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CONSERVATION AND CONVERSATION IN THE ANTHROPOCENE

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CONSERVATION AND CONVERSATION IN THE ANTHROPOCENE

By

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Dissertation

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Dedication:

To the myriad gardens I'll never get to see

Acknowledgements:

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Conservation and Conversation in the Anthropocene

Chairperson: Gordon Luikart

The driving questions of this dissertation consider both the scientific and communicative understanding of conservation and extinction in the Anthropocene. Overall, this dissertation portfolio explores this topic via genetic and genomic data, international policy, big data analytics, human values, and the performing arts. Chapter 1 analyzes the use of genetics and genomics in conservation, finding multiple case studies within and outside of peer-reviewed journals. Chapters 2 and 3 quantify and describe the use of genetic principles and tools in a global species extinction risk assessment, the IUCN Red List, and finds low overall use but high potential for genetics to improve risk assessments and facilitate conservation. Chapter 4 reviews and synthesizes the use of big data analytics in biodiversity conservation including tools, processes, case studies, and caveats. Chapter 5 extends the conservation toolbox to include philosophy of the Anthropocene, and both questions and qualifies the uniqueness and demarcation of a current sixth mass extinction in terms of extinction rates and human involvement in species loss. Chapter 6 addresses conservation via media products and science communication through a five-part video mini-series on the intersection of philosophy and climate change (https://www.youtube.com/natureleague/playlist), a YouTube channel focused on life on Earth (https://www.youtube.com/natureleague), and an internationally produced podcast featuring voices of less common stories of biodiversity conservation (https://ipbes.net/podcast). Finally, Chapter 7 considers the performing arts within the context of its own extinction due to COVID-19 and uses two case studies to demonstrate the use of science and technology to conserve performance art during the pandemic. This dissertation demonstrates the use of science, philosophy, and communication as an approach for conservation of both biodiversity and human cultural phenomena, while recognizing that in the Anthropocene, most conservation work begins and ends with human conversation.

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Introduction

By the start of the 21st century, scientists had introduced and popularized the term "Anthropocene"- a word describing the most recent geological epoch of distinct human impact on the Earth. While the Anthropocene has not yet been officially designated as a geological epoch by international stratigraphy working groups, the widespread impacts of humans on the Earth and Earth's systems is undeniable. One line of evidence for designating an Anthropocene is the current rapid loss of biodiversity directly and indirectly caused by humans via habitat destruction, overexploitation, climate change, and more. While human activities threaten approximately 20% to 40% of mammals, birds, reptiles, amphibians, plants, and other taxa with extinction over the next few decades (IUCN 2019), humans are simultaneously working to quantitatively assess these risks and identify and prioritize actions to slow this loss of biodiversity.

This dissertation considers science and technology as an approach to conserving biodiversity in the Anthropocene, while also considering the philosophical underpinnings of extinction designations and the impact of science communication to the public. Multiple tools and approaches are analyzed, beginning with conservation genetics and genomics. The recent expansion of conservation genetics into conservation genomics is an incredible technological feat, yet doubts exist about the extent of genomics in practice. Chapter 1 rebuts the claim that genomic data and techniques are far from being practically used in conservation and provides examples from conservation practitioners across countries and taxa. To quantify the use of genetic principles and tools globally, Chapters 2 and 3 analyze threat designations and listing rationales by the IUCN Red List, the largest and most influential worldwide source for information on the conservation status of extant species. Overall, this work finds low overall use of genetics throughout the Red List, but highlights areas of high potential for conservation application, including estimation of the effective population size when assessing a species' extinction risk.

Conservation in the Anthropocene is becoming increasingly data-driven, particularly in combination with remote sources and collaborative, shared online platforms. Big data analytics originated in the technology and business sectors, where they are applied to minimize cost and maximize efficiency- a highly relatable premise in the high-urgency, often triage-based field of biodiversity conservation. Chapter 4 reviews and synthesizes the use of big data analytics in biodiversity conservation including tools, processes, case studies, and caveats. While there is enormous potential for transformative change in the way conservation is done, caution is given for practitioners to recognize issues of equity, access, and the metaphorical arms race against those using these techniques to do harm.

With so many new and exciting tools available for conservation in the Anthropocene, there is an increasing need to consider the reasons for conservation itself, and whether the current extinction crisis is unique in Earth's history. Chapter 5 extends the conservation toolbox to include philosophy of the Anthropocene, and both questions and qualifies the labeling of a current sixth mass extinction. While science and technology are being used for conservation, many of the driving factors for action are human values informed by both media and culture. Chapter 6 addresses conservation via media products and science communication through a five-part video mini-series on the intersection of philosophy and climate change, a YouTube channel focused on life on Earth, and an internationally produced podcast featuring voices of less common stories of biodiversity conservation. Overall, these products offer educational experiences and explorations that include the nuance of human values as well as entertainment for audience engagement.

In 2020, human pressures on biodiversity and habitat contributed to a zoonotic pandemic of a novel coronavirus, COVID-19. While threatening the survival of our species, COVID-19 acutely threatened the survival of the performing arts, demonstrating a significant yet rarely considered connection between conservation of biodiversity and conservation of human culture. Chapter 7 considers the performing arts within the context of extinction due to COVID-19 and uses two case studies to demonstrate the use of science and technology to conserve performance art during the pandemic. Much like with biodiversity, there is a demonstrated need to add philosophy and communication to the science and technology being used to conserve the performing arts. As a whole, this dissertation demonstrates the use of science, philosophy, and communication as an approach to conservation of both biodiversity and human cultural phenomena, while recognizing that in the Anthropocene, most conservation work begins and ends with human conversation.

Chapter 1: Genomics in Conservation: Case Studies and Bridging the Gap between Data and Application

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We agree with Shafer et al. [1] that there is a need for well-documented case studies of the application of genomics in conservation and management as well as increased communication between academics and natural resource managers. However, we challenge Shafer et al.'s [1] relatively pessimistic assertion that 'conservation genomics is far from seeing regular application'. Here we illustrate by examples that conservation practitioners utilize more genomic research than is often apparent. In addition, we highlight the work of nonacademic laboratories [government and nongovernmental organizations (NGOs)], some of which are not always well represented in peer-reviewed literature. Finally, we suggest that increased agency–academic collaboration would enhance the application of genomics to real-world conservation and help conserve biodiversity.

There is substantial controversy and confusion surrounding the definition of 'genomics' versus traditional genetic approaches. Here we address this by expanding Shafer et al.'s [1] definition to include a broad- and narrow-sense definition to better illuminate the different ways that genomics contributes to conservation practice. We define broad-sense conservation genomics as the use of new genomic techniques and genome-wide information to solve problems in conservation biology (as in Shafer et al. [1] and Allendorf et al. [2]). Our narrow-sense definition also requires the use of approaches that are conceptually and quantitatively different from traditional genetics to answer questions that would be impossible using genetic data alone (e.g., detecting genome-wide adaptation, use of transcriptomics, epigenetics, using annotated genomes). This narrow-sense definition includes using hundreds to thousands of mapped or gene-targeted marker loci in combination with recent computational and conceptual approaches such as mapping runs of homozygosity, comparing neutral versus adaptive patterns of population structure or gene flow, and testing for signals of selection to assess adaptation.

Narrow-sense genomic approaches have been used for diverse conservation applications including identifying conservation units, assessing gene flow, and detecting local adaptation (Table S1 in the supplementary material online). We agree with Shafer et al. [1] and others [2] about the general and serious concern of erroneous identification of adaptive loci and their subsequent use (or misuse) in conservation practice. However, we remain cautiously optimistic given the recent efforts to use putatively adaptive loci to inform management practices. For instance, genome-wide scans using diversity array technology (DArTseq) in gimlet trees (*Eucalyptus salubris*) generated 16 122 neutral and putatively adaptive SNP markers used to uncover distinctive molecular lineages signaling adaptation to different environments. These genome-wide scans offered enhanced precision otherwise unavailable with traditional genetics or phenotypic traits alone [3] (Table S1). Such novel insights are important in seed choice for the ecological restoration of gimlet trees, a keystone species in the Great Western Woodlands of Australia, in the wake of wildfires [3].

In many broad-sense studies, next-generation sequencing (NGS) has enabled the discovery of management-informative markers that are subsequently screened in populations of conservation concern. For example, state management agencies in Washington and Idaho, USA used NGS to discover markers of introgression from hatchery broodstock into wild populations of salmonid fishes [4,5]. Other applications of broad-sense conservation genomics are evident (Table S1) and have been enabled by recent NGS and SNP genotyping technologies [6] (http://biorxiv.org/ content/early/2015/10/11/028837). These approaches allow genome-wide discovery and genotyping of highly informative markers, making cost-effective monitoring feasible using relatively small marker sets (e.g., 100–500 markers) [7].

Decreases in costs (e.g., sequencing, library prep, bioinformatics) are sparking the application of NGS to a broader set of conservation questions and taxa where funding is relatively more limited. In addition to the examples above, genomic data are currently applied in conducting parentage analyses in Pacific lampreys (*Lampetra tridentata*) and monitoring for disease in Tasmanian devils (*Sarcophilus harrisii*) [8,9] and fish (Table S1). Power analyses and cost-savings comparisons of using SNPs versus microsatellite markers in conservation genomics would be of great benefit, but such analysis is beyond the scope of this letter. However, using genomic approaches has been shown to provide more statistical power than microsatellites and cost less for genotyping and are as low as

1% of the cost of traditional Sanger sequencing for marker discovery [3,6,7,10] (Table S1).

We have included multiple case studies from salmonids because these species are of great conservation concern due to their ecological, commercial, and cultural importance in many Northern Pacific Rim river systems. For example, 30% or more of salmonid populations in the Columbia River Basin (USA–Canada) have been extirpated and many remaining populations are listed as endangered or threatened under the Endangered Species Act (ESA) or the Species at Risk Act in Canada because of, for example, over-harvesting, habitat degradation, pollution, and hydrological dams [11]. Therefore, more money and time is being spent on these species than other taxa due to their multiple conservation concerns (e.g., climate change, hybridization, over-harvesting). There are 12 nonacademic laboratories (e.g., federal, tribal, NGO, state agencies) using genomic data to work mostly or exclusively on salmonids in the Pacific Northwest of North America. Shafer et al. [1] insufficiently acknowledged one of the most significant contributions of genomics to conservation by not fully highlighting the work of these laboratories, particularly the Alaska Department of Fish and Game (ADFG), a leader in SNP and NGS tool development and application. ADFG genotypes approximately 100 000 fish annually for management using broad-sense conservation genomic approaches [12]. Such approaches are now feasible and being conducted in many other species thanks to declining costs of genomics, as mentioned above (Table S1).

We highlight recent applications of genomics in real-world management where some are published, but many similar studies are not published or widely disseminated. Some nonacademic laboratories have relatively limited incentive to publish or are delayed due to urgent deadlines reinforced by political, legislative, or legal constraints. For example, some agency laboratories produce reports or declarations used in litigation or the planning of harvest regulations or introductions (e.g., hatchery fish management plans), which can delay scientific publication. Nonacademics could potentially publish more by collaborating with academic groups who have strong incentives to publish (e.g., to 'publish or perish'). Academics could in turn achieve greater conservation impact by working closely with practitioners who can provide benefits such as large sample and data collections, funding and field staff, collection permits, and high-throughput, cutting-edge genomics platforms.

While research and publications from some nonacademic laboratories are often underappreciated or delayed, they can help the conservation biology community to understand the extent and feasibility of applying genomics to conservation. We hope by highlighting case studies we will expand discussions and applications of genomic techniques in conservation and encourage the closing of gaps between nonacademic laboratories and academia.

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Table S1. Selected case studies using genomics to address problems in conservation. All studies required the use of new genomic techniques [broad-sense (BS)] while some also use recent conceptual and computational approaches that would be impossible without genomics [narrow-sense (NS); see definition in text]. Studies listed as narrow-sense (NS) report the recent population genomic computational and conceptual approach used. Examples listed here represent a subset of the numerous studies found during the course of writing this piece with many collaborators. The studies were selected as representatives for each application or problem in conservation.[1]

Problem Addressed	**Case Study and broad- versus narrow-sense use of genomics (BS vs NS)**	**Refs**
Managing hybridization and introgression	Used next-generation sequencing (NGS) to discover a panel of 60 single-nucleotide polymorphisms (SNPs) distributed across all but 2 of 29 chromosomes. The panel is diagnostic in identifying individual Atlantic salmon (*Salmo salar*) as farmed versus wild. This panel development involved screening of 7,000 SNPs genome-wide, and was challenging because gene flow or genetic similarity between farmed versus wild populations made it difficult to identify hatchery-informative markers. This SNP panel is used to detect farmed escapees (and their offspring) in wild Atlantic salmon populations, and quantification of cumulative introgression is providing policy makers with new ways to address this situation. (BS)	[S1-S2]
	Used sequencing of expressed sequence tags (ESTs) and restriction site-associated DNA sequencing (RAD-seq) to screen thousands of SNPs to develop informative SNP chips to monitor introgression from hatchery-origin steelhead trout (*Oncorhynchus mykiss*) into wild steelhead populations. Due to continual introduction (release) of hatchery-origin steelhead and gene flow between wild and hatchery fish, the mean (genome-wide) F_{ST} was low and required the use of NGS to identify ~190 hatchery-informative markers now used to monitor for introgression. Hatchery informative SNPs are genotyped in thousands of fish annually to monitor for and quantify introgression from hatchery fish into wild populations. (BS)	[S3]
Identifying conservation	Recommended three ecotypes of killer whales (*Orcinus orca*) be elevated to full species status based on mitogenome	[S4-S5]

units: species, evolutionary significantly units (ESUs), distinct population segments (DPSs), designatable units (DUs), and management units (MUs)	sequencing, capture enrichment of 78 nuclear sequences, and genotyping-by-sequencing (GBS). Highly parallel sequencing techniques (NGS) were required to successfully sequence entire mitogenomes, which have extremely low levels of diversity, from hundreds of samples and was not feasible previously using Sanger sequencing. (BS)	
	Used over 10,000 RADseq SNP markers to assess stock structure in American lobster (*Homarus americanus*). The use of population genomics allowed the definition of populations that were previously unresolved using microsatellite markers and provided a powerful tool for population assignment. This work involved the collaboration of the Department of Fisheries and Oceans Canada in order to improve lobster fishery management. (BS)	[S6]
	Used SNPs to identify neutral and adaptive spatial structure in Atlantic salmon (*Salmo salar*) to help identify DUs. Genome scans, linkage maps, and 49 environmental variables were combined to provide insight into the links between environmental variation and both neutral and potentially adaptive genetic divergence. The discovery and use of putatively adaptive loci (e.g., F_{ST} outliers) to delineate DUs required NGS and thousands of SNPs. In addition, SNPs were found to have substantially improved power compared to microsatellite markers. (NS- use recent computational and conceptual approaches and neutral and putatively adaptive loci combined with linkage maps)	[S7]
Dispersal, gene flow estimates, and/or population assignment for harvest and management	Used genome-wide DArTseq scans (Diversity Arrays Technology) in Red Ironbark and Gimlet trees (*Eucalyptus tricarpa* and *Eucalyptus salubris*) to generate thousands of high-quality SNP markers useful in studying adaptive variation and barriers to gene flow. Potentially adaptive loci were correlated with climatic variables at the population level and variation in functional traits, providing evidence that they may, indeed, relate to climate adaptation and to functional responses. The results of this project are influencing seed collection zones for revegetation and general management strategies of this keystone species in the Great Western Woodlands (M. Byrne, pers. comm.; see: http://www.nccarf.edu.au/content/climate-resilient-	[S8-S9]

	revegetation-multi-use-landscapes-exploiting-genetic-variability). (NS- genome-wide neutral and candidate adaptive loci, recent computational and conceptual approaches testing for loci associated with climate and phenotype variation)	
	Used RAD-seq to develop a population-informative SNP panel for unprecedented power to monitor stock composition in sockeye salmon (*O. nerka*) to set fishing openings (and closures) and to delineate population units to harvest as discrete rather than mixed stocks to protect weak stocks from overharvest. Data provided relative abundance information within 3-4 days of capture (faster than most previous methods), allowing managers to shift fishing efforts based on return rates to stock of origin (noted in publication as pers. comm. with T.M. Sands, M.A. Jones, and P.G. Salomone in 2012). Similar work has been done in Chinook salmon (*O. tshawytscha*). (BS)	[S10-S11]
	Used 4723 SNPs to detect substantial gene flow and no adaptive differentiation between a potential source population of orange roughy (*Hoplostethus atlanticus*) and the intensively fished population it supplements. Results from AMOVA, STRUCTURE, discriminant analysis of principal components, BAYESASS and isolation by distance suggested high gene flow and demographic connectivity. A large number of genome-wide markers were required for a convincing case that there were not F_{ST}-outliers, and also to assess a key assumption (equal adaptation of migrants) of population growth modelling. (BS)	[S12]
	Used NGS to develop a population-informative SNP panel in chum and sockeye salmon (*O. keta; O. nerka*). The Alaska Department of Fish and Game's Western Alaska Salmon Stock Identification Program (WASSIP) used these SNPs to genotype 156,000 individuals collected from 3 years of marine fishery harvests along 3,000 km of Alaska coastline. In addition, baselines needed to be developed for each species by surveying 38,000 sockeye and 32,000 chum salmon across wide geographic ranges. The projects conducted by WASSIP directly informed decision making for management, allocating resources, and protecting weak stocks (see: http://www.adfg.alaska.gov/index.cfm?adfg=wassip.main).	[S13-S16]

	Similar work is being done by at the University of Washington, Washington Department of Fish and Wildlife, and Idaho Department of Fish and Game. (BS)	
	Used a genome-wide scan of 31,008 RAD-seq SNPs to inform restocking and delineate locally adapted populations of abalone (*Haliotis roei*), which are challenged by climate change and managed by fisheries programs in Western Australia (Beheregaray et al., unpublished; see: http://www.molecularecology.flinders.edu.au/molecular-ecology-lab/research-programs/research-projects/ecological-genomics-and-adaptation-to-climate-change/). Needed cost-effective screening of many samples and a high density of markers to reveal that most of the vast sampled areas had little differentiation, but three locations were differentiated by F_{ST} outliers. These were annotated using the transcriptome of a close relative and were found to be related to genes associated with heat stress or general immune tolerance. This putatively adaptive variation was spatially associated with thermal gradients. (NS- Recent computational and conceptual approaches; use of transcriptome functional annotations to outline potential adaptive differentiation among stocks)	
Effective population size (N_e) estimation and monitoring	Used RAD-seq to identify both neutral and putative adaptive genetic variation from ~4,000 SNPs to better estimate N_e and resolve stock structure in eulachon (*Thaleichthys pacificus*). This is enabling population monitoring in populations where census size is difficult to obtain. NGS was necessary to discover and genotype thousands of SNPs in this species with high gene flow. Similar work has been done in Chinook salmon (*O. tshawytscha*) by identifying more than 10,000 SNPs. (BS)	[S17-S18]
Parentage, relatedness, and inbreeding quantification	Used NGS to develop SNP genotyping panels to reconstruct pedigrees for hatchery broodstock steelhead trout (*O. mykiss*) and genetically tag offspring. This work laid the foundation for parentage-based tagging (PBT) in the Snake River Basin and has resulted in genetic tagging of ~95% of the thousands of steelhead and Chinook salmon in this region. (BS)	[S19]
	Used SNP markers to perform parentage analyses that detected successful reproduction in Pacific lamprey (*Lampetra*	[S20]

	tridentata). NGS technology was needed to find highly informative SNPs for parentage and selection detection for this particular non-model organism. This study discovered putatively adaptive outlier loci significantly associated with geography, run timing, and dwarf life history. 27 SNPs aligned with known genes or highly conserved genomic regions identified using the genome browser available for sea lamprey. This study provides both neutral and adaptive context for observed genetic divergence among collections. (NS- genome-wide neutral and candidate adaptive loci, recent computational and conceptual approaches testing for adaptive variation including use of genome browser and gene function annotation)	
	Sequenced the entire genome of wild-caught founders and first generation California condors (*Gymnogyps californianus*). NGS data and genomic calculations of kinships based on 4.2 million SNPs were used in the recent captive breeding plan for this species. This is apparently the first captive breeding plan to incorporate genomic data (pers. comm. Webb Miller). (BS)	
Environmental epidemiology, pathogen detection, and monitoring	Used SNPs to understand the origins, transmission, and diversity of Devil Facial Tumor Disease in the Tasmanian devil (*Sarcophilus harrisii*) in order to inform disease management, breeding programs, reintroductions and to manage genetic diversity. Using genomic techniques (NGS) enabled the creation of a reference genome, which led to the mapping of 99% of sequencing contigs to chromosomes and identifying 18,775 protein-coding genes. Understanding origins required sequencing multiple tumor genomes and comparing them to one another and to devil genomes. In addition, reference genomes from geographically separated individuals were necessary to choose individuals for breeding stocks that will preserve extant genetic diversity. (BS)	[S21-S22]
	Used SNPs from whole-genome sequences to uncover with sufficient resolution the geographic spread of the fungus (*Pseudogymnoascus destructans*) associated with white-nose syndrome in North American bats (Order: Chiroptera). This work has created a better understanding of the geographic scale necessary for protection and the results suggest much stronger connectivity among bat populations than previously recognized (J. Foster et al., unpublished). (BS)	

	Used gene expression profiling (16k loci), high throughput pathogen monitoring, and NGS to discover novel physiological mechanisms and disease infection trends associated with reduced survivorship during spawning migration in sockeye salmon (*O. nerka*). Mortality-related genomic signatures and pathogens associated with migration survival were only discoverable with genome-wide expression work and high-throughput pathogen monitoring tools. (NS- genome-wide gene expression and outlier concepts and tests)	[S23-S24]

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[1] All examples given in the table have at least one coauthor from a non-academic lab or who is an agency managers/conservation practitioner. With the inclusion of an agency coauthor, each study was considered likely to have been designed, or at a minimum conducted, with manager input or consultation. Examples were only included if there was clear evidence, either in the publication or in personal communication, that the work had a direct influence on conservation or management.

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Chapter 2: IUCN Red List and the Value of Integrating Genetics

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Abstract

Many species on endangered species lists such as the IUCN Red List (RL) are categorized using demographic factors such as numbers of mature individuals. Genetic factors are not currently used in the RL even though their explicit consideration, including effective population size (N_e) and expected heterozygosity-loss (H-loss), could improve the assessment of extinction risk. Here, we consider the estimation of N_e and H-loss in the context of RL species. First, we investigate the reporting of number of mature individuals for RL Endangered species, which is needed to estimate N_e and H-loss. We found 77% of species assessments studied here did not report methods used to estimate the number of mature adults, and that these assessments rarely report other important determinants of N_e (e.g., sex ratio, variance in family size). We therefore applied common rules of thumb to estimate N_e, and found that N_e was likely < 50 for at least 25% of the 170 RL Endangered species studied here. We also estimated mean expected H-loss for these species over the next 100 years, and found it to be 9–29%. These estimates of high H-loss and low N_e suggest that some species listed as Endangered likely warrant listing as Critically Endangered if genetic considerations were included. We recommend that RL and other assessment frameworks (i) report methods used for estimating the number of mature adults, (ii) include standardized information on species traits that influence N_e to facilitate N_e estimation, and (iii) consider using concepts like N_e and heterozygosity-loss in risk assessments.

