispersal decisions could be influenced by the extent to which surrounding areas are occupied by relatives (Zedrosser et al., 2007) and whether habitat resembles that of the native range (Edelaar et al., 2008; Sacks et al., 2004). Certain species inhabit a temporary landscape with moving territories, represented by polar bears (*Ursus maritimus*) (Kutschera et al., 2016) as well as Arctic foxes (*Vulpes lagopus*) and gray wolves (Canis lupus) in some areas (Carmichael et al., 2007). In wolves, dietary specialization may explain seasonal migrations over large areas in certain regions (Musiani et al., 2007) and genetic differentiation across short distances in others (Pilot et al., 2012; Stronen et al., 2014). Here landscape ecology and inherent social behaviour interact to produce location-specific hierarchies of spatial genetic structure. A study of a given species in one landscape may therefore find that a certain variable has a large effect on genetic differentiation, whereas its effects may appear much weaker and relatively less important elsewhere, which can be explained by differences in the degree to which the landscape composition and configuration limit gene flow (Cushman et al., 2013). In addition, history and biogeography can at times provide a better explanation for observed patterns than ecological or evolutionary developments (Warren et al., 2014). Sampling may also follow political boundaries that have no biological relevance; perhaps producing inflated population estimates (Bischof et al., 2016) or more genetic clusters than what an organized sampling through the overall range of the population would show. For wide-ranging species, the availability of "hard data" that e.g., confirms collared (or similarly tagged) animals traveling across heavily human-altered landscapes (Ciucci et al., 2009) and remarkable long-distance movements that can involve important ecological changes (Fuglei & Tarroux, 2019) also help limit speculation about wide-ranging wildlife species and promote science-based management involving different jurisdictions (Ciucci et al., 2009).

Furthermore, spatial genetic structure may coincide with natural landscape transitions without necessarily being shaped or influenced by these features (Bierne et al., 2011). Similarly, landscape and/or ecological transitions that occur naturally (i.e., independent from human activities) can result in spatial genetic structure (Muñoz-Fuentes et al., 2009; Pilot et al., 2012). The presence of such structure could easily remain unnoticed; although at times it may be well known to those intimately tied to the local natural history, for instance, local indigenous communities (Stronen et al., 2014). Current genetic structures can also reflect historical landscape features that no longer exist, exemplified by the corridor that permitted brown bears (*U. arctos*) from the Iberian lineage entry to the Scandinavia peninsula following retreat of the ice sheet after the last glaciation (Bray et al., 2013). In contrast, the genetic structure of a fast-evolving virus has been used to infer population genetic structure of its large carnivore host over a more recent time scale (Biek et al., 2006).

More attention toward environmental variation and selection. New methods have enabled the addition of new evolutionary perspectives to the classic approaches primarily focused on neutral genetic markers. However, even studies that genotype thousands of individuals at a large number of SNPs generally uncover only a small proportion of the heritable variation of a trait (Meirmans, 2015). The next step is improved design of studies that will enhance our ability to detect this genetic variation, especially in the presence of seemingly contradictory animal movement (Moura et al., 2014; Riley et al., 2006; Vander Wal et al., 2013). A further aim is to recognize the selective pressures driving genetic changes and to identify how and where genetic differences are expressed within the

genome. With large numbers of markers, completely avoiding false positives may be almost impossible. Adjustment of alpha levels or correction for multiple testing may help to a degree, but at the cost of inflating type II errors (Meirmans, 2015). Multiple testing approaches might help, but could lead to biases, at least in part, by the particularities and strengths of the given method (Narum & Hess, 2011; Stucki et al., 2017). A combination of methods may highlight genes, environmental factors, and/or potential driving processes behind genetic variation, which can point to priority areas for further investigation. Because various factors can confound the identification of ecotypes and their spatial distribution, it is important to consider that false-positive associations can occur if models fail to incorporate factors such as isolation by distance, shared demographic history, and cryptic relatedness (François et al., 2016). With an expanding toolbox of powerful techniques for genomic data analyses, careful attention is required to avoid overfitting models, while ensuring that they realistically capture the underlying biology (Liberles et al., 2013). A very small bias may have negligible effect in a microsatellite data set but become a strongly significant pattern in a nextgeneration sequencing project, which can cause overconfidence in the patterns observed (Meirmans, 2015). Conversely, a bias against negative results could mean that investigations not producing clear genetic structures are less likely to be published or undertaken, despite their importance for the public record. Theoretical investigations predicting and then simulating at what sample size or number of markers family structure and other effects will no longer be detected (or strongly influential) could provide a measure of sensitivity analysis to guide sampling design.

When interpreting genetic results, focusing more on biological relevance than on statistical significance is important; in the genomics era with thousands of loci, strong significance is easily obtained even for biologically marginal processes (Meirmans, 2015). Broad-scale landscape genetic studies must be carefully interpreted to avoid unwarranted extrapolation but provide key opportunities

for illuminating patterns and processes across geographical space and taxonomic groups (Richardson et al., 2016). From an ecological perspective, however, shifting the focus from the exact genes involved in adaptation toward the processes and environmental variables that lead to adaptation to the local climate could be valuable (Meirmans, 2015). This could aid investigation on the presence of local ecotypes, where multiple genetic variants may be under influence of the environmental and ecological forces under study. This approach may also help solve the problems related to having low statistical power. Especially in non-model organisms, the lack of statistical power can make it difficult to establish clear associations between adaptive genetic variation, phenotypes, and reproductive isolation (Foote, 2012). Past signatures of selection are not certain to indicate future adaptive potential, and it can often be difficult to determine the specific cause of selection (Stanton et al., 2019). Even if we have incomplete understanding of the underlying processes, identification of seemingly important genes can provide key advances for follow-up research and could further knowledge of connections among genes, communities, and ecological processes (Coulson et al., 2006). Good hypotheses often exist about climatic variables that may affect the study species, and there are usually fewer climatic variables than genes, leading to less testing and less need for correction (Meirmans, 2015). The emerging findings from genome-wide studies combined with sound ecological data provide rich opportunities to inform our understanding of biology and evolution, and can help us in setting thoughtful priorities for conservation at the species level and beyond. Moreover, data on responses to human activity following colonization of new habitats (Gompper, 2002; McPhearson et al., 2016), or responses to the local absence of predators (or competitors) and their possible implications for source-sink dynamics (Goldberg et al., 2014) could inform interpretations of genetic results and research design. Ecotypes may emerge and disappear following landscape and environmental alterations. Traits such as body size, which can show clear genetic and environmental components (Rivrud et al., 2019) and appear instrumental in ecological

genetic differentiation (Kays et al., 2010; Monzón et al., 2014) are often polygenic traits involving many genes each with a small effect. Accordingly, target genes may be difficult to detect with standard genome-wide association studies, although such traits could play a more important role in selection than that documented at present (Exposito-Alonso et al., 2018; François et al., 2016).

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