COMMENTARY

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Diverse data sources and new statistical models offer prospects for improving the predictability of anthropogenic hybridization

S. Eryn McFarlane[1] | Elizabeth G. Mandeville[2]

[1]Department of Botany, University of Wyoming, Laramie, Wyoming, USA

[2]Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada

Correspondence
S. Eryn McFarlane, Department of Botany, University of Wyoming, Laramie, WY, USA.
Email: eryn.mcfarlane@gmail.com

Anthropogenic hybridization, or the breakdown of reproductive isolation between two or more previously isolated species because of human intervention, is increasing (Grabenstein & Taylor, 2018), and can have negative effects on biodiversity (Todesco et al., 2016). However, mechanistic studies to understand the causal relationship between human activities and hybridization, particularly across multiple locations, are few and far between. A critical task for the field going forward will be to identify under what circumstances hybridization outcomes are consistent or variable across time and space, and which evolutionary and ecological forces promote or inhibit hybridization and introgression (Gompert et al., 2017). Identifying to what extent human activities (e.g., urbanization, climate change, translocation of novel species) affect hybridization, and how these variables interact, will be especially crucial to address anthropogenic hybridization practically as a conservation concern.

Hybridization is expected to increase with anthropogenic disturbance both as a consequence of altered mating patterns that increase propensity to hybridize, and because relative fitness of hybrids may be elevated in disturbed areas. A classic example of the former scenario is increasing hybridization with increasing eutrophication (nutrient loading and increased turbidity) in aquatic systems. In Lake Victoria cichlids, murky water makes it difficult for the fish to distinguish the color morphs of their mates (Seehausen et al., 1997). Similarly, eutrophication is believed to have caused speciation reversal in European whitefish (Vonlanthen et al., 2012). Hybridization between a rare species and a common species can also follow anthropogenic mortality of the rare species (i.e., allee effect, as is the case in red wolf and coyote hybridization; Bohling & Waits, 2015), or mating patterns could theoretically be disrupted by noise or light

pollution in cities. Once hybridization has occurred, human disturbance can change the fitness landscape to favor hybrids, as in southern tigrina *Leopardus guttulus* and Geoffroy's cat *L. geoffroyi* hybrids which are favored in anthropogenically modified ecosystems, resulting in a higher proportion of hybrid individuals than in a undisturbed habitat (Sartor et al., 2021). While few examples of anthropogenic disturbance promoting hybridization are well characterized, a larger-scale effort to quantify the effects of anthropogenic disturbance on hybridization is needed. The first necessary step is to estimate the relationship between human disturbance, the rate of hybridization and fitness of hybrids for a given species pair. However, completing these studies at the scale needed to achieve generality is quite challenging.

In their new paper, Grabenstein et al. (2022) demonstrate that the rate of hybridization between black capped and mountain chickadees (*Poecile atricapillus* and *P. gambeli* respectively) increases with increasing human disturbance. This is an exciting step forward for studies in anthropogenic hybridization, because in addition to demonstrating variation in hybridization rates across different habitats, Grabenstein et al. (2022) propose and test human disturbance as a mechanism leading to this hybridization. An innovative aspect of this study is that they test this pattern using both a smaller dataset of 409 birds at 81 replicate sites (genomic and phenotypic data), and using a community collected data resource (reports from eBird) that reports hybrids using phenotypic data only, but from many more locations. Notably, they also used a publicly available index of human disturbance that could be applied to all locations. By looking at rates of chickadee hybridization across the overlapping range, and controlling for sympatry, Grabenstein et al. (2022) provide convincing evidence for a causal relationship between human disturbance and chickadee hybridization. Furthermore, by including the eBird data

in the analyses, Grabenstein et al. (2022) show that the effect of disturbance on chickadee hybridization is likely to be a widespread phenomenon. If this relationship holds across variation in reproductive isolation across areas of sympatry between parental species, it is possible that understanding this mechanistic relationship will enable prediction of when reproductive isolation breaks down—a major question in conservation genetics when dealing with hybridization. While neither chickadee species is currently threatened, these results are encouraging for managing hybridization in threatened taxa as well. If, as has been done in Grabenstein et al. (2022), it is possible to predict the breakdown of reproductive isolation based on environmental factors, then wider conservation policies can be enacted for species of conservation concern, without substantial, costly genomic sampling across ranges.