Keywords

Biodiversity preservation · Conservation genetics · Extinction risk · Effective size · Number of breeders · Population bottleneck

Introduction

> *"The one process now going on that will take millions of years to correct is the loss of genetic and species diversity by the destruction of natural habitats. This is the folly our descendants are least likely to forgive us."*
>
> -Edward O. Wilson, 1984

Biodiversity loss is among the most urgent problems facing the world today. The most recognized worldwide index for biodiversity is the International Union for Conservation of Nature's (IUCN) Red List. This list results from a large, informative, and continually updated database dedicated to "providing the world with the most objective, scientifically-based information on the current status of globally threatened biodiversity" (IUCN 2001). For extant organisms with adequate demographic data, the IUCN Red List assigns an extinction risk category ("Least Concern", "Near Threatened", "Vulnerable", "Endangered", or "Critically Endangered") based upon a variety of criteria (Mace and Lande 1991; IUCN 2001). The IUCN bases most of its risk assessment on factors regarding number of mature individuals, trend, and geographic range. The IUCN recognizes genetic diversity as one aspect of species diversity and health (Norse et al. 1986, Reed and Frankham 2003); however, genetic factors are seldom used explicitly in RL assessments (Laikre et al. 2009), or in conservation policy or assessments in general (Pierson et al. 2016). For example, Laikre (2010) concluded that genetic diversity was not monitored, genetic change indicators were missing, and no strategy had emerged for including genetic aspects into global biodiversity targets, a point reiterated in Laikre et al. 2020.

Genetic principles and parameters have been useful in assessing conservation priority and risk assessment in a range of taxa, particularly when extinction risks are difficult to evaluate from ecological and demographic data alone (Dunham et al. 1999). Effective population size (N_e) is defined as the size of the ideal population with the same rate of genetic drift as in the actual population being considered (Fisher 1930; Wright 1931). N_e is among the most important genetic parameters in evolutionary and conservation biology because it influences the rate of inbreeding, loss of genetic diversity, efficiency of natural selection, and the maintenance of evolutionary potential (Newman and Pilson 1997; Waples et al. 2014; Beaumont and Wang 2019). This contrasts with the population census size, N_c, which is often defined as the number of mature (adult) individuals (e.g., Frankham1995; Waples 2005; Waples et al. 2014). N_e (and the N_e/N_c ratio) is often particularly small for species with high fecundity, high mortality in early life stages (type III survivorship), high sex ratio skew, polygamy, and/or heritability

of reproductive success (Waples et al. 2014; Kendall et al. 2016; Wang 2016; Greenbaum et al. 2017; Sun and Hedgecock 2017).

However, the main driver of low N_e and N_e/N_c ratios is typically high variation in reproductive success among individuals, which could be due to body size and fecundity variation (e.g., large trees or fish producing thousands of seeds or eggs), behavior (e.g., dominant males; Beletsky and Orians 1989), or chance. While some of the extremely low N_e/N_c ratios reported in the literature have been contested as potential artifacts of sampling (Hauser et al. 2002; Ficetola et al. 2010; Waples 2016), the ratios in many species are often small (< 0.10). N_e is often small (< 50) and/or declining which is problematic for population persistence, and thus is of concern to conservation biologists (Allendorf and Ryman 2002, Laikre et al. 2020).

N_e ranging from around 50 to several hundred is within the range where genetic variation is lost rapidly due to genetic drift and deleterious effects of inbreeding likely occur; N_e below 50 signals critical and rapid genetic erosion (Frankham et al. 2002; Hoarau et al. 2005). This is especially true if the population size has been small for multiple generations and was recently large, because large (outbred) populations carry a large genetic load (deleterious alleles; Allendorf et al. 2013; Spigler et al. 2017). At small and declining N_e, loss of allelic diversity is especially rapid and increases susceptibility to infectious disease and cancers (Ujvari et al. 2018). Thus, N_e could inform managers and other conservation stakeholders about a population's ability to persist and respond to environmental change, which is of great importance in the Anthropocene.

While there are increasingly useful genetic methods to estimate N_e (e.g., those based on linkage disequilibrium or sibship; Waples and Do 2008; Wang et al. 2016; Beaumont and Wang 2019) and genetic data are increasingly affordable, N_e need not be empirically measured with molecular markers for the N_e concept to be useful in assessing risk of a species or population. For example, the N_e for a species or taxonomic group is known to often be only 10% to 20% of the N_c (Frankham et al. 2014), and sometimes far less (e.g., $< 1\%$; Palstra and Ruzzante 2008). Biologists can estimate or approximate N_e from N_c using only demographic data such as the number of reproducing males and females, the adult sex ratio, longevity, family size variance, and more (Waples et al. 2013), if such information is available. This would allow explicit consideration that if $N_e \ll 50$ (e.g., 20 to 30), then inbreeding depression (and fixation of deleterious alleles) and loss of alleles is likely to threaten a population's growth and persistence (Bozzuto et al. 2019). Furthermore, N_e estimates allow estimation of the loss of heterozygosity (H-loss) expected over 100 years, for example, if the generation interval is known or approximated. Heterozygosity loss over 100 years (e.g., $> 5\%$ or 10%) has been proposed as threshold for population extinction risk and management concern (e.g., Allendorf and Ryman 2002).

Our overarching goal here is to consider the use of N_e concepts and estimates, and loss of heterozygosity for IUCN Red List assessment procedures. Our main objectives are to (1) assess the standardization of reporting the “number of mature individuals” as estimated and reported within the IUCN Red List to facilitate N_e estimation, (2) estimate the N_e for species listed as endangered (EN) on the IUCN Red List per Criterion D using a range of generally accepted and reasonable N_e/N_c ratios, (3) estimate the heterozygosity expected to be lost in the next 100 years based on those N_e estimations and generation interval estimates, and (4) identify which species listed as EN are at the most risk and could warrant listing as critically endangered (CR) if the N_e and heterozygosity-loss are considered. We predict that many species in the IUCN Red List are likely to have a small N_e/N_c ratio and $N_e < 50$ (for multiple generations) and thus could benefit from revision of Red List ranking along with monitoring or management actions to prevent excessive loss of genetic variation and reduced probability of persistence (Crow and Kimura 1970; Allendorf and Ryman 2002; Lacy 2019).

Methods

To assess and quantify standardization in the IUCN Red List reporting of number of mature individuals in a species, we first compared the text of recent available Red List guidelines, beginning from ones published in 2004 up to the most recent one, Version 14 (IUCN 2019). Similarities and differences between the guideline versions over time were recorded. We were interested in species listed as Endangered (EN) on the IUCN Red List as they are already of high conservation concern and are one risk category away from being Critically Endangered (CR), which is the most endangered category (except Extinct in the Wild). Under Criterion D, species with number of mature individuals < 250 are listed as EN, and < 50 are listed as CR.

To analyze the assessments of EN species listed under Criterion D, we filtered all species assessments currently available on the IUCN Red List (n = 105,732) to include only those species listed as Endangered (EN; n = 9754), and then filtered to include only those categorized as EN under Criterion D alone (n = 222). Our final filtering step kept all assessments with reported estimates for the number of mature individuals (n = 171). One assessment was written without an English translation, and was removed from the dataset. The final, working dataset of 170 assessments included all species on the IUCN Red List with available population size estimates in the endangered (EN) category listed under Criterion D (small population size; note that IUCN uses the term “population size” but this refers to the entire species not individual populations). All filtering was done within Microsoft Excel.

We investigated the estimation and reporting of population sizes (i.e., estimates of mature individuals) in each assessment in the working dataset in order to quantify discrepancies between species’ assessments. This included recording the number of assessments that provided primary sources (e.g., peer-reviewed publications) and methods of estimation (e.g., field surveys, camera traps, number of breeding pairs, etc.), as well as if the sources cited within the assessment (if applicable) provided methods of estimation. All information was retrieved from the text within the “Population” information segment of each assessment (available online at www.iucnredlist.org), as our working dataset contained species listed based on Criterion D alone (small population size) without consideration of habitat, threats, or other factors.

For species in the working dataset, we estimated N_e by multiplying the number of mature individuals reported in their assessments by 0.4 or 0.1, representing a common range of N_e/N_c ratios (Waples et al. 2011; Allendorf et al. 2013; Frankham et al. 2014). The maximum estimate was used for assessments that reported ranges of values for mature individuals. These species were then sorted into new IUCN Red List categories based on their estimated N_e in order to quantify the changes in risk categorization that would happen if the Red List considered N_e. Under a genetics viewpoint, if the N_e estimate was less than 50 individuals, the species might be moved from its original EN category into the critically endangered (CR) category, per IUCN Red List Criterion D guidelines.

Thirty-nine assessments of 170 within our working dataset reported generation length. For these 39 species, we estimated loss of heterozygosity over the next 100 years using the following equation (Wright 1931):

$$\% \text{ heterozygosity remaining} = [1-(1/(2*N_e)]^t$$

where N_e was estimated using the N_e/N_c ratios of 0.4 and 0.1, N_c is directly from the Red List assessment (reported as the number of mature adults), and t is the number of generations in 100 years. The number of generations (t) was estimated by dividing 100 by the generation length reported within the Red List assessments.

Results

Since 2001 and in the present guidelines, the number of “mature individuals” is defined as “the number of individuals known, estimated or inferred to be capable of reproduction”; therefore, population sizes for IUCN Red List listed species are contingent upon reproductive maturity (IUCN 2001; IUCN 2019). While the text in versions 6 through 14 (years 2006 to 2019) includes using lower population size estimations in cases of biased adult or breeding sex ratios, Version 13 (2017) added the following text explicitly regarding effective population size, which is still present in the current guidelines:

> “Note that effective population size (N_e) cannot be used as an estimate of the number of mature individuals. One reason is that reproductively suppressed individuals do not contribute to the calculation of N_e, but, as explained above, they may be counted as mature individuals.”

In our working dataset of 170 assessments, 96 (~ 56%) assessments did not report any primary, peer-reviewed literature within the “Population” section of text in relation to the estimate given for population size (i.e., the number of mature individuals). Sixty-three assessments of the 96 lacked any type of cited source for the estimation of mature individuals, and the other 33 cited secondary sources, personal communications, and unpublished results. Additionally, 131/170 (~ 77%) did not report the method of estimating the number of mature individuals. For the 39 assessments that provided a primary source citation for the mature individual estimates, 28 reported a methodology for the estimation. While 76/170 (~ 45%) of the assessments reported a range of values for this estimate, uncertainty of the estimate was never discussed or estimated within the "Population" section text.

No assessments in the final dataset relayed the information necessary to estimate N_e based on demographic data (e.g., sex ratio, variance in family size or reproductive success, etc.), verified by manual inspection. When using an estimated N_e/N_c ratio of 0.4, 42 species (24.7%) had an estimated effective population size below 50, and thus could warrant moving from the EN to CR threat category. When using an estimated N_e/N_c ratio of 0.1, 168 (98.8%) EN species had an estimated effective size < 50, and could likewise warrant moving into the CR category (Fig. 1; Online Resource 1).

When estimating loss of heterozygosity over the next 100 years, the average *H*-loss among species (estimated by 0.4 and 0.1 N_e /Nc ratios) was 9% for an N_e/N_c ratio of 0.4 and 29% for an N_e/N_c ratio of 0.1 (Fig. 2; Online Resource 2). Only 13 or 1 (using 0.4 and 0.1 N_e/N_c ratios) of these 39 species with reported generation times are expected to retain > 95% heterozygosity.

Discussion

Over the past decade, several calls have been made to apply conservation genetics to policy (Laikre 2010; Storfer et al. 2010; Hoban et al. 2013; Garner et al. 2016). In spite of several examples, there remains a frequent disconnect between genetic concepts and data and conservation policies and management (Santamaria and Mendez 2012). Here we used a range of common estimations to help bridge fundamental genetic concepts and one of the largest conservation instruments available, the IUCN Red List. Under current IUCN Red List guidelines, practitioners do not report effective population size (N_e) estimates, or metrics needed to estimate N_e, to compliment the number of mature adults (N_c), despite the utility of N_e in risk assessment for populations. There is reason for this- if some species were assessed using both N_e and N_c while others were assessed only by N_c, the Red List might be less useful for prioritizing or ranking conservation action, as species often need to be assessed with the same criteria. Nonetheless, the clear relevance of N_e for species and population survival cannot be ignored in the Red List or in conservation assessments broadly.

The Red List defines population size (again, note that for the IUCN Red List this refers to the species as a whole and not individual populations) as the number of mature individuals capable of reproduction; however, the number of individuals that *successfully* reproduce (and produce offspring that survive to maturity) is generally much lower than the number that are capable of reproducing. Furthermore, in many cases there is a large variance in reproductive output, so the concept of effective population size is a highly useful complement to N_c when assessing population viability (Frankham 1995; Lacy 2019).

In our analyses, we found several issues in how IUCN assessments report on the number of mature individuals; addressing these issues would make it easier to more precisely estimate N_e and loss of heterozygosity. We strongly recommend reporting demographic metrics necessary for estimating N_e (e.g., number of mature or reproducing males and females, adult sex ratio, longevity, family size variance, etc.). This will help practitioners to calculate N_e and also collaborate with geneticists (as recommended by Holderegger et al. 2019) to improve threat categorizations and reduce extinction risk and rates. Additionally, to improve standardization in reporting, we recommend assessors provide details of methods used and more explicitly highlight uncertainty in estimates of population size. It would be also valuable if information could be included, in a standardized way, on the history of a species' demographic decline (e.g., historic population size estimates and timing of decline), which could facilitate much more precise estimation of metrics including loss of heterozygosity (sensu Hoban et al. 2014) and number of generations at small N_e. We recognize that both time and expense is a significant consideration when collecting data on the biological characteristics mentioned here. In situations where conditions are rapidly changing and a species is at a high risk of extinction, there might not be time to collect these data. Therefore, we do not argue that these measurements be taken no matter what, but rather that biologists should include them in assessments when possible as there is definitive value in recording such information.

The majority of species in our working dataset were plants, with ~ 17% belonging to the *Sorbus* (rose family) genus. This bias likely reflects that there are many rare species in this genus, but may reflect disproportionate Red List contributions from certain botanists or countries. To investigate a potential taxonomic bias in the results, we removed these species from the working dataset and re-calculated the percent of species with an estimated effective population size below 50 (and thus potentially warranting a move from the EN to CR threat category), again using N_e/N_c of 0.4 and 0.1. However, the results we obtained when removing these species were similar to the original results, with 17.1% when using $N_e/N_c = 0.4$ (compared to 24.7% before the removal of *Sorbus* species) and 99.3% when using $N_e/N_c = 0.1$ (compared to 98.8% before the removal of *Sorbus* species).

Additionally, we found that close to ¼ (51/222) of the assessments listed as EN under Criterion D (i.e., population size < 250) didn't report a population size estimate, despite Criterion D being contingent upon this estimate. In cases like this where populations are small but estimating a census size is difficult, the use of genetic markers and an acceptance of N_e as a metric under Criterion D could provide more information that what is currently available. Sometimes it is easier to estimate N_e using genetic markers than to estimate N_c by traditional methods, because genetic markers can be applied to scat, hair, feathers, or other remnants of an individual (Taberlet et al. 1999). Genetic markers can be used to estimate N_c through capture-mark-recapture (CMR) methods, and additionally, genetic analysis costs are plummeting and transfer of markers between species is increasingly feasible (e.g., Andrews et al. 2016).

Effective population size estimates can vary widely depending on sampling, assumptions, the estimator, and more. While our “rule of thumb” estimates of N_e/N_c equal to 0.4 and 0.1 represent a wide range and a simplistic approach, they are still useful in determining the range of likely actual N_e value. Using the larger 0.4 estimate still resulted in close to ¼ of the EN species having an estimated $N_e < 50$, meaning they could be candidates for the CR category. Other groups have suggested that an N_e/N_c ratio of 0.14 is actually an overestimate for many species (Palstra and Ruzzante 2008), meaning our results using a ratio of 0.1 could often be closer to reality. In the 0.1 case, all but two of the 170 species would be moved into the CR category. Though it is theoretically possible that species sorted into threat categories based on small population sizes could have experienced genetic purging and are less susceptible to genetic effects, most threatened species are recently declining and have not been at low populations over long periods of time. While we recognize the potential pitfalls in using the same N_e/N_c ratio across taxa, this study represents a critical starting point and highlights a key message—many species are in a critical situation due to small effective population size, inbreeding, loss of variation fixation of deleterious alleles, and reduced long-term viability. The IUCN Red List status of “endangered” (EN) may not highlight the urgency of this situation, and we aim to make clear to non-genetics experts the scope of this problem.

One major asset of the Red List is its relatively unchanged nature over time, and hence the ability to track temporal changes. Nonetheless, our findings suggest many species may have effective population sizes substantially below recommended conservation thresholds ($N_e < 50$) and that the Red List criteria overlook important genetic and evolutionary processes like strong genetic drift, inbreeding, and loss of heterozygosity. This and previous findings that genetic diversity is not well predicted by RL status argue that there is room for improvement in the incorporation of genetic considerations into the IUCN Red List. Willoughby et al. (2015) examined the relationship between IUCN RL category and microsatellite diversity and determined whether IUCN criteria are effective at identifying low genetic diversity species; generally, genetic diversity did not correlate with IUCN Red List category. The team suggested a genetic IUCN criterion with a conceptual outline that includes estimation of census size, effective population size, neutral genetic diversity, reference genetic diversity, and number of generations until reaching a certain heterozygosity-loss cutoff value. Here, we are also suggesting that Ne (and the predicted loss of heterozygosity) be considered as additional important information to supplement reporting and assessments because genetic factors (e.g., drift, inbreeding depression) reduce population persistence (Allendorf and Ryman 2002; Lacy 2019).

Feasible solutions may include a new category for listing, e.g., “Category F: Effective Population Size < 50”, or creation of an alternative (additional or independent) list including genetic factors in assessments (e.g., a “Red-Genes List”). Lists complementary to the Red List, e.g., the Green List, have proven successful (Akcakaya et al. 2018). Other assessment devices exist including the national endangered species lists, the NatureServe list, BGCI ThreatList, and the European Union Habitats Directive, and these could consider N_e. Additionally, IUCN guidelines could be updated to include suggested, but optional, fields for reporting demographic and life history metrics (e.g., sex ratio, family size variation, mating strategy, birth and death rates, reproductive output) when possible, which can be used by conservation geneticists and other practitioners to estimate N_e separately and precisely for each species.

Our results also have usefulness in the context of the Convention on Biological Diversity Target 13 on “genetic erosion”. The Red List Index is currently an indicator for this Target but we suggest that a rule of thumb such as $0.4N_c$ below thresholds such as 50 and 500 could be complementary with more genetic relevance and a better predictor of extinction risk (Laikre et al. 2020, Hoban et al. 2020). We acknowledge that this approach is imperfect, but including genetic factors (which have known influences on population persistence) is an improvement over no indicators at all. We hope these results and perspectives motivate improved risk assessment and conservation of threatened species while advancing quantitative biodiversity monitoring broadly.

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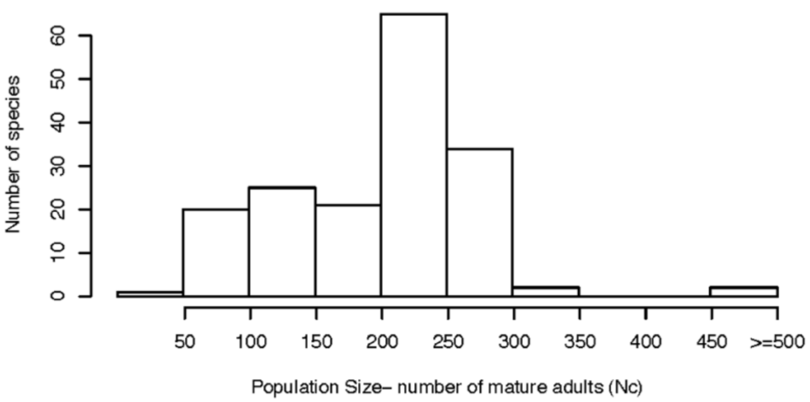
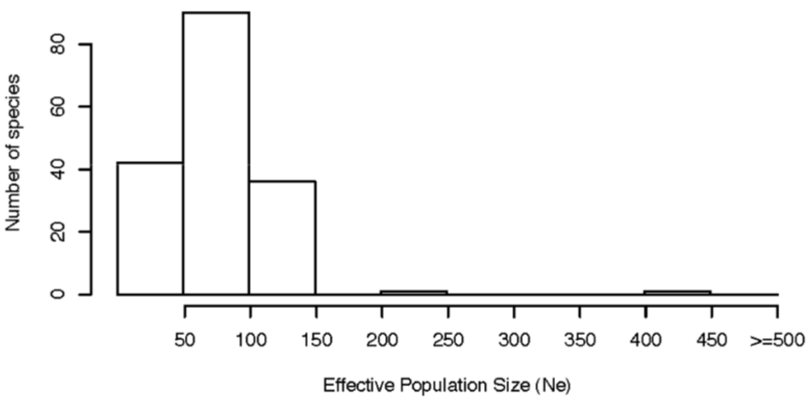
(a) Nc



(b) Ne using Ne=0.4*Nc



(c) Ne using Ne=0.1*Nc

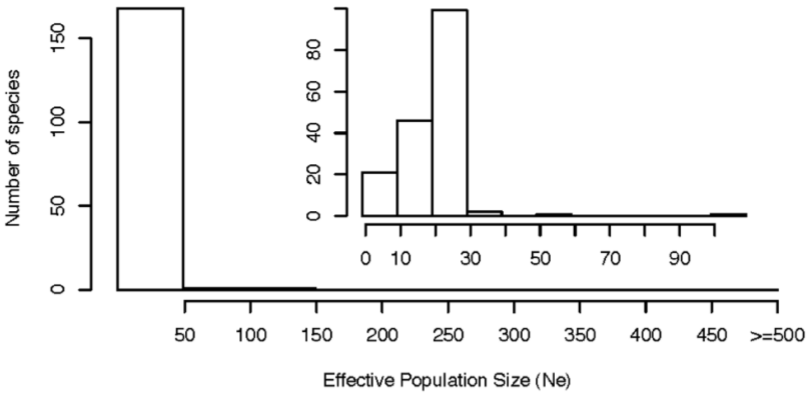


Figure 1. Histograms of a population census size N_c (i.e., number of mature individuals reported within the Red List), b 0.4 N_c (representing $N_e/N_c = 0.4$), and c) 0.1 N_c (representing $N_e/N_c = 0.1$)

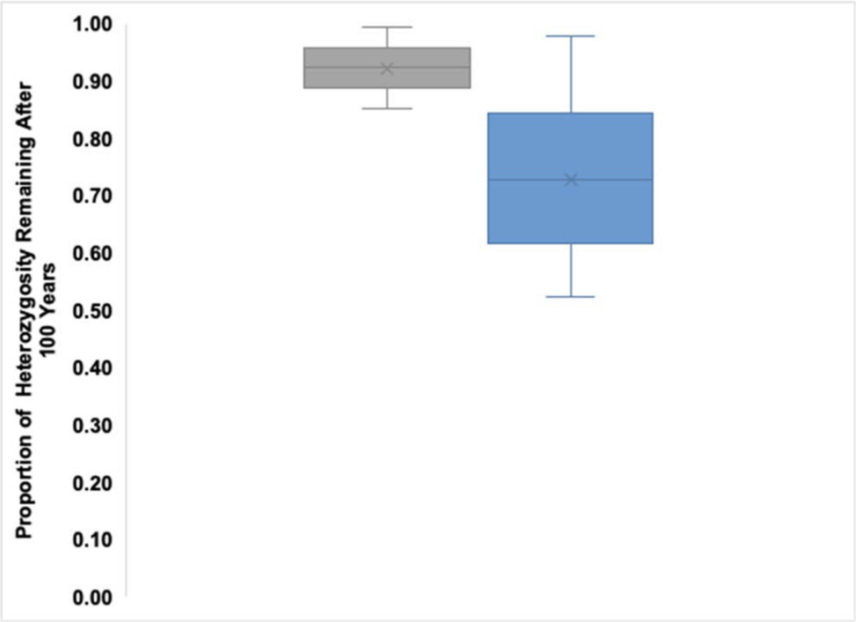


Figure 2. Box plots showing the estimated remaining heterozygosity for 39 species after the next 100 years assuming an N_e/N_c ratio of 0.4 (grey), and 0.1 (blue)

Online Resource 1. Effective population size estimates for all species in final dataset (n=170) based on 0.4 and 0.1 estimates of the N_e/N_c ratio. N_c is the number of mature individuals or adults reported in the IUCN Red List. This number is commonly used and reported as the "population census size" in the literature. This final data set includes all EN (endangered) species assessments listed under Criterion D with a reported population size estimate. We highlighted in red those species with an estimated N_e <50 (i.e., those that would move into the CR category) for the 0.4 and also the 0.1 N_e/N_c ratio-based estimation of N_e.

Scientific Name	**N_c max.**	**0.4 N_c**	**IUCN Category**	**0.1 N_c**	**IUCN Category**
Berlinia rabiensis	4	1.6	CR	0.4	CR
Sorbus leighensis	52	20.8	CR	5.2	CR
Sorbus eminentiformis	54	21.6	CR	5.4	CR
Dypsis schatzii	60	24	CR	6	CR
Dypsis ceracea	60	24	CR	6	CR
Sorbus wilmottiana	60	24	CR	6	CR
Sorbus herefordensis	60	24	CR	6	CR
Sorbus admonitor	60	24	CR	6	CR
Sorbus adeana	70	28	CR	7	CR
Sorbus haesitans	70	28	CR	7	CR
Sorbus leptophylla	74	29.6	CR	7.4	CR
Zoogoneticus tequila	80	32	CR	8	CR
Nepenthes tenuis	80	32	CR	8	CR
Kindia gangan	86	34.4	CR	8.6	CR
Ostrya trichocarpa	90	36	CR	9	CR

Platanthera yosemitensis	90	36	CR	9	CR
Diomedea amsterdamensis	92	36.8	CR	9.2	CR
Dypsis moorei	99	39.6	CR	9.9	CR
Limonium poimenum	99	39.6	CR	9.9	CR
Dypsis boiviniana	99	39.6	CR	9.9	CR
Acmadenia candida	99	39.6	CR	9.9	CR
Paludomus ajanensis	100	40	CR	10	CR
Sorbus subarranensis	100	40	CR	10	CR
Parodia hausteiniana	100	40	CR	10	CR
Paraboea chiangdaoensis	100	40	CR	10	CR
Nepenthes paniculata	100	40	CR	10	CR
Pedicularis sanguilimbata	100	40	CR	10	CR
Sorbus amici-petri	100	40	CR	10	CR
Sorbus cordigastensis	100	40	CR	10	CR
Sorbus fischeri	100	40	CR	10	CR
Sorbus ratisbonensis	100	40	CR	10	CR
Lecomtedoxa plumosa	100	40	CR	10	CR
Marcetella maderensis	100	40	CR	10	CR
Sorbus roopiana	100	40	CR	10	CR
Silene orphanidis	100	40	CR	10	CR
Magnolia viridipetala	100	40	CR	10	CR
Sorbus thaiszii	100	40	CR	10	CR
Sorbus magocsyana	100	40	CR	10	CR
Deutzia yaeyamensis	100	40	CR	10	CR
Sorbus stenophylla	100	40	CR	10	CR
Centranthus trinervis	112	44.8	CR	11.2	CR
Sorbus cuneifolia	122	48.8	CR	12.2	CR
Xysmalobium samoritourei	130	52	EN	13	CR
Bassia saxicola	135	54	EN	13.5	CR
Dypsis acuminum	140	56	EN	14	CR
Duellmanohyla uranochroa	149	59.6	EN	14.9	CR
Rhinopoma hadramauticum	150	60	EN	15	CR
Lonchorhina fernandezi	150	60	EN	15	CR
Dypsis fanjana	150	60	EN	15	CR
Barbarea lepuznica	150	60	EN	15	CR
Sorbus subcuneata	150	60	EN	15	CR
Sorbus bristoliensis	150	60	EN	15	CR
Sorbus hoppeana	150	60	EN	15	CR
Raphionacme caerulea	150	60	EN	15	CR
Sorbus madoniensis	150	60	EN	15	CR

Poa riphaea	150	60	EN	15	CR
Lynx pardinus	156	62.4	EN	15.6	CR
Pterodroma madeira	160	64	EN	16	CR
Marsdenia exellii	160	64	EN	16	CR
Sorbus cambrensis	170	68	EN	17	CR
Equus ferus	178	71.2	EN	17.8	CR
Gluema korupensis	178	71.2	EN	17.8	CR
Edolisoma nesiotis	180	72	EN	18	CR
Copsychus sechellarum	190	76	EN	19	CR
Pisonia sechellarum	190	76	EN	19	CR
Pterodroma cahow	196	78.4	EN	19.6	CR
Dypsis corniculata	199	79.6	EN	19.9	CR
Namkungia biryongensis	200	80	EN	20	CR
Inversodicraea pepehabai	200	80	EN	20	CR
Acrostira tenerifae	200	80	EN	20	CR
Penelope albipennis	200	80	EN	20	CR
Magnolia angustioblonga	200	80	EN	20	CR
Dypsis bosseri	200	80	EN	20	CR
Paraboea rabilii	200	80	EN	20	CR
Ravenea albicans	200	80	EN	20	CR
Ravenea dransfieldii	200	80	EN	20	CR
Toussaintia patriciae	200	80	EN	20	CR
Magnolia odoratissima	200	80	EN	20	CR
Narcissus albimarginatus	200	80	EN	20	CR
Nepenthes adnata	200	80	EN	20	CR
Euphorbia rugosiflora	200	80	EN	20	CR
Sorbus pseudothuringiaca	200	80	EN	20	CR
Sorbus doerriana	200	80	EN	20	CR
Anas nesiotis	200	80	EN	20	CR
Ognorhynchus icterotis	212	84.8	EN	21.2	CR
Thinornis novaeseelandiae	220	88	EN	22	CR
Atlapetes pallidiceps	226	90.4	EN	22.6	CR
Petroica traversi	230	92	EN	23	CR
Hypotaenidia sylvestris	232	92.8	EN	23.2	CR
Echinodontium ballouii	240	96	EN	24	CR
Myotis planiceps	240	96	EN	24	CR
Aloe cremnophila	240	96	EN	24	CR
Amazona imperialis	240	96	EN	24	CR
Pholidoscelis corax	249	99.6	EN	24.9	CR
Ramalina confertula	249	99.6	EN	24.9	CR

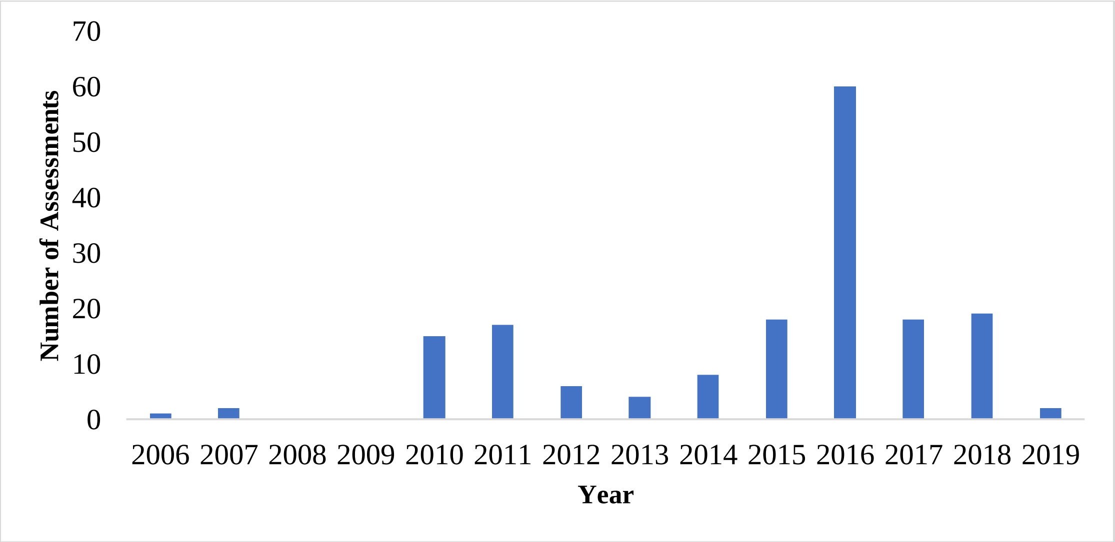
Saltuarius eximius	249	99.6	EN	24.9	CR
Gastrotheca dendronastes	249	99.6	EN	24.9	CR
Ramalina timdaliana	249	99.6	EN	24.9	CR
Ducula galeata	249	99.6	EN	24.9	CR
Etlingera kenyalang	249	99.6	EN	24.9	CR
Bystropogon maderensis	249	99.6	EN	24.9	CR
Centrolene medemi	249	99.6	EN	24.9	CR
Hottea miragoanae	249	99.6	EN	24.9	CR
Gymnocalycium amerhauseri	249	99.6	EN	24.9	CR
Eriosyce sociabilis	249	99.6	EN	24.9	CR
Raphionacme keayi	249	99.6	EN	24.9	CR
Gaertnera spicata	249	99.6	EN	24.9	CR
Cipocereus laniflorus	249	99.6	EN	24.9	CR
Nymphoides herzogii	249	99.6	EN	24.9	CR
Rhynchostegium strongylense	249	99.6	EN	24.9	CR
Seligeria carniolica	249	99.6	EN	24.9	CR
Sticta alpinotropica	249	99.6	EN	24.9	CR
Dichapetalum potamophilum	249	99.6	EN	24.9	CR
Geronticus eremita	249	99.6	EN	24.9	CR
Epipactis olympica	249	99.6	EN	24.9	CR
Erythropitta palliceps	249	99.6	EN	24.9	CR
Alopecoenas rubescens	249	99.6	EN	24.9	CR
Erythropitta caeruleitorques	249	99.6	EN	24.9	CR
Megalurulus rufus	249	99.6	EN	24.9	CR
Geissois bradfordii	249	99.6	EN	24.9	CR
Haematopus chathamensis	249	99.6	EN	24.9	CR
Artisornis sousae	249	99.6	EN	24.9	CR
Chlorophoneus kupeensis	249	99.6	EN	24.9	CR
Nesospiza wilkinsi	249	99.6	EN	24.9	CR
Rhyticeros narcondami	249	99.6	EN	24.9	CR
Cyclopsitta coxeni	249	99.6	EN	24.9	CR
Grus americana	249	99.6	EN	24.9	CR
Fringilla polatzeki	249	99.6	EN	24.9	CR
Camellia huana	249	99.6	EN	24.9	CR
Hibbertia margaretae	249	99.6	EN	24.9	CR
Meistera stephanocolea	249	99.6	EN	24.9	CR
Junco insularis	249	99.6	EN	24.9	CR
Garra dunsirei	250	100	EN	25	CR
Wagenitzia lancifolia	250	100	EN	25	CR
Hexalectris warnockii	250	100	EN	25	CR

Exsertotheca baetica	250	100	EN	25	CR
Ulota macrospora	250	100	EN	25	CR
Saxifraga presolanensis	250	100	EN	25	CR
Cercopithecus dryas	250	100	EN	25	CR
Sorbus sognensis	250	100	EN	25	CR
Labidochromis zebroides	250	100	EN	25	CR
Gypsophila papillosa	250	100	EN	25	CR
Aster sorrentinii	250	100	EN	25	CR
Linaria tonzigii	250	100	EN	25	CR
Stipa veneta	250	100	EN	25	CR
Asarum hatsushimae	250	100	EN	25	CR
Cailliella praerupticola	250	100	EN	25	CR
Sorbus legrei	250	100	EN	25	CR
Sideroxylon canariense	250	100	EN	25	CR
Pomarea mendozae	250	100	EN	25	CR
Allophylus samoritourei	250	100	EN	25	CR
Cheirolophus massonianus	250	100	EN	25	CR
Sorbus subpinnata	250	100	EN	25	CR
Sorbus klasterskyana	250	100	EN	25	CR
Crinodendron brasiliense	250	100	EN	25	CR
Xenopoecilus bonneorum	250	100	EN	25	CR
Manilkara lososiana	250	100	EN	25	CR
Euphorbia uniglans	250	100	EN	25	CR
Argyranthemum thalassophilum	250	100	EN	25	CR
Musschia wollastonii	250	100	EN	25	CR
Asarum nazeanum	250	100	EN	25	CR
Hymenostylium gracillimum	250	100	EN	25	CR
Arvernella microclada	250	100	EN	25	CR
Molendoa taeniatifolia	250	100	EN	25	CR
Magnolia lacei	260	104	EN	26	CR
Porphyrio hochstetteri	280	112	EN	28	CR
Epipactis cupaniana	300	120	EN	30	CR
Otus insularis	300	120	EN	30	CR
Sorbus slovenica	500	200	EN	50	EN
Alopecoenas sanctaecrucis	1070	428	EN	107	EN

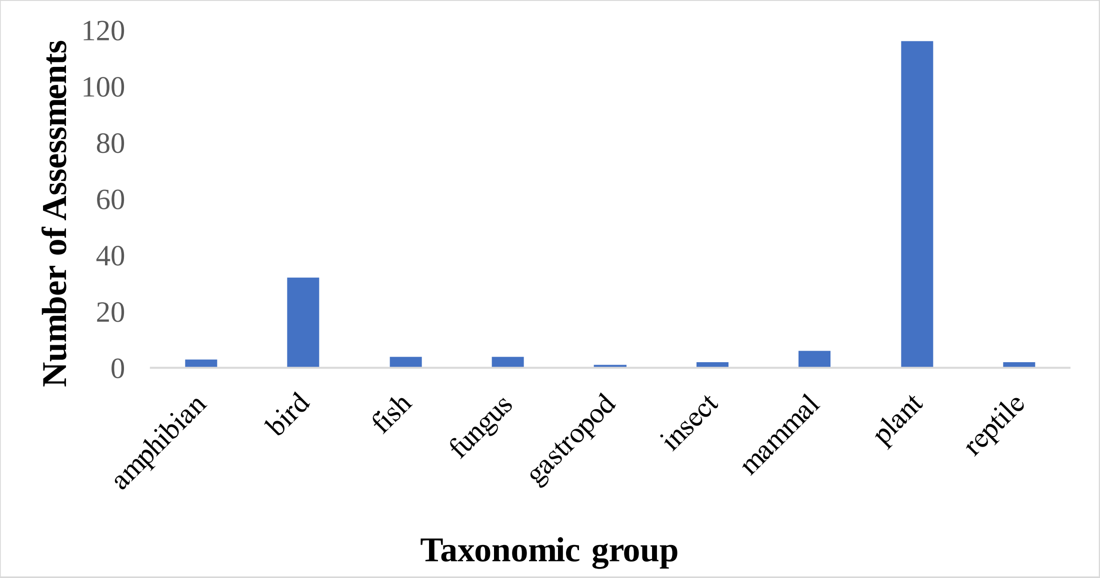
Online Resource 2. Estimation of proportion of heterozygosity (*H*) remaining after 100 years, based on N_e/N_c ratios of 0.4 and 0.1. Generation length was provided within the Red List assessment for each species. Highlighted in red are species with <95% H remaining.

Scientific Name	**Gen. length (years)**	**Gens. in 100 years**	**N_c max est.**	**0.4 N_c**	**0.1N_c**	**0.4 prop. *H* remain**	**0.1 prop. *H* remain**
Labidochromis zebroides	1	100.00	250	100	25	0.61	0.13
Hypotaenidia sylvestris	3.4	29.41	232	92.8	23.2	0.85	0.53
Megalurulus rufus	3.6	27.78	249	99.6	24.9	0.87	0.57
Artisornis sousae	3.6	27.78	249	99.6	24.9	0.87	0.57
Copsychus sechellarum	3.6	27.78	190	76	19	0.83	0.48
Junco insularis	3.6	27.78	249	99.6	24.9	0.87	0.57
Otus insularis	3.7	27.03	300	120	30	0.89	0.63
Nesospiza wilkinsi	3.8	26.32	249	99.6	24.9	0.88	0.59
Atlapetes pallidiceps	3.8	26.32	226	90.4	22.6	0.86	0.56
Erythropitta palliceps	4.2	23.81	249	99.6	24.9	0.89	0.62
Erythropitta caeruleitorques	4.2	23.81	249	99.6	24.9	0.89	0.62
Chlorophoneus kupeensis	4.4	22.73	249	99.6	24.9	0.89	0.63
Edolisoma nesiotis	4.6	21.74	180	72	18	0.86	0.54
Cyclopsitta coxeni	4.8	20.83	249	99.6	24.9	0.90	0.66
Penelope albipennis	5.7	17.54	200	80	20	0.90	0.64
Fringilla polatzeki	5.7	17.54	249	99.6	24.9	0.92	0.70
Alopecoenas rubescens	6.6	15.15	249	99.6	24.9	0.93	0.74
Anas nesiotis	6.6	15.15	200	80	20	0.91	0.68
Ducula galeata	6.6	15.15	249	99.6	24.9	0.93	0.74
Alopecoenas sanctaecrucis	6.6	15.15	1070	428	107	0.98	0.93
Thinornis novaeseelandiae	6.7	14.93	220	88	22	0.92	0.71
Pomarea mendozae	6.9	14.49	250	100	25	0.93	0.75
Namkungia biryongensis	7	14.29	200	80	20	0.91	0.70
Petroica traversi	7	14.29	230	92	23	0.93	0.73
Ognorhynchus icterotis	7.5	13.33	212	84.8	21.2	0.92	0.73
Geronticus eremita	8	12.50	249	99.6	24.9	0.94	0.78
Porphyrio hochstetteri	9.8	10.20	280	112	28	0.96	0.83
Nepenthes tenuis	10	10.00	80	32	8	0.85	0.52
Amazona imperialis	12.3	8.13	240	96	24	0.96	0.84
Grus americana	13.1	7.63	249	99.6	24.9	0.96	0.86
Haematopus chathamensis	13.7	7.30	249	99.6	24.9	0.96	0.86
Pterodroma cahow	15.6	6.41	196	78.4	19.6	0.96	0.85
Echinodontium ballouii	17	5.88	240	96	24	0.97	0.88
Rhyticeros narcondami	19	5.26	249	99.6	24.9	0.97	0.90
Diomedea amsterdamensis	27.2	3.68	92	36.8	9.2	0.95	0.81
Pterodroma madeira	28	3.57	160	64	16	0.97	0.89

Sorbus subarranensis	30	3.33	100	40	10	0.96	0.84
Sorbus subpinnata	30	3.33	250	100	25	0.98	0.93
Allophylus samoritourei	100	1.00	250	100	25	1.00	0.98
Average						**91%**	**71%**



Online Resource 3. Number of assessments in final dataset (n=170) that were completed each year, sorted by year.



Online Resource 4. Number of assessments in final dataset (n=170) sorted by broad taxonomic group.

Chapter 3: Extinction Risk and Improved Use of Genetics in the IUCN Red List

Brittany A. Garner, Sean Hoban, Gordon Luikart

Abstract

The International Union for Conservation of Nature's (IUCN) Red List of Threatened Species is the most comprehensive and global set of species' conservation and risk assessments. The list is based on rigorous criteria, primarily a species' demographic status (e.g., abundance) and geographic range. The Red List seldom incorporates genetic threats or principles, despite wide recognition of genetic diversity as a fundamental level of biodiversity, and its association with extinction risk. We investigated the extent to which genetic threats and principles are mentioned within all IUCN Red List threat assessment rationales (n = 98,512) using automated and manual search methods. This study is the largest global analysis of genetic considerations in threat assessments to date, analyzing >90,000 species assessments with a standardized methodology. We calculated the proportion of species assessments that explicitly consider genetics in their threat determination across different Red List categories and criteria, taxonomy, habitats, biogeography, and assessment years. In addition, we compared types of genetics applications (e.g., different questions or threats) and quantified the use of effective population size (N_e) within Red List assessments. Only 263 out of 98,512 available Red List assessments explicitly used genetic data, principles, concepts, or tests (0.267%), while only 0.010% used N_e. Genetic diversity was more frequently mentioned in higher threat categories (e.g., Endangered or Critically Endangered), and in certain habitats, regions, and taxonomic groups, and in more recent years. Hybridization was the most frequent genetic topic mentioned, followed by gene flow and genetic diversity. Our results point to several suggestions for increasing the effective use of genetics in biodiversity assessments, including within the IUCN Red List. Quantifying trends and biases in use of genetics will allow practitioners to reassess and improve the use of genetics in assessments, leading to more well-informed and comprehensive assessments and ultimately conservation action.

Keywords

IUCN Red List; policy; effective population size; conservation genetics; population viability; threat assessment

Introduction

Loss of biodiversity is a mark of the Anthropocene- a geological epoch where humans are the dominant force shaping the trajectory of biotic and abiotic processes across the globe. While human activities threaten approximately 20% to 40% of mammals, birds, reptiles, amphibians, plants, and other taxa with extinction over the next few decades (IUCN 2019), humans are working to quantitatively assess these risks and identify and prioritize actions to slow this loss of biodiversity. The largest and most influential worldwide source for information on the conservation status of both animals and plants is the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species. For extant organisms with adequate population-level data, the Red List assigns an extinction risk category: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), or Critically Endangered (CR). Species are assigned to risk categories based upon five primary criteria: A (past, present, and/or projected population decline), B (geographic range size, and fragmentation, decline or fluctuations), C (small population size and fragmentation, decline, or fluctuations), D (very small population or very restricted distribution), and E (quantitative analysis of extinction risk) (Mace & Lande 1991; IUCN 2012). The Red List is used to inform decision makers, allocate scarce conservation resources to species of high need, measure progress on international biodiversity commitments, inform conservation planning, and raise awareness.