From a conservation perspective, the potential to predict rates of hybridization using ecological variables would be extremely useful. Once hybridization has begun, if there is not strong selection against hybrid individuals or strong assortative mating, then the proportion of hybrids in the population is always expected to increase if hybridization dynamics remain constant through time, as all of the offspring of hybrids are themselves hybrids (Epifanio & Philipp, 2000). This means that the best policy for controlling unwanted anthropogenic hybridization is to stop it before it begins. If, as is the case for black capped and mountain chickadees, hybridization generally increases with disturbance, then this increased risk

must be accounted for when planning future conservation priorities. Natural stochasticity across hybrid zones can lead to substantially different outcomes, even before accounting for ecological variation (McFarlane et al., 2022). This means that to predict the rates of hybridization of unsampled sites, studies must be carefully designed to maximize generality across ecological gradients (Figure 1).

Predicting hybridization is an extremely challenging problem. Repeated sampling across hybrid zones may shed light on both local and global patterns of hybridization and introgression, but we must be cautious to not assume that replicates will necessarily be predictive of other replicates or unsampled sites. Prediction ability depends largely on what mechanisms constrain or promote hybridization. For example, geographic distribution of hybridizing species, as well as the dispersal mode and capacity of study organisms, is likely to be quite important in defining independence of replicate sites, and may influence decisions about statistical treatment of comparisons (McFarlane et al., 2022). One solution is to use hierarchical models, as has been explored by Grabenstein et al. (2022) who accounted for site-specific and year-specific variation while examining patterns across the range of chickadees. This is an excellent first step, and we hope that future studies will incorporate further advances to address the need to account for additional covariates while propagating error from genomic analyses by incorporating genotype uncertainty and uncertainty in hybrid ancestry. This will require development of new statistical methods. However, models to predict

FIGURE 1 Sampling potentially hybridizing species across variable ecological gradients (like the urbanization gradient depicted above) allows for the estimate of both local hybridization patterns at the population-level and global patterns when all populations are considered in a hierarchical framework. Hybrid individuals (two species of chickadees) can be identified phenotypically (binoculars) or genetically (double helix), and here we have depicted variation in both urbanization and tree cover. The different widths of arrows represent that different sampling sites, specifically those with more sampled individuals or more variation along the gradients of interest, will contribute more to the estimate of the global patterns. By combining data from multiple sources—that is, both phenotypically and genetically identified hybrids—there is more statistical power to identify relationships between anthropogenic disturbance and hybridization outcomes. [Colour figure can be viewed at wileyonlinelibrary.com]

hybridization outcomes are only as good as the empirical data going in, which depends strongly on sampling design, sequencing strategy, and bioinformatics choices. We must temper our expectations for what can be predicted from our inferential work, especially if replicate hybrid zone sampling is done haphazardly, making it difficult to compare sites that are similar in all ways except for our parameter of interest. At present, mechanistic understanding of the causes and consequences of ecological variation across replicate hybrid zones is sometimes hampered by a disconnect between those statistical methods typically used in ecological fields, and those used in population genetics. To make progress, we need to bring these heuristics together to be able to answer questions about how ecology influences population genetics, and vice versa.

If we can build models to predict the risks, benefits, and potential outcomes of hybridization by integrating ecological data with population genetics, then true focus can be put on the systems where hybridization is a conservation risk. If models of anthropogenic hybridization have strong predictive ability, then expensive conservation genomics can be partially bypassed, or paired with crowd sourced monitoring or ecological data that may be easier to collect across time and space, like the eBird data used in Grabenstein et al. (2022). With more studies of replicate hybrid zones, particularly with a focus on independence between sites, and control of confounding variables, we can rigorously test how predictable hybridization can be. Growing availability of genomic and citizen science datasets, with parallel in-progress methods development for comparing replicate hybrid zones, will make this an exciting avenue of research that will hopefully open up new insights into how anthropogenic disturbance is likely to drive hybridization outcomes in our changing world.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

S. Eryn McFarlane https://orcid.org/0000-0002-0706-458X

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