The criteria noted above all pertain to demographic status; however, genetic parameters are also useful in assessing conservation priority and risk assessment, particularly when extinction risks are difficult to infer from ecological and demographic data alone (Dunham et al. 1999; Frankham 2010; Allendorf et al. 2013). Overall, genetic processes like inbreeding depression (Frankham 2005), loss of genetic diversity (Spielman et al. 2004), and a reduction in gene flow (Frankham 2015) can contribute to the extinction risk of a species. Leaving out genetic factors in population vulnerability or risk assessments can be misleading or result in biased conclusions (Allendorf & Ryman 2002; Wade et al. 2016, 2017; Pacioni et al. 2018). Additionally, genetic parameters like genetic diversity are widely recognized as a main level of biodiversity deserving of conservation (United Nations 1992), suggesting that effective, comprehensive conservation efforts would include genetic data and principles.

In addition to factors like genetic diversity and gene flow, the effective size of a population, N_e, is well suited for predicting and monitoring populations at risk of extinction. N_e is defined as the size of the ideal population with the same rate of genetic drift as in the actual population being considered (Fisher 1930; Wright 1931), and is often only between <5% and 20% of adult abundance (N_c). Thus, a hypothetical population with $N_c = 5\ 000$ may experience genetic erosion at a much higher rate than expected because its N_e may often be 1000, or even as low as 250. N_e is mathematically related to heterozygosity, and can aid in assessing and predicting changes in genetic diversity and inbreeding within populations at risk. For example, N_e ranging from around 50 to several hundred is within the range where deleterious effects of inbreeding may develop and genetic variation may be lost rapidly due to genetic drift (Frankham et al. 2002; Hoarau et al. 2005; Jamieson & Allendorf 2012). Populations with low N_e are also less able to adapt to changing environments, because the effectiveness of natural selection is weak relative to genetic drift. Therefore, a significantly small (and declining) N_e is problematic for genetic “health” and long-term population persistence, and thus is of concern to conservation biologists (Allendorf & Ryman 2002).

Genetic data and principles have been considered for assessing extinction threats in international frameworks, including within the IUCN Red List (Laikre 2010; Frankham et al. 2014; Rivers et al. 2014). Frankham et al. (2014) investigated relationships between effective population size, minimum viable population size, and IUCN Red List criteria. They concluded that IUCN Red List population size thresholds are derived from N_e concepts, but that the methods for incorporating genetic risks into the categorization should be revised to increase cut-off values for Red List population size criteria.

Additionally, Willoughby et al. (2015) investigated relationships between IUCN Red List categories and microsatellite diversity and determined which IUCN criteria (A-E) are most correlated with genetic diversity. Overall, the authors found that vertebrate populations listed in threatened categories on the Red List generally had more reduction in genetic diversity than populations listed as Near Threatened or Least Concern, but that the specific Red List criteria A-E did not systematically identify species with low genetic diversity. In addition, the same authors concluded that these criteria do not necessarily identify species with low N_e, and recommended that the IUCN Red List incorporate both N_e and genetic diversity in determining threat categories.

Despite these and other findings of limited genetics use in policy and listing, several groups are currently making progress toward incorporating genetic metrics and principles, in part due to the increasing availability and decreased cost of genetic data. For example, Aichi Target 13 of the Convention on Biological Diversity is explicitly aimed at preserving genetic diversity, the IUCN has established a Conservation Genetics Specialist Group, and both GEOBON and the Society for Conservation Biology have launched working groups to provide conservation genetic guidance. These efforts demonstrate an increasing policy emphasis on genetics in conservation; however, taxonomic biases in conservation biology and genetics research have been documented (Clark & May, 2002; Pérez-Espona 2017). For example, species with existing genetic tools may receive disproportionately more genetic consideration. Similarly, wealthy countries might incorporate genetics more often simply due to availability of resources. Analyzing and quantifying trends and biases in the use of genetics will allow practitioners to reassess and improve the use of genetics in assessments, leading to more well-informed, comprehensive assessments and conservation action.

As the IUCN Red List is the largest global biodiversity assessment platform, we directed our analyses toward the text of risk assessments for species on this registry. In this study, we filtered all assessments in the Red List to only include those that demonstrated a direct consideration of genetic data and principles in the threat determination of the species. This allowed us to quantify a) how often genetic data, parameters, and principles are used in the IUCN Red List, b) what biases exist within that usage, to identify why genetics is used in some assessment rationales and not others, and c) the types of genetic concepts or metrics used in species-level threat assessments. We hope that quantifying and reporting the current use of genetic data and biases in IUCN listings will allow conservation scientists and working groups to identify and address barriers to entry for using genetics in conservation, thereby improving and increasing the use of these concepts and data in biodiversity conservation.

Methods

To quantify the use of genetics and use biases within the IUCN Red List, we analyzed the risk category "Rationale" sections within all available Red List version 2019-1 assessments using automated and manual methods. We calculated proportions of assessments using genetics for different Red List threat categories, Red List criteria, taxonomic kingdoms and classes, habitat systems, biogeographical realms, and assessment years. In addition, we compared the types of conservation genetics topics addressed and quantified the proportion of assessments that use effective population size (N_e).

Source material and search terms:

We directly downloaded all available IUCN Red List species assessments (n = 98 512) through the online Red List search portal at www.redlist.org. Assessment text included full taxonomy, Red List threat category (e.g., Vulnerable, Endangered, etc.), year of assessment publication, rationale for the assigned threat category, population size estimates, population trend, range description, documentation of use and/or trade, habitat system, biogeographical realm, and current conservation actions. The "Rationale" section includes the justification for both the Red List category and Red List criteria each species is listed under, and we mined the text of each assessment's "Rationale" section within Microsoft Excel for entries in a genetics word list (Table A1).

We derived this comprehensive list of terms from several general categories within the field of conservation genetics, with input from subject matter textbooks and experts. A table of terms related to each of these general categories was constructed (Table A1), then text matching duplicates were removed from the list. The script returned a "TRUE" or "FALSE" response for each species assessment, where "TRUE" was returned if any terms within the genetics word list appeared in the assessment. Each "TRUE" entry was then manually inspected in a series of filtering steps (Figure 1A; Table A2).

Filtering:

The list of entries reporting "TRUE" for the initial search was manually filtered in a series of steps. First, unrelated or coincidental instances of genetics terms were removed, e.g., "locus typicus" used as a Latin descriptor but not related to a gene "locus" in English. Then, assessments were removed that recommended genetics as a next step, instead of being considered at present. A final filter removed assessments that mentioned a potential/likely genetic factor at play within the population or species. In these cases, genetics terms/concepts from the text list were mentioned and relevant, but included wording like "suggesting", "probably", "likely", etc. These were removed so that the only remaining assessments not only mentioned the use of genetics but included text that demonstrated a direct consideration of genetics in the threat determination of the species. These steps resulted in a final set of assessments that explicitly use actual empirical genetic data or principals in their IUCN Red List threat category determination. Overall proportions of assessments that passed all filtering steps were calculated for the total Red List (n = 98,512) in additional to several subgroups in further analyses.

Analyzing biases and types of genetics use:

In order to assess potential biases in genetics use throughout the IUCN Red List, we quantified and compared the final set of assessments across Red List threat category, Red List criteria, taxonomic kingdom and class, habitat system, biogeographic realm, and the year of assessment. In addition to quantifying differences in the overall use of genetics within these subgroups, we also quantified the types of uses of genetic data in order to investigate the relative use of specific genetics applications. These were categorized as genetic diversity, gene flow, abundance, taxonomy, and hybridization (Table 1), and assessments were sorted into one or more of these specific application categories (assessments with more than one application were counted in each category). All subsequent analyses within subgroups were conducted in order to understand where and how genetics is being used most often, and where and how it might be applied more effectively in the future. All statistical differences in proportions between groups were calculated using a X^2 test statistic within R (R Core Team 2016) using a Holm adjustment (Holm 1979). For small sample sizes, we used the Fisher exact test.

Effective population size:

We also quantified the use of empirical estimates and conceptual uses of effective population size (N_e) in the IUCN Red List. We searched all 98 512 available IUCN Red List assessments for text relating to both N_e and a related concept, the effective number of breeders (N_b). The "Rationale" section of each assessment was mined within Microsoft Excel for entries in an effective population size word list (Table A1). The script returned a "TRUE" or "FALSE" response for each species assessment, and each "TRUE" entry was manually inspected in a series of filtering steps (Figure 1B; Table A2).

The first filtering step removed false positives that were unrelated to the concepts in the list (e.g., a population section mentioning "range in NE India", where "NE" flagged a "TRUE" response). The second filter kept only those assessments that explicitly used N_e or N_b concepts to justify the threat category. The last filter kept only those that gave an empirical estimate of N_e or N_b. The proportion of assessments remaining after each filter was calculated for each Red List threat category, Red List criteria, taxonomic kingdom, habitat system, biogeographical realm, and year of assessment. Significant differences between proportions were calculated with paired X^2 tests and exact tests when sample sizes were small.

Results

Use of genetics in different Red List threat categories and criteria

In total, only 263 out of 98,512 available Red List assessments explicitly mentioned genetic data, principles, concepts, or tests in their "Rationale" sections (0.267%). We calculated use proportions and comparisons for all major threat categories (e.g., LC, NT, VU, EN, and CR) in the Red List (Figure 2). Assessments in threat category "Critically Endangered" (CR) had the highest proportion of genetics use (45 out of 9,175 EN assessments; 0.215%), and the "Least Concern" (LC) category had the least (46 out of 49,010 LC assessments; 0.09%). The proportion of assessments using genetics in the LC threat category was significantly lower (i.e., $P < 0.05$) than in all other threat categories (e.g., NT, VU, EN, and CR). The proportion of assessments using genetics in the NT and VU assessments were significantly different ($P < 0.05$) than the proportion of use in both the EN and CR categories. Overall, the use of genetics in assessments increased as the Red List threat category moved from LC to CR.

In addition to Red List categories, assessments with use of genetics ($n = 263$) were sorted and compared based on the IUCN Red List criteria used to assign species to IUCN Red List categories (e.g., Least Concern, Endangered). Broadly, these criteria are A (population size reduction), B (geographic range), C (small population size and decline), and D (very small or restricted population), and each assessment can be listed under multiple criteria. Criteria E (quantitative analysis) is listed within the Red List documentation but did not appear within this analysis. The highest proportion of usage was in criteria C (47/2,595; 1.81%), and the lowest proportion of usage was in criteria B

(106/17,677; 0.60%) (Figure A1). Statistically significant differences were found between proportions in criteria A and B, A and C, B and C, and C and D.

Type of genetics use within Red List threat categories

Assessments that passed all filtering steps (n = 263) for use of genetics were sorted into categories based on the type of genetic principal(s) and/or concepts(s) that were involved in their assessment's "Rationale" section (Figure 3a). The most significant difference between the proportion of assessments that explicitly used genetic diversity was between LC assessments and CR assessments. For gene flow, significant differences existed between LC assessments and all other threat categories, as well as between EN assessments and NT and VU assessments. For both gene flow and genetic diversity, the most significant differences in proportions were between LC assessments and EN and CR assessments, where the latter incorporated both gene flow and genetic diversity significantly more. There were no significant differences across threat categories between the proportions of assessments using genetics for both population abundance and taxonomy resolution. For hybridization, both LC and CR assessment use were significantly different than all other threat categories. Overall, the percentage of assessments sorted into the genetic diversity category increased as threat increased in the threatened categories (VU, EN, and CR). The highest proportion of assessments sorted into the hybridization category was in the CR threat category.

Overall use and type of use within taxonomic groups

Proportions of assessments with use of genetics (n = 263) were sorted and compared based on taxonomic kingdoms that were represented within the IUCN Red List in order to test for usage biases in different groups of species. There were statistically significant differences between proportions of genetics use in kingdoms Animalia and Fungi, Animalia and Plantae, and Fungi and Plantae. Kingdom Fungi had the highest proportion of overall use (6/91; 6.59%), whereas Kingdom Chromista had the lowest (0/15; 0.00%). In terms of genetic use type, the majority of assessments using genetics within Kingdom Fungi were sorted into the “abundance” and “taxonomy” use type categories, differing from patterns seen in Kingdom Animalia and Plantae (Figure 3c).

Within kingdom Animalia, 13/31 classes had assessments with direct use of genetics. The highest proportion of genetics use was in class Merostomata (1/4; 25%; Figure A1); however, there was only one assessment that used genetics, and the high proportion is due to a low total number of species in class Merostomata. In terms of raw numbers, the kingdom Animalia class with the highest usage of genetics was Actinopterygii, with n = 62 assessments passing all filtering criteria. One of five classes in kingdom Fungi used genetics (Agaricomycetes), as well as three of 18 classes in kingdom Plantae (Liliopsida, Magnoliopsida, and Pinopsida). In terms of raw numbers, when all classes with non-zero proportions were combined (Figure A1), class Merostomata (Kingdom Animalia) had the highest use, followed by class Agaricomycetes (Kingdom Fungi). Within Kingdom Animalia, classes Actinopterygii, Amphibia, Aves, Chondrichthyes, Gastropoda, Insecta, Mammalia, and Reptilia all had use proportions that were statistically significant different than at least one other class. No significant differences between classes were found in Kingdoms Fungi or Plantae.

Overall use within habitat systems, biogeographic realm, and assessment years

The highest proportion of usage was in Terrestrial/Marine (11/484; 2.27%), and the lowest proportion of usage was in Terrestrial/Freshwater (15/11,599; 0.13%) (Figure 4a). The most statistically significant differences were between Terrestrial/Marine assessments and Freshwater, Marine, Terrestrial, and Terrestrial/Freshwater assessments. Among biogeographical realms, the highest proportion of usage was in the Antarctic (2/272; 0.74%), and the lowest proportion of usage was in Oceanian (6/4,058; 0.15%) (Figure 4b). Statistically significant proportion differences existed between Neotropical assessments and Afrotropical, Indomalayan, Nearctic, and Palearctic assessments. By year, the highest proportion of assessments with an explicit use of genetics was 2015 (41/4,618; 0.89%), and on average, the percentage of assessments using genetics over time increased by 0.02% per year (Figure A1), with statistical tests revealing a significant deviation from the null hypothesis of no linear relationship (P = 4.52E-07).

Effective Population Size Metrics and Concepts

Overall, there were no assessments containing words and phrases related to N_b; therefore, the results all apply only to N_e and N_e concepts or principles. Words in the N_e text list (Table A1) were mentioned in the Rationale information section for only 432 out of 98,512 assessments (0.439%). After filtering, ten assessments (0.010%) remained that explicitly used N_e within the rationale for determining the Red List threat category, and four (0.004%) gave empirical estimates of N_e. The majority of assessments filtered out were coral species with a mention of assumed effective population size, but did not actually use the concept or provide an estimation within the threat category rationale.

The highest proportion of effective size explicit usage was in the Red List category VU (5/12,070; 0.041%), and the lowest proportion of usage was in category NT (= 0). The highest proportion of usage by Red List criteria was in criteria C (4/2,595; 0.154%), and the highest proportion of usage across taxonomic kingdoms was in Animalia (8/70,119; 0.011%). By system, the highest proportion of use was in terrestrial (10/56,500; 0.018%). By realm, the highest proportion of use was in Oceanian (1/4,058; 0.025%). The only statistically significant difference found within subgroups was in Red List criteria, between criteria B and C. There was no significant linear trend across assessment years, though there was a general increase in use over time (Figure A2).

Discussion

Overall, genetic concerns or data were seldom explicitly used in IUCN Red List assessments to determine the threat category of listed species (<<1% of all assessments). This is consistent with previous examinations of the use of genetic data and concepts in state, country, and global analyses, despite the utility and importance of genetic principles and measurements in assessing a population's risk of extinction endangerment (Laikre 2010, Taberlet et al., 2012; Hoban et al. 2013; Pierson et al. 2016; Bowman et al. 2016). The first comprehensive analysis within the United States was by Hoekstra et al. in 2002, which searched a database of the USA Endangered Species Act (ESA) listing decisions (i.e., recovery plan review projects, n = 195 species) and found no mention of genetic data or principles within the study's representative sample of recovery plans. Laikre (2010) documented a lack of genetic data and principles in several global monitoring programs, including National Biodiversity Strategy and Action Plans, the UN World Environment Program and the Convention on Biological Diversity. In 2014, Rivers et al. conducted an initial survey of 8,897 scientific journal articles on the topic "Red List" and 5,505 papers on "conservation genetics" (years 2004-2013) and found that <1% of papers included both topics, a result similar to the one we report here.

Despite the low use of genetics in the Red List assessments, we found the proportion of assessments using genetics did increase overall as IUCN Red List threat category increased, reflecting a relatively high use of genetics in species at the highest risk of extinction. This makes sense because genetic concerns increase as populations become smaller and more isolated, and these population processes are reflected within IUCN Red List threat categories. However, genetics could be used on Vulnerable or Endangered species before they become Critically Endangered and are eminently threatened with extinction. When we further explored specific types of genetics use, we found significant differences in the applications of genetic principles and data between threat categories, criteria, and taxonomic kingdoms. The consideration of hybridity and admixture was most present in the Critically Endangered threat category and criteria D (very small or restricted population), which could suggest that issues of maintaining the last individuals of certain genetic lines is of high importance to conservation practitioners when populations are highly threatened with extinction (e.g., Scottish wildcats, Senn et al. 2019). Genetics was hardly used for taxonomy, which is somewhat surprising given the importance of verifying taxonomic status for endangered species protection. The use of genetics also increased over time, and may be predicted to rise in the future.

More recently, Pierson et al. (2016) examined how often genetics factors are considered in threatened species recovery planning in Europe (n=110), the U.S. (n=100), and Australia (n=108). In their analysis, three categories of genetic data were addressed: population-genetic (genetic variation and structure, gene flow, and N_e), fitness-related (inbreeding, inbreeding depression, hybridization, and outbreeding depression), and life-history (mating system, chromosome variation, and clonal propagation). Overall, Pierson et al. (2016) found that the host country and taxonomic group may have some influence on the use of genetic factors (e.g., North American species recovery plans were more likely to include genetic factors)- a finding similar to the taxonomic trends we report here. Despite extensive evidence that inbreeding depression negatively affects fitness (Keller & Waller 2002; Biebach & Keller 2009; Frankham 2010, 2015; Frankham et al. 2017; Barmentlo et al. 2018), they found that fitness-related parameters were overlooked in all regions and taxa, leaving them to recommend an “international standard, similar to an IUCN Red List framework, that requires explicit consideration of genetic aspects of long-term viability”.

Of the 263 assessments that explicitly used or considered genetics in threat assessment found within this study, there were similar biases in taxonomy and geography. In terms of vertebrate taxonomy, mammals and fish were disproportionately represented in genetic use when compared to their overall Red List threat index. For example, even though one-third of IUCN Red List assessed amphibian species are threatened, only one amphibian assessment contained explicit use of genetics. Despite their relative endangerment, amphibians are not as charismatic or economically important as mammals or fishes, which is likely why amphibians are underrepresented in genetic work within the IUCN Red List. In terms of biogeographical realm, species within Palearctic and Nearctic had the highest proportional use of genetics within assessments, despite having lower biodiversity than Neotropical and Oceanian realms, which had the lowest proportional use. This is likely due to higher funding availability for genetic analyses outside of the tropics; however, this may change in the future as the costs of genetic data acquisition and analysis are going and will continue to go down.

There are several areas of uncertainty within this study, particularly in the determination of genetics use within an IUCN Red List assessment. While our list of genetics search terms was created with input from subject matter textbooks and experts, it is possible that taxon- or industry-specific words or phrases could have been missed. It is also notable that we are working with extremely small numbers of assessments after filtering (especially for the use of N_e), and as more assessments add the use of genetic data these proportional trends in taxa, geography, etc. may shift. However, the most likely source of uncertainty is the possibility of Red List assessors that do consider genetic data in their listing decision, but do not describe the genetic data or methodology within the Rationale section of the species assessment on the IUCN Red List. In fact, genetic data are routinely considered in management decisions for conservation but are not in the peer-reviewed literature, and instead exist in state or federal agency reports, making the actual frequency of use difficult to quantify (Bowman et al. 2016; Garner et al. 2016). The same discrepancy between use, publication, and description/incorporation into the assessment rationale could potentially be occurring within the IUCN Red List. A future study could analyze other aspects including the Works Cited portion of the assessment, as in Bowman et al. (2016).

Considering the increasing recognition of the importance of genetic diversity in the ability of species to adapt and for resilient ecosystems, we make several suggestions for increasing the use of genetics in biodiversity assessments, including the IUCN Red List. First, conservation geneticists and practitioners must both increase efforts to acquire, share, and interpret genetic data (which is often already published in some form) within the risk assessment framework of the IUCN Red List. Global databases of genetic information such as Dryad can help in making the data accessible, but standardized simple analyses or easy to use “pipelines” for the non-expert, and guides to interpretation, are still lacking. For example, the GEO BON genetics working group or the IUCN Conservation Genetics Specialist Group (CGSG) could create a document that outlines relevant genetics concepts (allelic diversity, gene flow, inbreeding, N_e, etc.) that guides Red List species assessors toward ingesting and applying genetics literature and results.

Simultaneously, Red List species assessors could make a greater use of the IUCN CGSG for consultation in trying to apply genetic principles and interpret genetic data and results. Conservation geneticists can also become involved in Red Listing workshops, in which expert Red List assessors work on a large number of taxa.

Second, conservation genetics practitioners should consider directing time and financial efforts toward species in taxonomic groups that are highly threatened, like corals and amphibians, and that efforts are directed toward regions of high biodiversity instead of areas with high funding. Finally, our work suggests a need for a long-term goal of explicitly incorporating N_e into the criteria used to determine overall threat categories within this international framework (perhaps including the well-known thresholds of 50/500 as “red zones” for inbreeding and loss of response to natural selection). For example, identification of species that experienced a severe reduction in N_e and has had $N_e < 50$ for multiple generations is likely at increased extinction risk and perhaps merits listing as Critically Endangered instead of Endangered, even if its census size is large (Garner et al. 2020). Such revised listing could help identify and conserve species at most risk of extinction, especially if assessments included estimation of census size, effective population size, neutral genetic diversity, reference-population genetic diversity, and number of generations until reaching certain heterozygosity-loss cutoffs (Willoughby et al. 2015; Garner et al. 2020). This is admittedly difficult because the Red List has great value in its consistency over decades, and changes in the criteria would disrupt the temporal tracking of Red List changes.

Conclusions

This study on the use of genetics within conservation assessments is the largest ever in scope, looking at >90,000 species assessments with a single, shared methodology and filtering schema including many crucial genetics search terms and phrases. While it has its own limitations, it is orders of magnitude larger than previous studies and is global in scope, in addition to utilizing a standardized methodology; as such we believe these results will be widely applicable across disciplines to improve the use of genetics. There are likely hundreds or thousands of peer-reviewed genetic studies on threatened and endangered species with relevant information on genetic erosion, drift, inbreeding, altered gene flow, and N_e that have not been explicitly used in IUCN Red List threat assessment processes. We hope the results of this study prompt greater consideration of these data, useful resources, and genetic principles in future Red List rationales and other conservation assessments.

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Table 1. Five categories of genetics applications or questions, the genetic concept or metric, and example Red List species assessment text that mentions genetics.

Genetics application	**Included concepts or metrics**	**Example Excerpt from "Rationale" Section**
Diversity	Genetic diversity, heterozygosity, homozygosity, inbreeding (depression)	"The remnant subpopulations were small and widely dispersed, as a result, this species has low genetic diversity" -*Enhydra lutris*, sea otter
Genetic structure	Flow of genes, genetic structure, barriers to gene flow, connectivity	"Genetic results indicate that two major subpopulations exist" -*Rhincodon typus*, whale shark
Abundance	Population presence and abundance estimates based on genetic data	"…intensive observation of wolf packs in recent years which yielded an estimate of 25 adult wolves, and was corroborated by DNA fingerprinting in 2008 (which identified 23 individuals)" -*Canis simensis*, Ethiopian wolf
Taxonomy	Taxonomic or phylogenetic classification of populations and species based on genetic data	"*Leopardus guttulus* has only recently been acknowledged as a valid species, separate from the former *Leopardus tigrinus*, due to their genetic uniqueness and differences." -*Leopardus guttulus*, southern tiger cat
Hybridity	Genetic purity, genetic integrity, hybridization, introgression, admixture	"The main causes of decline include water extraction, sedimentation and pollution, and ongoing hybridisation with other *Barbus* spp." -*Barbus caninus*, brook barbel

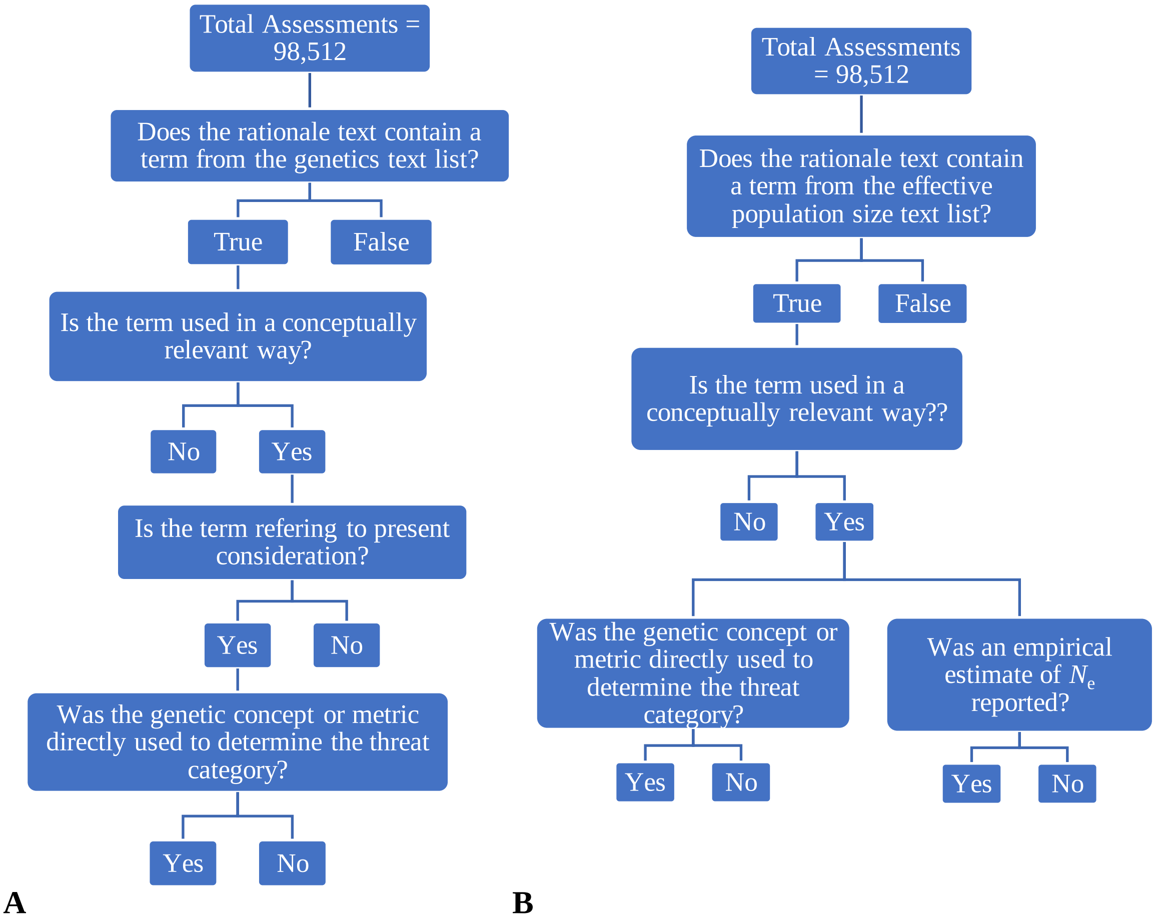

Figure 1. Manual filtering steps for identifying (a) the use of genetic principles, concepts, or empirical data and (b) the use and empirical estimation of effective population size within the "Rationale" section of IUCN Red List assessments.

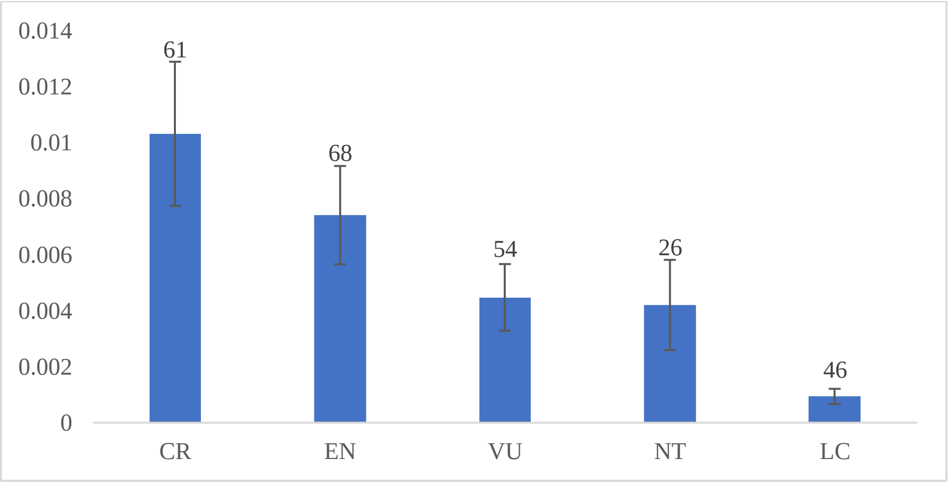

Figure 2. Proportion of assessments in each IUCN Red List threat category that passed all filtering criteria for genetics use. Error bars represent the margin of error using a 95% confidence level. Numbers above each bar represent the raw number of assessments passing all filtering steps for each Red List category.

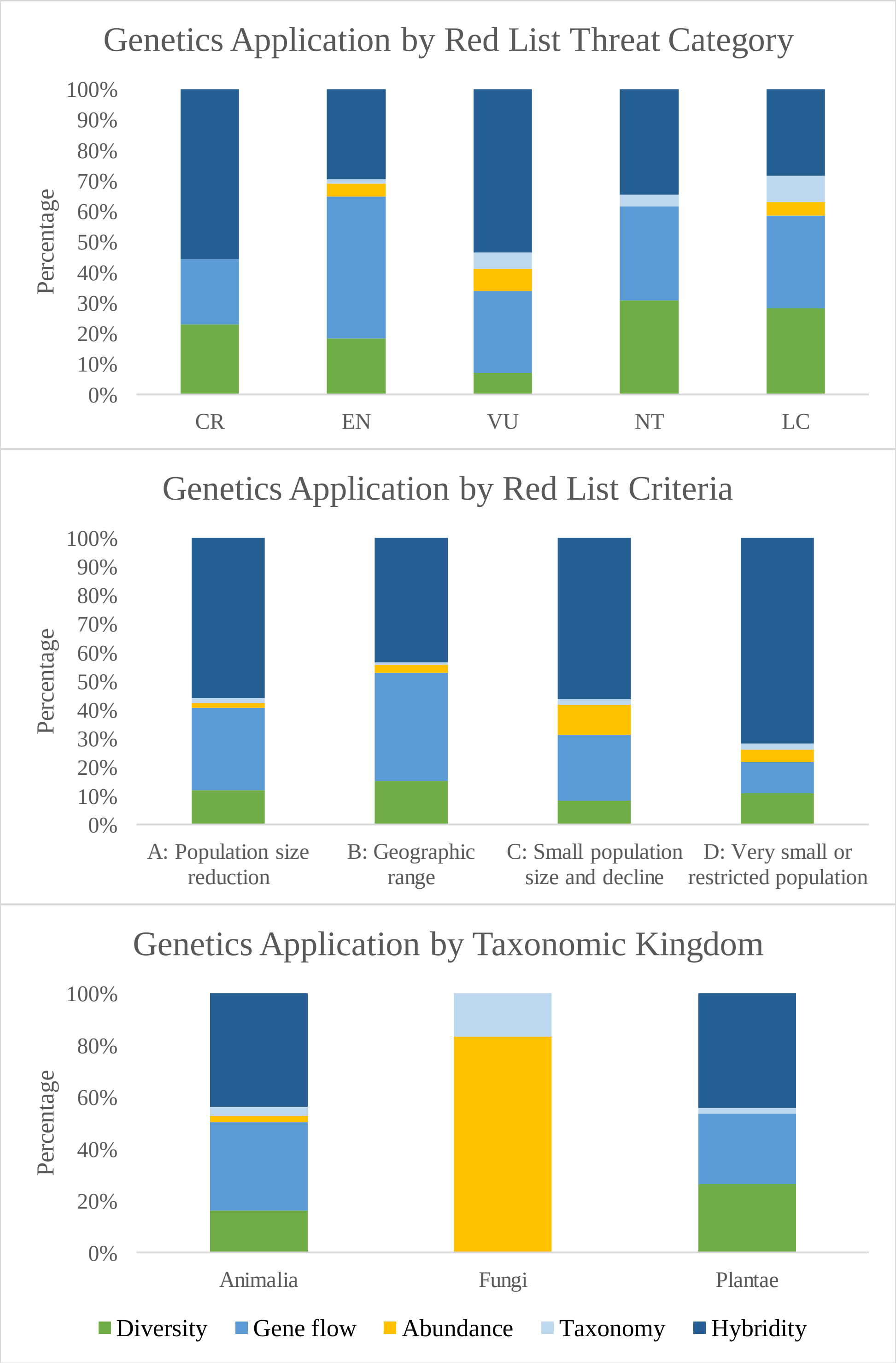

Figure 3. Percentage of specific genetics applications (i.e., use of principles or concepts) cited within assessments in each a) IUCN Red List threat category, b) IUCN Red List criteria, and c) taxonomic kingdom that passed all filtering criteria.

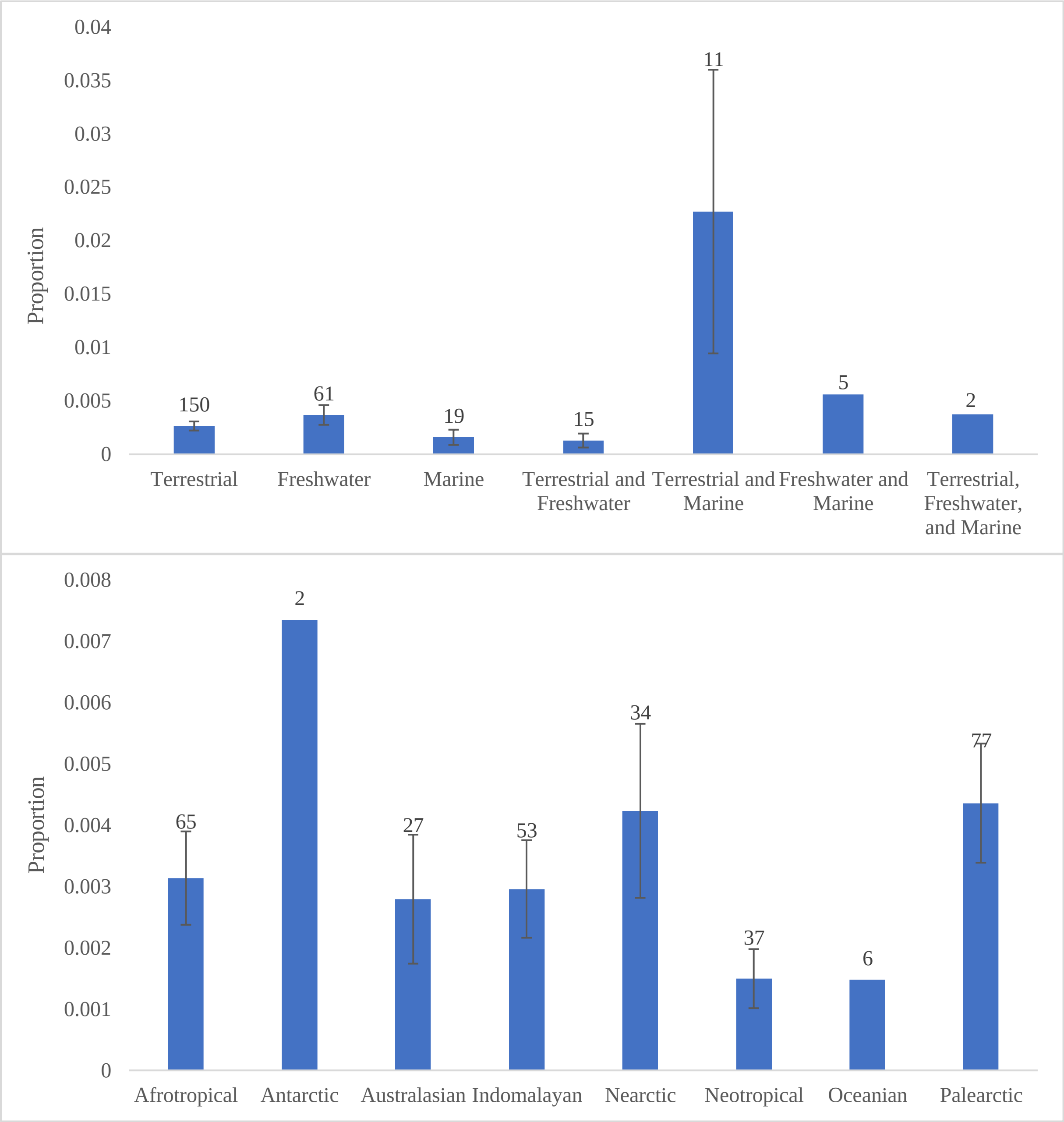

Figure 4. Proportion of assessments in each a) habitat system and b) biogeographical realm that passed all filtering criteria for genetics use (Figure 1). Error bars represent the margin of error using a 95% confidence level. Numbers above each bar represent the raw number of assessments passing all filtering steps for each habitat system.

Supporting Appendices

Table A1. Conservation genetics categories, filtering methods, and text lists.

Original text search terms:

Conservation genetics category	**Word, phrase, and symbol search**
Effective population size	Effective population size or effective size; effective number of breeders; N_e, N_b
Population structure	F_{ST}; F_{IS}; G_{ST}; *R*st; genetic subdivision; genetic structure; spatial structure, genetic differentiation, population structure; population subdivision
Genetic distinctiveness	Genetic divergence; evolutionary significant unit; genetically divergent; genetically distinct; genetic uniqueness; phylogenetic; phylogenomic; phylogeography; evolutionary tree
Change in Gene flow	Reduced gene flow; population genetic fragmentation; genetic rescue; genetic restoration; restored gene flow; increased gene flow and loss of local adaptation; mal-adaptive gene flow; adaptation to captivity
Genetic drift	N_e; random genetic drift; genetic stochasticity; random genetic change;
Inbreeding	Inbreeding coefficient; F; identity by descent; mating between relatives; increased homozygosity; decreased heterozygosity
Hybridization	Hybrid*; introgression; admixture; genetic mixing; genomic extinction; genetic mixing
Loss of genetic diversity	H_e; H_o; allelic diversity; allelic richness; gene diversity; loss of genetic variation
Inbreeding depression	Inbreed, Inbreeding coefficient; F; genetic load; expression of deleterious alleles; fitness decline
Outbreeding depression	Breakdown of coadapted gene complex; local adaptation
Genetic concepts	All of the above (as concepts/metrics) Bottleneck, coefficient of relatedness (r), effective population size, effective size, fitness, gene diversity, gene flow, gene frequencies, genetic distance, genetic drift, genetic markers, genome, genomic, genotype, genotyping by sequencing, Hardy-Weinberg, heritability, heterozygosity, homozygosity, marker, minimum viable population size, panmixia, panmictic, PCR, phylogeography, primer, probe, recombination, relatedness, sequencing, transversion
Genetic regions/markers	Allele, allozyme, autosome, base pair, chromosome, inversion, DNA, exon, haplotype, intron, isozyme, karyotype, locus, microsatellite, minisatellite, mitochondrial DNA, mtDNA, nucleotide, RNA, SNP, DNA fingerprint,

Genetics text list for mining in Excel:

```
=SUMPRODUCT(--ISNUMBER(SEARCH({"genetic"," gene "," genes "," genome "," genomic"," Fst "," Fis "," Gst ","genetic subdivision","genetic structure","genetic population structure","genetic divergence","evolutionary significant unit","genetically divergent","genetically distinct","genetic uniqueness","phylogenetic","phylogenomic","phylogeograph","evolutionary tree","genetic load","deleterious alleles","fitness decline","inbreeding coefficient","inbred","inbreed","inbreeding","identity by descent","identical by descent","mating between relatives","homozygosity","heterozygosity","homozygous","heterozygous","genotype","hybrid","introgression","introgressed","admixture","admixed","allelic diversity","allelic
```

richness","gene diversity","genetic diversity","loss of genetic variation","gene flow","flow of genes"," allele ","allozyme","autosome ","base pair","chromosome"," inversion "," DNA "," exon ","haplotype"," intron ","isozyme","karyotype"," locus "," loci ","microsatellite","microsat","minisatellite","minisat","mitochondrial DNA","mtDNA","nucleotide"," RNA "," SNP ","DNA fingerprint"},G2)))>0

Ne text list for mining in Excel:

=SUMPRODUCT(--ISNUMBER(SEARCH({“effective size”,“effective population size”,“number of breeders”,“effective number of breeders”,“effective breeder”,“ Ne “,“ Nb “},B2)))>0

Table A2. Examples of filtering steps used to determine if a) genetic concepts and/or empirical data and b) N_e was used or estimated explicitly within the “Rationale” sections of each Red List assessment.

a)

Species	**“Rationale” Assessment Section Text**	**Filter 1**	**Filter 2**	**Filter 3**
Atlantica putrescens, a snail	“This species is endemic to the Island of La Palma in the Canary Islands (Spain) from where it is only known from the locus typicus…”	No	x	x
Procambarus brazoriensis, Brazoria crayfish	“Further research is needed to determine if this species is in fact undergoing hybridization with neighbouring species…”	Yes	No	x
Trachemys taylori, Cuatro Ciénegas slider	“The species is potentially subject to hybridization by an invading relative…”	Yes	Yes	No
Shorea leprosula, red meranti	“The genetic diversity of this species has been widely studied and it is still considered a genetically diverse species however as forest fragmentation and logging occurs this will decline.”	Yes	Yes	Yes

b)

Species	**“Rationale” Assessment Section Text**	**Filter 1**	**Filter 2**	**Filter 3**
Begonia samhaensis, a begonia	“The cliffs where it grows catch precipitation and mists (principally from the NE monsoon)...”	No	x	x

Psammocora stellata, a coral	"…therefore is likely to be more resilient to habitat loss and reef degradation because of an assumed large effective population size that is highly connected and/or stable with enhanced genetic variability…"	Yes	No	X
Chaetophractus vellerosus, screaming harry armadillo	"This absence of genetic diversity observed in the 10 individuals sampled within the Oruro region suggests a local reduction of effective population size…"	Yes	Yes	No
Tympanocryptis pinguicolla, grassland earless dragon	"…may have an effective population size of as few as 106 individuals..."	Yes	Yes	Yes

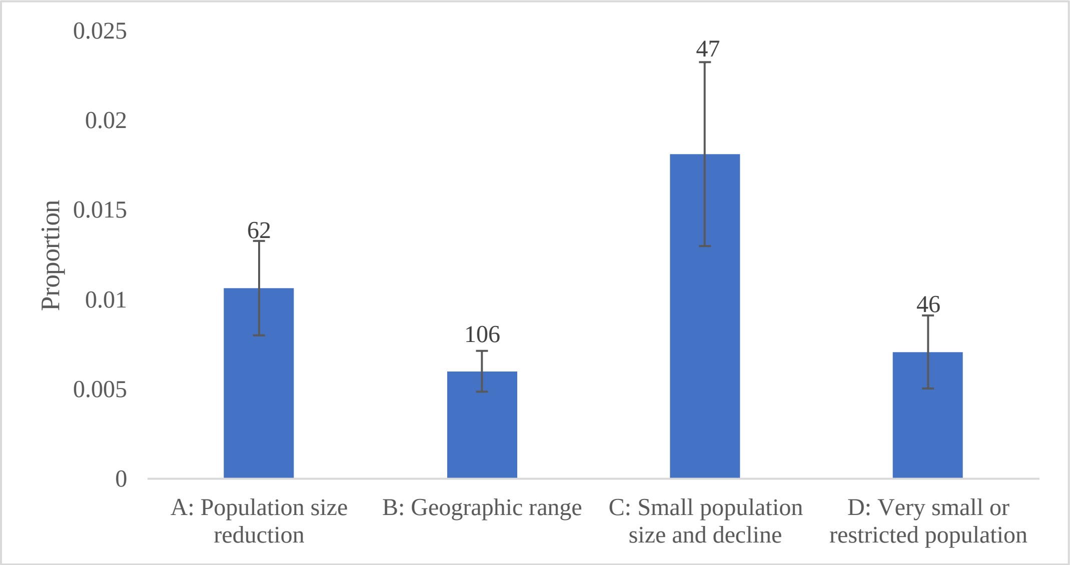

Figure A1. Proportion of assessments in each IUCN Red List criteria that passed all filtering criteria for genetics use. Error bars represent the margin of error using a 95% confidence level. Numbers above each bar represent the raw number of assessments passing all filtering steps for each Red List criteria.

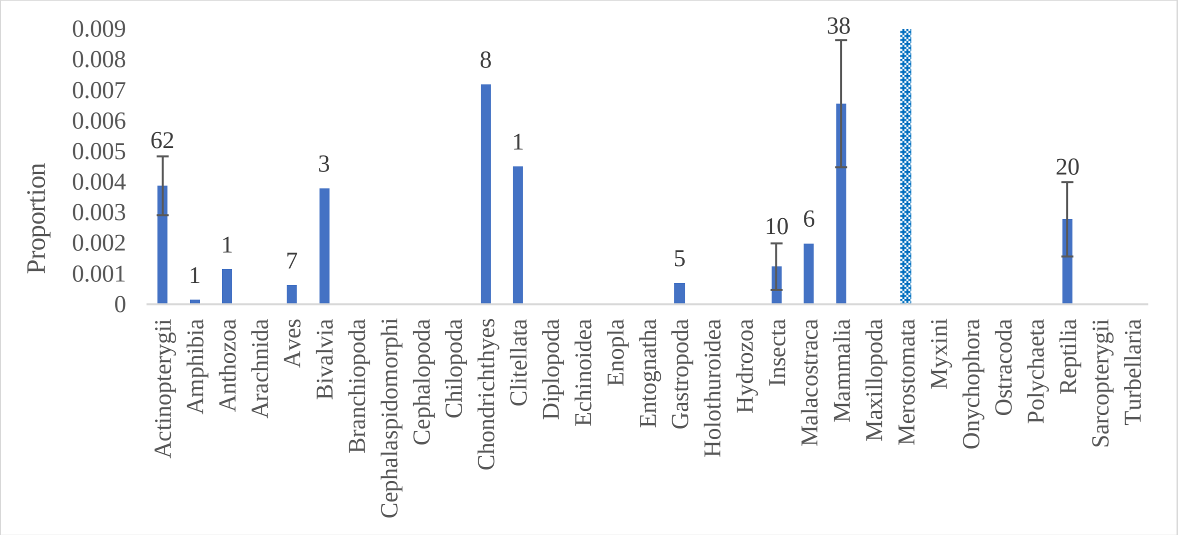

Figure A2. Proportion of assessments in each class within kingdom Animalia that passed all filtering criteria for genetics use. Error bars represent the margin of error using a 95% confidence level. Numbers above each bar represent the raw number of assessments passing all filtering steps for each class. Merostomata is an outlier (n=1; p=0.25) and not visible within the bounds of the graph.

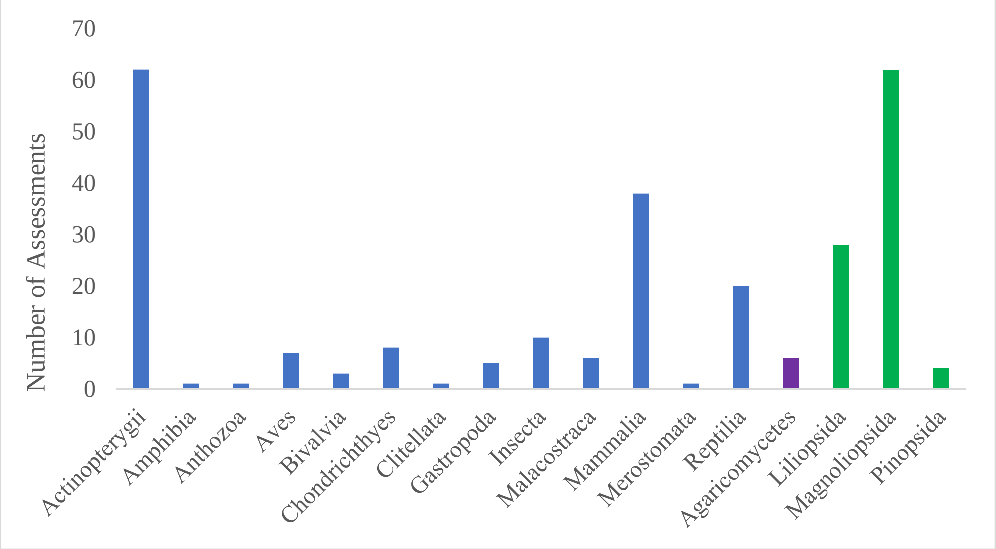

Figure A3. Raw number of assessments explicitly using genetics, separated by taxonomic class. Blue = Kingdom Animalia, Purple = Kingdom Fungi, and Green = Kingdom Plantae.

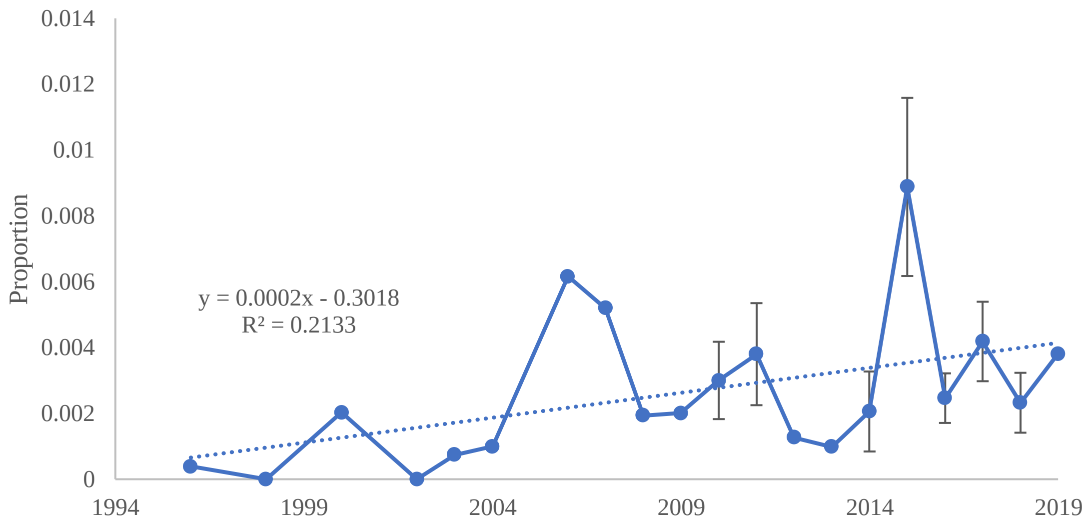

Figure A4. Proportion of assessments in each assessment year that passed all filtering criteria for genetics use. Error bars represent the margin of error using a 95% confidence level.

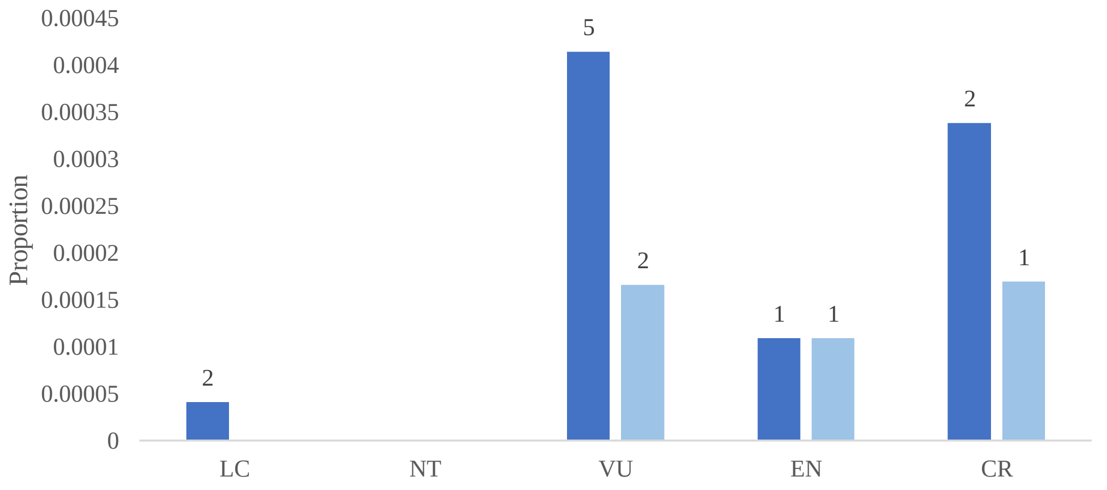

Figure A5. Proportion of all IUCN Red List assessments that explicitly use N_e within the threat Rationale information section, separated by Red List threat category. Light blue bars are proportion of assessments that report an empirical estimate of N_e. Numbers above each bar represent the raw number of assessments passing all filtering steps for each Red List category.

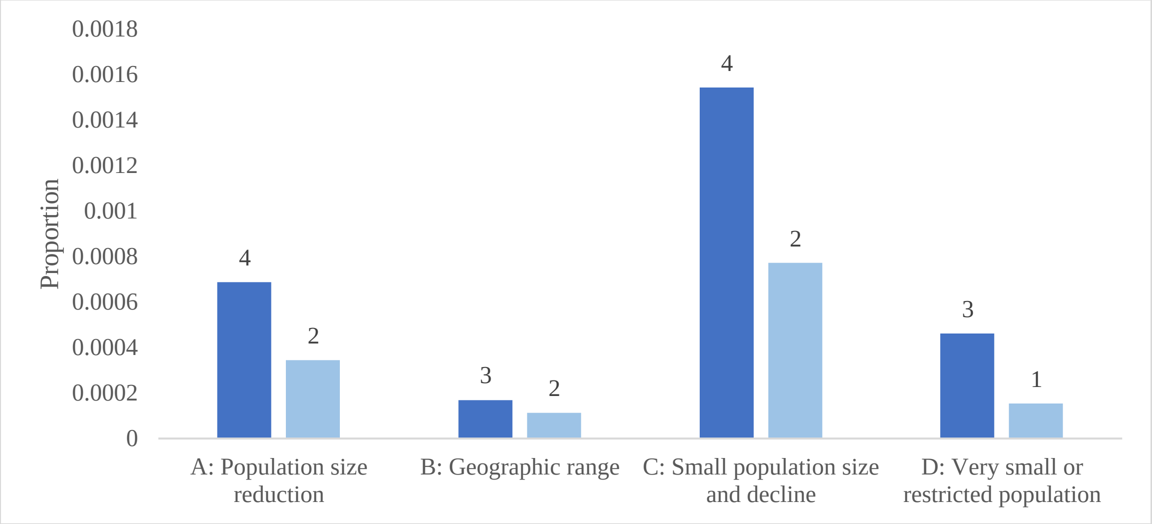

Figure A6. Proportion of all IUCN Red List assessments that explicitly use N_e within the threat Rationale information section, separated by Red List criteria. Light blue bars are proportion of assessments that report an empirical estimate of N_e.

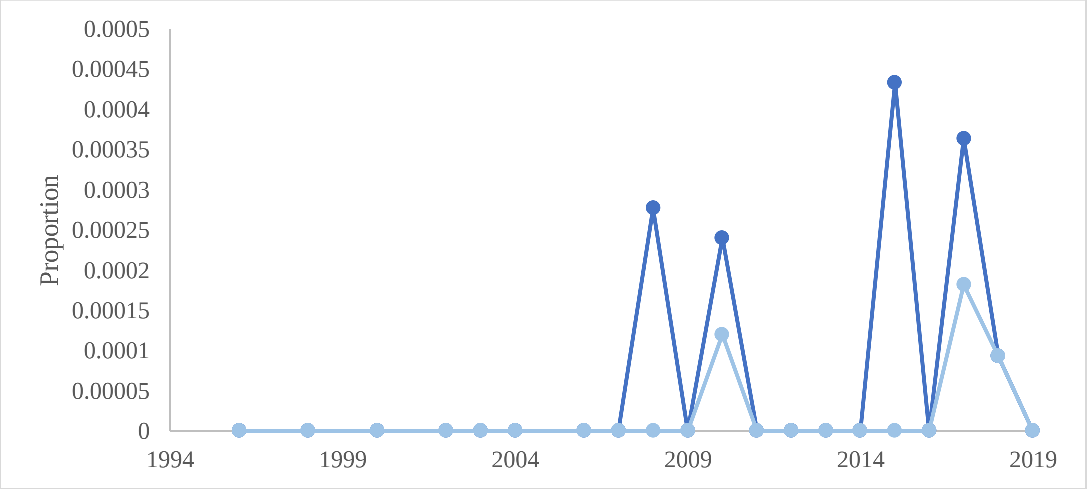

Figure A7. Proportion of all IUCN Red List assessments that explicitly use N_e within the threat Rationale information section, separated by year of assessment. Light blue bars are proportion of assessments that report an empirical estimate of N_e.

Chapter 4: Applications of Big Data for Biodiversity Conservation

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Abstract

The advent of big data (characterized as data of large volume, short latency, and variable structure and uncertainty) and the artificial intelligence-based analytics with which they are utilized has revolutionized many applied fields in business and science, technology, and engineering. This review surveys and synthesizes current applications of big data analytics in biodiversity conservation across descriptive, diagnostic, predictive, and prescriptive applications to highlight the diversity and rapid growth of tools available to conservation scientists. We also explore the intersections of big data analytics and conservation policymaking, and address potential ethical, social, and operational issues brought about by the rise of big data in biodiversity conservation.

Biodiversity Conservation in the Information Age

Rapid environmental change is driving biodiversity loss and ecosystem degradation at global scales. These losses impact human health and societal sustainability through increased environmental perturbation, resource depletion, and emerging disease, among other factors [1,2]. Conservation research and action are needed at a global scale to address this biodiversity and societal crisis [3,4]. The advent of the Big Data Revolution (see Glossary) [5] has yielded new data sources and disciplines with huge potential for upscaling and facilitating biodiversity conservation to meet this challenge [6,7].

Big data, the latest technological paradigm shift in the **Information Age**, has impacted nearly all academic and applied quantitative disciplines. Big data are typically defined in terms of the “4 V’s”: volume (amount of data), variety (unstructured or variable data formats), velocity (speed or latency of data collection), and veracity (authenticity and associated uncertainty). The exploration of complex and evolving relationships among big data, called **big data analytics**, is a paradigm shift in quantitative analysis developed as a response to those characteristics that make big data difficult to manage using conventional data handling and statistical methods. Big data analytics originated in the technology and business sectors, where they are applied to minimize cost and maximize efficiency- a highly relatable premise in the high-urgency, often triage-based field of wildlife conservation. With the explosive growth of environmental big data and rapid development of new analytical techniques, review and synthesis are a priority to facilitate and enhance the incorporation of big data analytics into conservation biology.

The growth in large, varied, and streaming biodiversity datasets results from the proliferation of high-throughput sources like remote sensing [8], genomics [9], social media, image recognition, text mining [10], citizen or community science [11], automated dataloggers and autonomous vehicles [12], and camera traps and acoustic and video recorders as sensor networks (the **Internet of Things**) [13]. Even technologies designed for non-conservation purposes, but as ubiquitous as automobiles are viewed as potential sources for collecting biodiversity data [14].

Although the relevance of big data to other environmental fields has been discussed (e.g. [15-17]), no such work has been completed for the highly dynamic, interdisciplinary field of conservation biology, which has greater time sensitivity, a distinctly applied focus, and different practical needs than other fields. Now is a critical time to explore the role of big data in transforming international conservation efforts. Here, we describe and highlight a diversity of big data applications in conservation to explore and enhance the impact and role of these methods in advancing this important field.

We pay special attention to applications of big data analytics to achieve global conservation goals, including those set by international frameworks like the United Nations 2030 Agenda for Sustainable Development and Post-2020 Global Biodiversity Framework (Table 1). We organize this review using a classification of big data applications from the business sector: descriptive, diagnostic, predictive, and prescriptive, which we define below (see also Figure 1). Our review focuses on capturing as much as possible the taxonomic, geographic, and methodological diversity of research in this discipline while illustrating the multiple avenues for the application of big data to addressing the global extinction crisis (Figure 2).

Descriptive Analytics

Descriptive analytics quantitatively summarize and highlight key characteristics and patterns within a system. The most frequent uses of descriptive analytics can be subdivided into 3 different categories: classification, monitoring, and describing genomic data. Below we provide examples for each of these uses. Big data analytics for monitoring typically describe current trends in important ecological parameters like population size and functional diversity, or social parameters like visitation rates to natural areas [18], and illegal wildlife sales [19]. For example, motion- or soundactivated camera traps and audio recorders collect enormous quantities of video footage, imagery, and sound for monitoring biodiversity. **Machine learning** of such unwieldy datasets has been used to monitor the occupancy and abundance of diverse mammal species in North America [20] and waterbirds in globally important wetlands [21] when image or sound processing by individual technicians would have been time- and cost-prohibitive. Essential Biodiversity Variables (*sensu* [22]) are an excellent example of descriptive products synthesized from monitoring information that can inform global-scale conservation decision-making; machine learning and big data analytics are considered key parts of advancing the implementation of these variables.

Deep learning, a sophisticated sequential form of machine learning known for impressive accuracy [23-25], and participatory citizen science initiatives [26-28] are effective descriptive analytics for classifying big data arising from imagery collected by targeted sources like camera traps and survey instruments and opportunistic, non-targeted imagery, crowd-sourced from social media. For example, machine learning methods were implemented in a mobile app that can identify endangered parrots from user images and help customs officials prevent illegal trade [29]. In the marine realm, machine learning and image recognition have been effective for monitoring important conservation parameters like species richness, bleaching, and recovery in coral reefs [30-32], size and species of catches in commercial fisheries to regulate harvest [33], and fish abundance in threatened seagrass ecosystems [34].

Digital conservation approaches and applications [35] like **conservation culturomics** and **iEcology** [10] utilize user-generated (i.e., crowd-sourced) data from social media platforms to monitor environmental and biodiversity variables. Recent applications include detecting illegal wildlife trade [36], spatial patterns in the use of ecosystem services [37], and an index of community engagement with the Aichi targets and sustainable development goals [38]. Sentiment analysis combined with text mining has been used to gauge prevailing social attitudes toward conservation actions or listed species [39,40], helping conservation scientists and managers keep a finger on the pulse of public opinion. Similarly, text mining has been used for an index for monitoring the commitments of individual nations to conserving agrobiodiversity given the use of relevant language in official documents [41].

Although such automated tools are invaluable for exploiting these new and burgeoning data sources, issues with veracity, especially known biases of social media data and sampling algorithms, are a persistent challenge [35,42]. Issues with veracity are also commonplace in large-scale citizen science research, which integrates observations from non-professional observers with varying degrees of processing and validation [27,28], presenting additional difficulties with unstructured data that must be accounted for in analysis. Smartphone technologies for community-based environmental monitoring greatly increase the potential for citizen participation in conservation science, making these issues of variety and veracity especially timely and important [43].

Data mining and machine learning are necessary for deriving useful information from the high volume of genetic data produced by modern DNA sequencing methods [15, 44]. There will be ample opportunities for innovation in using unstructured data in global genetic databases (e.g., GenBank) encompassing a growing number of molecular data types. The manifold applications of genomic big data for conservation are reviewed in [9], including delineating population units for protection and management and the identification of traits for disease resistance. A compelling example being the identification of genes responsible for the regression of transmissible tumors in endangered Tasmanian devils (*Sarcophilus harrisii*; [45]). Large-scale genetic data are critically needed for broad conservation efforts like the IUCN Red List that do not currently take full advantage of genetic information [46]. Big data and 3rd-generation DNA sequencing (e.g., Nanopore, MinION) may eventually be used for real-time on-site species identification for wildlife forensics and law enforcement (e.g., [47]).

Big data analytics can also aid in simultaneous monitoring of multiple taxa at the community level using metabarcoding [44] and the growing Barcode of Life Data System (BOLD; www.boldsystems.org). This monitoring may soon be feasible using autonomous vehicles and instruments for real-time sampling and analysis of DNA from the environment (eDNA) [48]. Big data analytics can be applied to characterizing gut microbiome communities and their effect on nutrition and immune function in captively-bred and closely monitored wild populations. For example, Wu et al. [49] characterized seasonal shifts in gut microbiome in giant pandas (*Ailuropoda melanoleuca),* a species of conservation concern. Microbiomes from the gut (feces), saliva, or breath (e.g., whale blow) may eventually be monitored remotely by combining genomics with non-invasive sampling using drones [50].

The advent of drones and hyperspectral sensors has made remotely sensed spatial information more abundant and accessible for researchers and vastly increased the volume of spatial environmental data being collected [8,51]. Machine learning algorithms facilitate the spatial delineation of habitat types, hydrological variables, monitoring of illegal fishing activity, [52] detection of invasive plant species [53], and functional diversity and carbon storage of forest habitats [54] from remotely sensed imagery.

Diagnostic Analytics

Diagnostic analytics introduce an element of inference into the big data workflow, elucidating key impacts and drivers of system dynamics. This can take the form of regression and correlation analyses [55] or mechanistic inquiries into the causal agents of an event or phenomenon (i.e., root cause analysis) through algorithms such as **decision trees** [56]. Diagnostic analytics can be performed with or without a-priori hypotheses. Where hypotheses are not involved, the Random Forest algorithm provides consistently good results over a wide variety of data without the need for model tuning [57]. Bayesian hierarchical models are an excellent method allowing for the flexible use of prior knowledge (i.e., ancillary data sources) handling of multiple data types (i.e., variety or unstructured data), and explicit accounting of data uncertainty (veracity; [15,58]).

Data mining, which makes use of artificial intelligence, automates the process of inference, and employs model-building algorithms to find patterns and potential causal relationships in large datasets with higher throughput than traditional approaches [59]. Data mining is an excellent way to continually draw inferences from rapidly updated (high-velocity) data without needing to manually re-parameterize and re-design cumbersome statistical models. Because quantitative inference inevitably involves making key model assumptions that, if violated, can invalidate model results, the veracity of big datasets becomes an important issue in diagnostic analytics.

Bioinformatic analysis of genomic data is increasingly important for elucidating the role and drivers of disease impacts on wildlife populations [60]. Diagnostic analytics are also applied to big data from citizen science and social media sources. For example, these data have been mined from Twitter and Flickr to evaluate how visitation increased impact risk on imperiled species in Important Bird Areas [61], and others have shown that the release of wildlife documentaries had detectable impacts on public interest in nature and environmental topics [62]. The study of animal movement, increasingly tied to conservation objectives like connectivity, is an especially strong example of the use of diagnostic analytics and data mining for causal inference due to the rise of high-volume and high-velocity data generated by sensor networks and tracking technology [63,64]. Both machine learning and Bayesian hierarchical models are common for elucidating the features driving animal movement patterns and behavioral states, especially when combined with remotely sensed environmental covariates [65]. Machine learning and tri-axial accelerometers, which collect acceleration data in three dimensions, have been used in conjunction with movement data to identify important habitats and behaviors in threatened species, for example, foraging patterns and locations in endangered whale sharks (*Rhincodon typus;* [66]).

Machine learning and text mining have also been used to automate meta-analyses for testing key hypotheses in invasion biology [67] and elucidating key drivers of conservation-motivated consumer boycotts of palm oil [68]. The potential for these methods has been emphasized in evaluating and improving forestry policies at the global scale [69], and in using geotagged images on social media to quantify user visitation rates to protected areas in Southeast Asia, finding that non-biodiversity attractions drove heterogeneity in tourist traffic [18].

Predictive Analytics

Predictive analytics examine trends and patterns in historical data, extending inferences from diagnostic analytics or observed patterns from descriptive analytics to predict system behavior. Predictive analytics are at the core of ecological forecasting and are especially helpful in a conservation context, which necessitates proactive management [58,70].

Machine learning and in particular deep learning are inherently predictive in functionality and design, and are seeing diverse and powerful uses in conservation [24,25]. These approaches have been demonstrated to predict poaching and illegal fishing activity, fluctuations in market demand for threatened species, and wildlife-vehicle collisions [71-73], and have even been used to predict pro-conservation attitudes among private landowners to streamline efforts for ecological restoration [74; see also Box 1].

Big data are also being increasingly employed for global change ecology [16] in predicting spatial shifts in species distributions [75], the adequacy of protected areas for the ranges of endangered taxa [76], and forest cover dynamics [77] under future climate scenarios. The use of predictive big data analytics in species distribution models is especially important for invasive species management, where forecasting and invasion prediction are essential for early detection and rapid response [78]. Researchers have also applied machine learning to GenBank data to characterize the phylogenetic diversity of 19,039 plant taxa across the United States and predict changes in regional taxon diversity in response to climate and environmental change [79]. At a finer scale, another study combined hydrological information from automated sensors with several machine learning algorithms to reliably predict flooding patterns of an ecologically important wetland in South Korea [80]. Machine learning methods have also been employed in predicting whether data-deficient taxa are likely to be of 'least concern' conservation status [81]. Similar approaches have been used to predict species that will likely be affected by wildlife trade as traded species become scarce or extinct [82].

Veracity becomes an especially large challenge for predictive analytics, where data errors are rapidly compounded with model extrapolation, and inference beyond the sampled range makes analyses especially vulnerable to sampling bias; this problem can be exacerbated by differing predictions among models [16]. Interestingly, data with higher variety (e.g., non-randomly sampled) can perform equally to systematically controlled data for some ecological applications of big data analytics [83]; many machine learning and data mining techniques are somewhat robust to these difficulties, although the interpretability of model outputs and predictions can be problematic [16].

Prescriptive Analytics

Prescriptive analytics are specifically employed to inform or automate steps in the decision-making process, usually relying on predictive analytics to frame potential outcomes. In biodiversity conservation, this primarily takes the form of decision-support for management and policy around endangered taxa and natural resources. Surveillance of key decision-relevant biodiversity parameters is being increasingly automated and enhanced by the use of networked sensors and cloud-based computing resources [84,85], greatly increasing the velocity with which information reaches decision-makers. Natural language processing and text mining can also automate literature synthesis and meta-analysis for evidence-based conservation, for example assessing the efficacy of artificial reefs for increasing fish diversity [86] and analyses of forestry policy and governance (e.g., assessing stakeholder needs or regulatory compliance) [69], when traditional methods could not handle the heterogeneity and volume of these data sources. Machine learning plays an increasing role in spatial prioritization for conservation, including strategic conservation planning for protected areas [87,88]. Prescriptive analytics have also been [89] used to spatially prioritize areas for increasing connectivity or creating ‘reservoir’ herds for wisent (*Bison bonasus*) [89], and suggested as a way to enact real-time closures and patrol areas for fisheries enforcement [72].

Beyond decision support, prescriptive analytics will likely encompass more and more of the decision-making process, with the potential end result of decisions made by artificial intelligence independently of humans [90,91]. Research and innovation in this field are especially rapid in anti-poaching efforts to protect endangered wildlife, with particular attention paid to automated sensor surveillance. For example, one study [92] proposed a framework based on actual practices in South Africa to optimize poacher deterrence and interception using networked aerial drones outfitted with infrared cameras. The future of this technological trajectory may be an adaptive and continuous feedback between monitoring, automated analysis, and decision rules for conservation interventions, which has been likened to the “kill chain” used for military applications in drone warfare [91].

Caveats, Best Practices, and Future Directions

Although the enthusiasm for big data analytics in biodiversity conservation is certainly warranted, there are legitimate concerns about the rise of conservation big data that are worthy of consideration. Access to big data and necessary analytical tools has implications for equity in research, where a data divide may manifest between scientists in countries with sufficient resources to collect and manage big data and those that do not. For open-access big data repositories, questions around attribution, authorship, and ownership of data still remain to be completely resolved; paper authorship may be dominated by those with access to big data analytics and not those who collect data in the first place [93,94].

There is a great need for online data infrastructures (e-infrastructures) for storing and sharing conservation big data [15], which has been partly addressed by some current initiatives (e.g., Global Invasive Species Information Network, www.gisin.org), but with substantial room for improvement [95]. There are also major concerns with inherent biases in big datasets, many of which are constructed from found data or samples of convenience that may not adequately represent the population of interest [17,96]. The rapid proliferation of big data sources has greatly outpaced user understanding of their shortcomings, leading to concerns about data quality, reporting standards, and metadata [97-99].

Continued improvements in big data workflows, especially involving data mining, generate a potential conceptual conflict between the hypothesis-driven scientific method and analytics which detect patterns based on data not specifically designed for that purpose [100]. Additionally, self-reinforcing academic reward structures which see big data papers published in higher-impact conservation and ecology journals are pushing scientists, especially early-career professionals, away from field work and single-species studies [101]; this pattern may be simultaneously eroding the field-based practice upon which these studies rely. It is also important to note that there is enormous conservation value in studying human behaviors and patterns in addition to non-human species and systems (Box 1), as humans are causal agents for many current threats to biodiversity.

Finally, the increased automation of biodiversity conservation via artificial intelligence and automated surveillance creates potential ethical problems, with major social risks for conservation imperialism and coercive conservation through a militarization of methods and philosophical approaches. This trajectory could exacerbate and perpetuate environmental racism and existing unjust power structures wherein access to ecosystem services is controlled by those in power and marginalized groups are criminalized and excluded [91,102,103]. Artificial intelligence capabilities and open-access big data may also enable greater exploitation of ecosystems and biodiversity by legal or illegal extractive economies [104], in addition to increased emissions and energy use from the necessary hardware for data centers [105]. It is also critical to recognize that the same tools being used for conservation can be applied to threatening the species we are working to conserve. For example, an arms race of sorts exists between the poachers using big data to avoid being detected and the law enforcers using big data to detect said poachers- as with any rapidly evolving technology, the larger question will be how it is used and why.

Concluding Remarks and Future Perspectives

In this review, we present a broad sampling of the range of applications of big data analytics to biodiversity conservation through the use of both targeted and incidental data (Table 2). Descriptive analytics appear to be the most extensively developed, with a rich literature of applications for handling the many targeted and incidental sources of big data arising from technology in the Information Age. Typically, targeted use occurred when researchers collected large and unwieldy datasets, such as the aggregation of millions of photographs, and required a data mining or artificial intelligence approach to categorize the subjects of the photos in existing species categories. In a related sense, researchers can readily collect 100Gb to 1Tb of genomics data per analysis and need descriptive analytics to help identify either individual genes or categorize species in these massive datasets. However, descriptive analytics also use incidental data collected from social media platforms or scraped from websites to detect illegal activities harming wildlife or even changes in social values regarding conservation activities.

While big data analytics for conservation are concentrated primarily in descriptive analytics, we are beginning to see an emergence of diagnostic, prescriptive, and especially predictive analytics in conservation applications. Some of the most promising and exciting uses of these categories of tools are the automated processes of model building at a rapid speed, meaning that complex models can be linked to rapidly updated datasets and thus themselves updated frequently [106]. New ways of conducting such diagnostic, predictive, and prescriptive analyses would be of significant value to the field, especially where they could better accommodate and communicate issues around uncertainty and potential data biases.

Challenges remain in addressing the logistical and ethical concerns introduced by big data applications in conservation, and collaboration with social scientists and community stakeholders should be an integral part of how these challenges are met (see Box 2). As the worlds of science, social media, and technology converge, big data analytics mark a significant and much-needed engine for innovation and use of information to guide global biodiversity conservation. Exciting, transformative uses of big data in conservation are not only feasible but rapidly expanding, and collaborations and caution are needed to maximize the efficacy of these applications to slow the loss of global biodiversity.

Acknowledgments

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Glossary

iEcology (internet Ecology) – An emerging research approach that quantifies patterns and processes in nature using data from digital sources collected for other purposes. Online data is used to understand species distributions, interactions, and dynamics of organisms and their environment.

Information Age – A period beginning in the mid-1900s, characterized by a shift from industry and the Industrial Revolution to an economy primarily based upon information technology. Also called Computer Age or Digital Age.

Big Data - Datasets that are so large (volume), heterogenous in structure (variety), have such small latency (velocity), or varying degrees of uncertainty (veracity) as to necessitate a paradigm shift in analytical approaches.

Big Data Analytics - Quantitative approaches for analyzing big data, often drawing upon tools and frameworks from computer science, statistics, and data science.

Big Data Revolution – The advent of datasets and associated data management and analytical methods beyond the traditional human-centered scale of analysis that use automated and artificial intelligence approaches.

Conservation Culturomics - A new discipline that assesses human-nature interactions as detectable using growing digital information. The interactions can help understand patterns associated with human interest, knowledge, and opinions towards nature and conservation.

Data Structure - The degree to which data were collected and are reported in a consistent fashion, with sufficient metadata for conventional data storage. Unstructured data, common in citizen science approaches, are one form of big data and require validation or analytical accounting of differences in data quality and associated uncertainty. Data structure pertains to data *variety* and *veracity*.

Bio- and Ecoinformatics - Interdisciplinary fields that combine biology/ecology with mathematics, programming, information and computer science and programming to enable the analysis, visualization, and management of big data.

Data Mining (and Machine Learning) - A sub-field of artificial intelligence that leverages computer algorithms to systematically derive higher order information from data sets with minimal human guidance.

Internet of Things - Technologies and research disciplines that enable the internet to extend into the real world of physical objects, connecting multiple sensors and devices through an integrated network where data can be shared and integrated across devices and physical space.

Cloud Computing - On-demand services (e.g., computational resources, data sharing and storage) made available through the Internet or other remote servers and without direct management of physical resources (i.e., data servers) by the user.

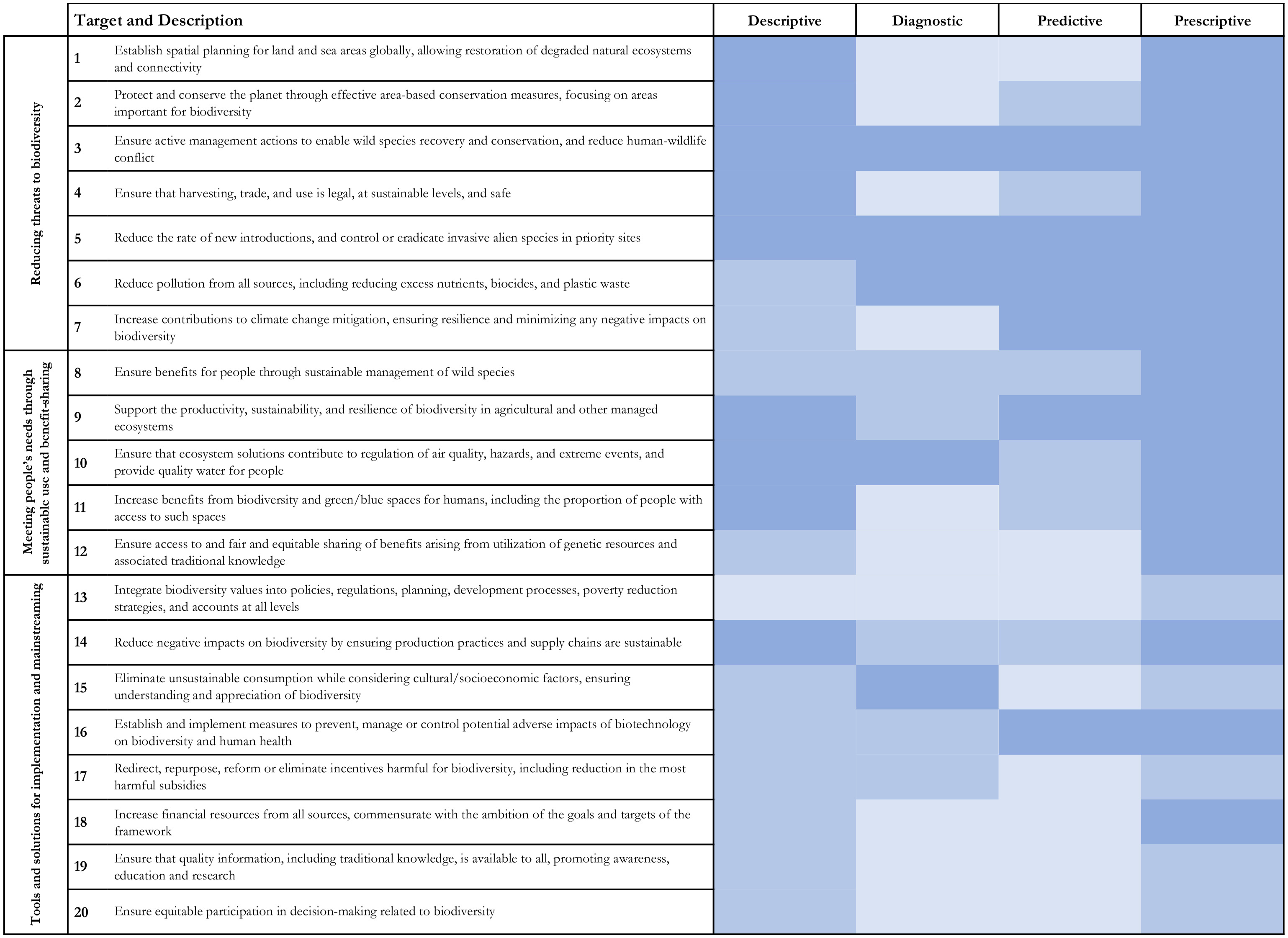
Deep Learning - A subset of machine learning approaches in which algorithms “self-teach” discriminative patterns across multiple levels of abstraction directly from raw data

Decision Tree - A form of machine learning that hierarchically organizes data across attribute value ranges designed to explain or predict one attribute of the data in terms of others.

Bayesian Hierarchical Model - A multi-level modeling framework in which the parameters estimated in one stage are used to parameterize the next stage of modeling. Prior probability distributions allow the construction of customized error structures accounting for different levels of uncertainty among data types (variety and veracity).

Table 1. The Policy Connection

A simplified summary of the 2030 action targets listed in the Convention on Biological Diversity (CBD) post-2020 framework, split into three categories according to draft policy communications from the CBD. Big data analytics types are listed at the top, and the boxes are colored according to an estimation of their use potential in addressing the action target listed to the left (low, medium, and high).



	Target and Description		Descriptive	Diagnostic	Predictive	Prescriptive
Reducing threats to biodiversity	1	Establish spatial planning for land and sea areas globally, allowing restoration of degraded natural ecosystems and connectivity	▓	░	░	▓
	2	Protect and conserve the planet through effective area-based conservation measures, focusing on areas important for biodiversity	▓	░	▒	▓
	3	Ensure active management actions to enable wild species recovery and conservation, and reduce human-wildlife conflict	▓	▓	▓	▓
	4	Ensure that harvesting, trade, and use is legal, at sustainable levels, and safe	▓	░	▒	▓
	5	Reduce the rate of new introductions, and control or eradicate invasive alien species in priority sites	▓	▓	▓	▓
	6	Reduce pollution from all sources, including reducing excess nutrients, biocides, and plastic waste	▒	▓	▓	▓
	7	Increase contributions to climate change mitigation, ensuring resilience and minimizing any negative impacts on biodiversity	▒	░	▓	▓
Meeting people's needs through sustainable use and benefit-sharing	8	Ensure benefits for people through sustainable management of wild species	▒	▒	▒	▓
	9	Support the productivity, sustainability, and resilience of biodiversity in agricultural and other managed ecosystems	▓	▒	▓	▓
	10	Ensure that ecosystem solutions contribute to regulation of air quality, hazards, and extreme events, and provide quality water for people	▓	▓	▒	▓
	11	Increase benefits from biodiversity and green/blue spaces for humans, including the proportion of people with access to such spaces	▓	░	▒	▓
	12	Ensure access to and fair and equitable sharing of benefits arising from utilization of genetic resources and associated traditional knowledge	▒	░	░	▓
Tools and solutions for implementation and mainstreaming	13	Integrate biodiversity values into policies, regulations, planning, development processes, poverty reduction strategies, and accounts at all levels	░	░	░	▒
	14	Reduce negative impacts on biodiversity by ensuring production practices and supply chains are sustainable	▓	▒	▒	▓
	15	Eliminate unsustainable consumption while considering cultural/socioeconomic factors, ensuring understanding and appreciation of biodiversity	▒	▓	░	▒
	16	Establish and implement measures to prevent, manage or control potential adverse impacts of biotechnology on biodiversity and human health	▒	▒	▓	▓
	17	Redirect, repurpose, reform or eliminate incentives harmful for biodiversity, including reduction in the most harmful subsidies	▒	▒	░	▒
	18	Increase financial resources from all sources, commensurate with the ambition of the goals and targets of the framework	▒	░	░	▓
	19	Ensure that quality information, including traditional knowledge, is available to all, promoting awareness, education and research	▒	░	░	▒
	20	Ensure equitable participation in decision-making related to biodiversity	▒	░	░	▒

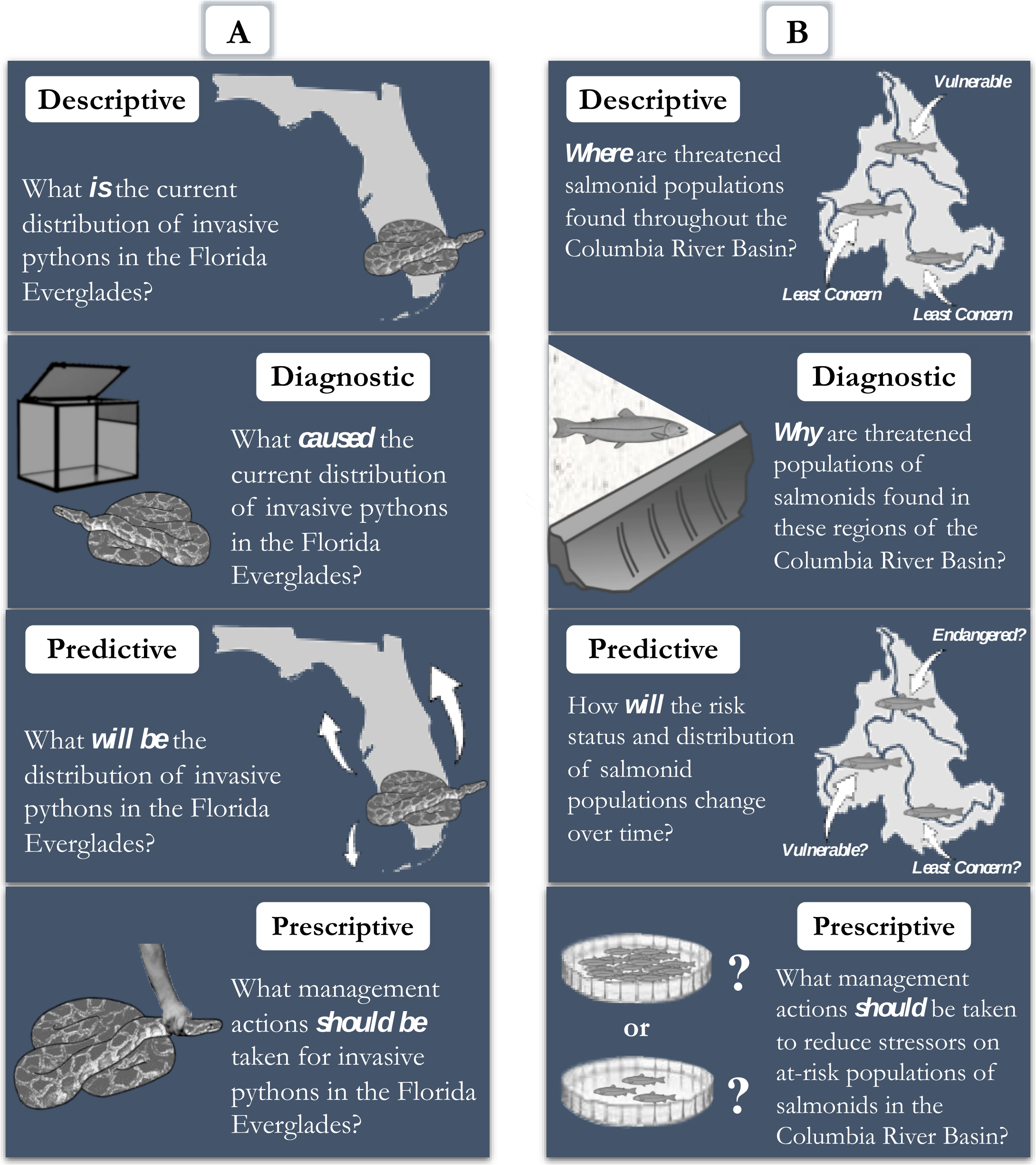
Table 2. Recent Case Studies of Big Data in Conservation

Examples of big data and big data analytics applied to addressing questions related to each of the main drivers of current biodiversity loss.

References: [52, 71, 75, 89, 107, 108]

Abbreviations: AUC = Area Under the Curve; RGB = red/green/blue; R-CNN = Regions with Convolutional Neural Network features; ROC = Receiver Operating Characteristics; TSS = True Skill Statistic; GLM = Generalized Linear Models; GAM = Generalized Additive Models

		Research Aim	Dataset	Approaches/Methods	Benefits/Outcomes	Ref.
Habitat Disruption		Identifying reintroduction sites for European bison	• Bison occurrence points from telemetry and field data • Environmental predictor variables	• Maximum entropy modelling (Maxent) • AUC analysis • Least-cost path calculations	• Identified three highly promising reintroduction patches that could both connect existing populations and establish reservoir herds	[89]
Overexploitation	Marine	Identifying illegal fishing activity	• Optical ocean surface imagery and vessel images • Fleet location and size data • Optical night imagery	• Convolutional neural network built in TensorFlow	• Demonstrated ability to transparently monitor fisheries by identifying previously unmonitored vessels and determining their country of origin and behavior	[52]
	Terrestrial	Identifying when and where poaching of rhinos occurs	• Aerial RGB images from drones and Google Images • Thermal images from ground-based cameras	• Data processed in TensorFlow and Pillow • Object detection using Faster R-CNN • Drone system uses local Wi-Fi to stream video to a field or remote server	• Successfully field tested a novel machine learning and drone approach to near real-time detection of rhinos and cars	[71]
Climate Change		Predicting how climate change will affect the distribution of tigers and leopards	• Tiger and leopard occurrence data from scat and camera trap photos • Climatic, topographic, landscape composition, vegetation, and human-influenced variables	• Univariate and multi-scale Random Forest models • AUC-ROC and TSS analysis • Environmental niche models	• Suggested importance of dense forest habitats with direct impact on regional and landscape planning for the future	[75]
Disease		Identifying diseased corals and classifying disease	• Images of corals from the Persian Gulf • Images of corals from Australian and Florida datasets	• Convolutional neural network	• 95% accuracy in classification of diseased corals	[107]
Invasive Species		Determining present and future distributions and abundance of an invasive rabbit	• Rabbit abundance from scat on randomly sampled plots • Abiotic, biotic, and human explanatory variables from public repositories	• GLM, GAM, and Random Forest	• Created rabbit distribution maps to aid management in identifying priority areas	[108]



What ***is*** the current distribution of invasive pythons in the Florida Everglades?

What ***caused*** the current distribution of invasive pythons in the Florida Everglades?

What ***will be*** the distribution of invasive pythons in the Florida Everglades?

What management actions ***should be*** taken for invasive pythons in the Florida Everglades?

Where are threatened salmonid populations found throughout the Columbia River Basin?

Why are threatened populations of salmonids found in these regions of the Columbia River Basin?

How ***will*** the risk status and distribution of salmonid populations change over time?

What management actions ***should*** be taken to reduce stressors on at-risk populations of salmonids in the Columbia River Basin?

Figure 1. Types of Analytics Applied to Conservation
Descriptive, diagnostic, predictive, and descriptive analytics can be used in many different parts of the scientific process. Figure 1 provides generic examples of each as applied to the conservation issue of invasive pythons in the Florida Everglades (A), and the distribution of at-risk salmonids species in the Columbia River Basin (B).

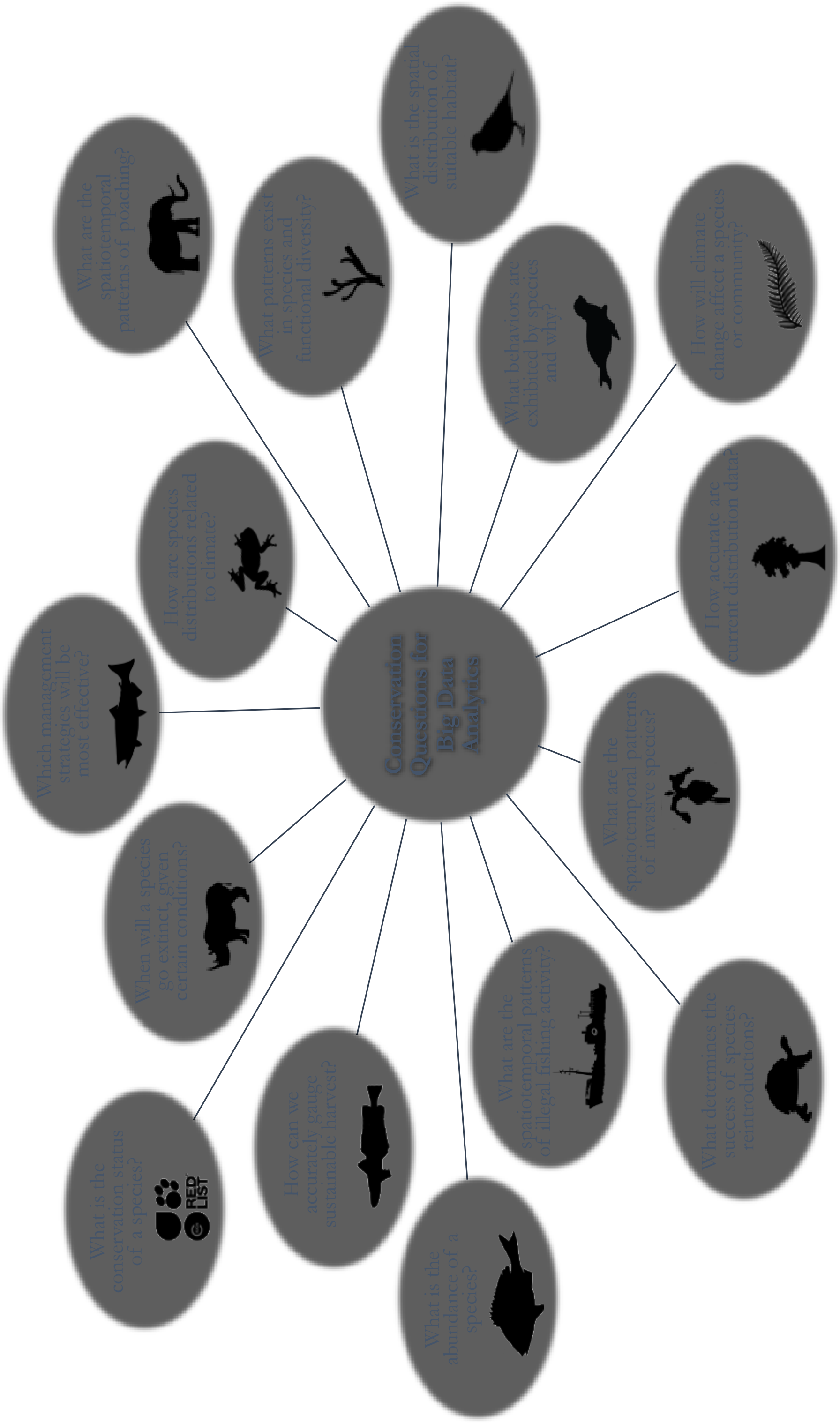


Figure 2. Conservation Questions for Big Data Analytics

The questions in conservation biology are currently being addressed by big data and big data analytics. Each bubble corresponds to a specific study, and the icon represents the species or system studied. References: [32, 33, 34, 39, 53, 79, 81, 84, 109, 110, 111, 112, 113, 114, 115

Box 1: Conservation and Big Data: The Human Connection

Understanding the patterns of species is a critical piece of conservation biology. In the Anthropocene, humans are arguably the most influential species on the planet; therefore, a fundamental piece of conservation big data is uncovering patterns of human behavior and understanding how these affect other species and systems.

Humans and other species benefit when human-wildlife conflicts are mitigated or minimized. Using machine learning methods, risk prediction algorithms for wildlife-vehicle collisions that consider spatial and temporal factors have been created, validated, and tested [73]. This forecasting element can be implemented inside cars via mobile applications to allow drivers to dynamically understand wildlife collision risks in real time and adjust driving behaviors. As the human population grows and roads increase in number and size, predicting the risk of wildlife-vehicle collisions is a significant step forward in the conservation of large, highly mobile species.

Big data analytics have resulted in massive efficiency and financial gain in the sectors of advertising and marketing, enabling businesses to more easily target and advertise to people that are more susceptible and likely to act on marketing materials. These same microtargeting approaches can be applied to myriad initiatives, including determining individuals' propensities toward conservation behaviors. This has been applied to private landowners in important riparian systems, successfully differentiating landowners who would participate in restoration programs from those who would not [74]. When applied to conservation program participant recruitment, this method improves on efficiency while minimizing cost.

Knowing where and when humans exist on the global landscape is key to understanding threats to biodiversity, yet quantifying and qualifying human presence and spatial variation requires extensive amounts of unstructured and varied data. However, data mining increasingly large amounts of geolocated pictures, texts, and videos on social media platforms provides a robust indicator of these human patterns. For example, these data have been used to assess human use and visitation appeal of global Important Birds and Biodiversity Areas (IBAs) [61]. Areas were identified and prioritized for enhanced monitoring, regarding both the amount of pressure exerted by tourists as well as minimization of negative impacts.

Human-environment and human-wildlife interactions will only increase in time as the human population increases, meaning that mitigation and resolving of conflicts will be a key aspect of future conservation efforts. Overall, this human connection makes it increasingly necessary to explore more dynamic and interdisciplinary research that includes synthesizing big data from social, economical, and ecological modeling.

Box 2: Outstanding Questions

How can artificial intelligence-based big data analytics be integrated into hypothesis-based conservation science?

What new opportunities for conservation monitoring and real-time management will be enabled by the advent of 5G wireless technology?

How can metadata, especially pertaining to data uncertainty and potential biases, be better built into analyses of found data?

What is the best way to ensure that access to big data in biodiversity conservation is broadly available and does not perpetuate institutional, economic, and disciplinary inequalities?

Would enhanced, cloud-based storage and computing for big data analytics increase opportunities for researchers without institutional resources to harness big data for biodiversity conservation?

How can the necessary interdisciplinary collaborations between conservation biologists, resource managers, data scientists, and computer scientists best be fostered to enhance the efficacy of big data analytics for preventing biodiversity loss?

Do the benefits of using big data and big data analytics to answer conservation questions outweigh the environmental cost of the materials and energy used to create and power the machines involved?

In which situations is big data the right tool for the job? Are there questions in conservation biology that are better answered using traditional analytical approaches?

Chapter 5: Anthropocene Biodiversity Conservation: A Little Science, a Lot of Values

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Abstract

In this paper, I give justification for the non-uniqueness of the current mass extinction; argue that comparing current extinction rates/causes against pre-human rates/causes is legitimate only if we define humans as “unnatural”; and apply Ereshefsky’s 2007 thesis on ecological preservation to biodiversity conservation. Overall, I conclude that the distinctness of humans is neither sufficient nor necessary to argue for the uniqueness of the current mass extinction and the need for conservation action. Rather, deciding why/how to conserve biodiversity is a value-based consideration that can and ought to be empirically informed once we decide what we value and why.

Introduction

On November 22nd, 2017, an article by Dr. Pyron of George Washington University was published in the Washington Post and lit the conservation world on fire. In this perspective piece, Pyron argued that extinction is natural and a driver of evolution, that humans should conserve biodiversity for themselves and not for the planet or other species, and that biodiversity will rebound after the current mass extinction event. At first read, it’s easy to think that Dr. Pyron held these beliefs because he was not learned in conservation biology and perhaps belonged to a field like economics or political science. However, Dr. Pyron is an assistant professor of biology, and has dedicated his career thus far to examining methods in phylogenetics using amphibians and reptiles as model systems. Dr. Pyron did not write his opinion piece from a place of ignorance, but rather from a place of revolution- in short, he asked the conservation biology world to look itself in the mirror and determine the real reasons why biodiversity should be conserved.

There was immediate outrage following the publication of Pyron's opinion piece, both from scientists and citizens around the world. Just a few days after publication, Dr. Antonelli and Dr. Perrigo, the director and coordinator of the Gothenburg Global Biodiversity Centre, respectively, created a shared Google Doc open to people all around the world. The goal of this shared document was to draft a rebuttal argument to oppose the views posited by Pyron. This argument was submitted on December 3rd, 2017 that was signed by more than 3,700 scientists and citizens from more than 88 countries, and a final version was published by the Washington Post on December 15th, 2017. In this rebuttal, the authors argue that Pyron's views are at odds with both facts and the moral responsibility of humans, that bequest and future use values of species are paramount, that the outcome of mass extinction is preventable, not inevitable, and most importantly, that extinction is natural, but the current rate is not (when compared to pre-human rates).

The rebuttal piece was only ~200 words long, and made these arguments without investigating the nuances of each topic. This is most likely because the sentiments expressed in the rebuttal are shared by most conservation biologists worldwide, and the status-quo nature of these opinions has led to a reiteration of the same ideas without the challenge of base arguments. I argue that the most interesting text is not Pyron's original article, or the short rebuttal, but rather the 43 pages of comments by over 100 scientists in the shared Google Doc online file. In a preliminary text analysis of this document, I created a word cloud for the top 20 occurring words while removing stop words and title keywords such as "species" and "extinction" (Figure 1). In a similar fashion, I created a second word cloud using text scraped from the comment section (n = 3,799 comments) of

Pyron’s original Washington Post perspective piece (Figure 2). The word clouds representing the top 20 word occurrences of the Google Doc rebuttal text and the comment section of the original article quickly tell an interesting story. More than half of the top 20 words in both sets of texts are shared between the two, and there is an overarching theme of both humans/people and nature/natural.

In a deeper examination of the rebuttal Google Doc text, it becomes clear that the signatories deem the current biodiversity extinction event as unique in two regards: the rate at which it is occurring, and the fact that a single species, *Homo sapiens*, is the root cause. Hence, these authors argue that what is occurring now is “unnatural” and therefore must be mitigated.

After examining the arguments made by the thousands of biologists in response to Dr. Pyron in the Washington Post, I am writing this paper to ask whether this appeal is accurate, and more importantly, if it is relevant to global biodiversity conservation. The conclusion of the scientists rebutting Pyron’s article relies heavily on the notion that the current mass extinction is unnatural.

In this paper, I will: (1) give justification for the non-uniqueness of the current mass extinction in terms of both rate and a single species root cause; (2) argue that biologists measuring the current mass extinction against the benchmark of pre-human rates and causes is legitimate only if we define humans as “unnatural” and briefly review the philosophical literature on the distinction between humans and nature; (3) apply

Ereshefsky's 2007 thesis on ecological preservation to biodiversity conservation to form a conclusion.

Overall, I argue that the current mass extinction is not unique from a scientific point of view in terms of the involvement of humans and that even if it were, this is not relevant to the choices conservation biologists make. Rather, deciding why and how to go about biodiversity conservation is a value-based and ethical consideration that can and ought to be empirically informed once we decide what we value and why.

Justification for the Non-Uniqueness of the Current Mass Extinction

In the philosophy of science literature, there are several ways in which an entity or process can be distinguished from nature: (1) as supernatural; (2) as displaying distinct and unique features; (3) as disturbing conditions on a system. In the published version of the rebuttal text in the Washington Post, the conservation biologists appeal mostly to (2). The most common arguments for treating the current global extinction crisis as an unnatural event in Earth's history involve the rate at which it is occurring and the fact that a single species, in this case humans, is causing it. However, a close look at Earth's previous mass extinctions reveals a different narrative.

Rate

The biologists who penned the rebuttal to Pyron's piece argue that the uniqueness of the current mass extinction is apparent when comparing current rates to pre-human rates. In their piece, they write, "Yes, extinction is natural. However, the scale at which it is occurring is not. Today, species are disappearing up to 1,000 times faster than pre-human rates." However, in terms of extinction rates, habitat fragmentation (a leading cause of current biodiversity loss) is occurring at a slower rate than some cataclysmic events of previous mass extinctions (Gould 1989; Primack 1993). The nuclear winter caused by a meteor strike, or a volcanic eruption, would arguably cause a faster rate of extinction than what is occurring at present. Ridley (1993) argued that the rate of current extinction caused by humans is not unique, and previous mass extinctions wiped out far more species than what is happening now. This is supported by evidence in the fossil record, specifically when looking at the End Permian and End Triassic mass extinctions. During the End Permian extinction ~251 MYA, the Earth lost ~96% of its species over an estimated 60,000 +- 48,000 years (Burgess et al. 2014). Close to 80% of species on Earth went extinct during the End Triassic mass extinction ~200 MYA due most likely to volcanic eruptions, and this was estimated to have occurred over ~5,000 years (Whiteside 2007).

Single Species Root Cause

The current mass extinction is inarguably being caused almost exclusively by humans, either directly or indirectly. While our cognizance and capacity to consider morality may be unique (and deserves its own consideration in a different article), it is untrue that a single species causing mass extinction effects is uniquely human over the course of Earth’s history. In the Great Oxygenation Event when the Earth was newly forming, cyanobacteria so drastically changed the environment that many species died off. The Late Devonian mass extinction, ~375 MYA, is thought to have been caused by land plants that released nutrients and caused eutrophication in the ocean, and in the End Permian mass extinction, the Siberian eruption is thought to have caused methanogenic bacteria to emit methane in such high amounts that the oceans acidified and set off hydrogen sulfide. While it is difficult to discern from the fossil record the exact number of species involved in causing these extinctions, and therefore problematic to name these are single-species root causes, these examples nonetheless give us ways of considering human uniqueness in causation.

Another Option?

Therefore, the rate and single species cause of the current mass extinction are not completely unique characteristics, and do not alone justify considering the current mass extinction as unnatural, and therefore needing intervention. If the claim of the conservation biologists is to stand, we must find another way to substantiate the claim in terms of unnaturalness. With the uniqueness of rate and single species cause now falsified, then the “unnatural” character of the current mass extinction must simply come from the fact that humans, the arguable cause, are unnatural. It is therefore now prudent to find if there is a notion of natural/unnatural in the philosophy literature that could possibly make sense of this reasoning.

The Distinction between Humans and Nature: A Brief Review

Main Distinctions

In order to understand how this view fits into the larger narrative of man's place in nature, we must consider the philosophical literature to date on the topic of the distinction between man and nature. There are three ways that environmental philosophers have commonly drawn the distinction between humans and the rest of nature: (1) the way human actions are unnatural; (2) human's distinctive influence on Earth's environment and (3) uniqueness of human culture. However, I will argue that none of these will do the work that needs to be done to salvage the argument that the current mass extinction is unnatural (and hence must be corrected).

In terms of (1), Brennan (1988) and Katz (1997) both argue that unnatural human actions are those that were not selected by natural selection. However, this is at odds with contemporary biology in several ways (Sober 1980, 1986; Lewontin 1983; Ereshefsky 2007). First, there is no biological distinction between an organism's "natural state" and population genetic/phenotype by environment interactions (i.e., all phenotypes are equally "natural"). The unnatural human actions concept is also at odds with Lewontin's (1983) niche construction observation, i.e., that environments of organisms are in part caused by the organisms themselves. Again, the ability for an organism, human or not, to change its environment and thus create new selective pressures does not make the organism unnatural under Brennan and Katz's criteria; indeed, these are processes acting under natural selection and should be considered natural according to their criteria.

Environmental philosophers also consider the influence of humans on Earth when defining the lines between man and nature. Taylor (1986) suggests that the naturalness of an ecosystem can be measured in degrees of human interference; however, this raises the following question- why are human modifications unnatural whereas those made by non-humans are natural? One answer is that the degree of effect is considerable, as humans affect the environment more drastically than, say, beavers when building dams. However, there are instances of non-human forces causing widespread destruction, and both Callicott (1996b) and Elliot (1997) make this argument by citing forces such as volcanic eruptions and floods. Callicott, one of the most prolific authors on this topic, argued that humans are natural because they resulted from evolutionary forces (Callicott 1991), and his contributions to the discussion will be addressed later on in this paper.

The third established basis for distinguishing humans from nature is the existence and uniqueness of human culture. Environmental philosophers have argued that there are three distinctive features of human culture: non-genetic transfer of information, complex tool and technology development, and insulation from natural selection. But are these unique to humans? And even if they are unique, does that equate to being unnatural? Callicott (1996a) argues that human culture does not make us unnatural, but it does represent a significant distinction between us and the rest of the world. However, each of these distinctive features may not be as unique to humans as originally thought. Consider non-genetic transfer of information, for example. Other species have been documented to transmit information through learning, like in bird songs (Avital and Jablonka 2000), and epigenetic changes due to environment are heritable without modifying the genetic code. In my own personal work with whales and dolphins, I've witnessed first-hand high level cultural learning and interactions comparable to those of humans, an observation supported in the scientific literature (Foote 2016; Fox 2017).

The last distinctive feature of humans argued by philosophers like Elliot (1997) is our ability to shield ourselves from the effects of natural selection, specifically by using our tools and technology. However, I argue that this is both (1) non-specific to humans and (2) not a relevant distinction in the consideration of natural selection. First, the development of complex tools and technology is not unique to humans (consider chimpanzees, Mercader 2002). The use of tools and technology is not different in *kind*, though the level of complexity might be different in *degree*. Regarding (2), I argue that there are no ways to separate the adaptations of humans (e.g., technology) from those of non-human organisms. In particular, there are counter-examples to the notion that our technology shields us from natural selection. Namely, some of the ways that we insulate ourselves from natural selection, e.g., antibiotics, are causing negative long-term effects in the overall evolutionary race between ourselves and microbes (e.g., antibiotic resistance). Overall, I argue that none of these distinctive human features mentioned in the literature are completely unique to humans, so separating humans from nature based on distinct human features is not factually accurate.

Callicott's Contributions

Callicott contributed two additional reasons for rejecting nature as being separate from humans: (1) a separation is socio-politically oppressive in that it may deny cultural rights to aboriginal human groups living "natural" areas and the creation of nature reserves after designation of naturalness evicts native groups and (2) this stems from an outdated Christian and Cartesian mind/matter dualism that is incompatible with our being a result of evolutionary processes like all other living things. One issue with the latter point is that this outdated dualism also feeds the "unperturbed except for by humans" idea of the balance of nature, which downplays the fact that changes and perturbations are constantly occurring in the ecological world.

Callicott also calls upon scale and rate of change when distinguishing man from nature while still considering man as "natural". His ecocentrism was inspired by Aldo Leopold's "Land Ethic" and derives two main principles of action, namely mimicry of the scales of natural change (i.e., eco-mimicry) and the harmony with nature principle (both appeal to notions of naturalness belonging to classical ethicists like Aristotle). Leopold's principle of eco-mimicry argues that humans are not a damaging or unnatural force if they make modifications to the land or ecosystems that are slow and local (similar to evolutionary changes). Callicott (1996a) emphasizes that human-caused perturbations are more frequent, widespread, and regularly occurring (as opposed to random perturbations like extreme weather), and updates Leopold's "Land Ethic" as "a thing is right when…disturb it only at normal spatial and temporal scales…" (Callicott

2013). Callicott (1996b) argues that human actions and influences are natural, but that humans are unique and different from the rest of nature because they cause a “wildly abnormal” rate of extinction. Specifically, abnormal in that the rate of extinction caused by humans outpaces speciation. In a counter-argument most relevant to this paper, Shrader-Frechette (1990) objects to this Callicott idea, stating that an explanation is required and is missing as to why the scale of change makes a significant difference: “Nor can the criterion be merely that it is wrong for humans to do quickly (e.g., cause lake eutrophication) what nature does more slowly. One would need an argument (given neither by Callicott nor Leopold) that accelerating ecosystemic changes is bad, even if the changes themselves are natural.” As a conservation geneticist, I argue that there is also empirical evidence against the Callicott claim that the rate of extinction caused by humans outpaces speciation. Though our understanding of gene-environment interactions is relatively new, there is preliminary evidence that species might be able to rapidly adapt via epigenetic and transposable element processes and keep pace with anthropogenic pressures (Liebl 2013; Rey 2016; Torda 2017).

Humans as Disturbing Conditions

In a recent article on the topic of whether humans are “natural”, Inkpen (2017) begins by stating that ecologists have treated humans as exogenous, disturbing conditions, and that this treatment of humans is an idealization, a term defined by the author as, “an intentional theoretical distortion that is in fact false of many target systems”. “Disturbing” in this case is defined in a philosophical sense, i.e., “class of exogenous factors that, when present, inhibit the applicability or accuracy of a model, mechanism, theory, etc.”. In addition to classifying this treatment as an idealization, Inkpen argues that the treatment is an intentionally introduced theoretical distortion, particularly when we consider how long ecologists have known that humans play a dominant role in many ecosystems. The treatment of humans as disturbing conditions is surprising as well- we have terms like the “Anthropocene”, showing that we clearly recognize how pervasive humans are. The author continues by making the case that ecologists have long attempted to study systems that are most-removed from human contact, despite knowing that humans are pervasive and may in fact represent a more “natural” system. He cites a meta-analysis of ecological field sites that showed a clear bias for sites with minimal human presence (Martin 2012). Additionally, even the definitions of “ecology” and related disciplines do not draw a distinction between human and natural (Sagoff, under review).

Inkpen (2017) provides a partial framework for evaluating the justification of this idealization, namely by giving illustrations of how ecologists have treated humans as disturbing conditions. The author splits these examples up into four different categories: language, choice of research site, experimental practice, and theory development/application. In terms of language, Inkpen states that phrases are regularly used to differentiate between presence/absence of humans in studies and that these phrases (e.g., “in nature”) seem to be important qualifiers (Shrader-Frechette and McCoy 1995; Haila 1997) despite their potentially seeming unnecessary to, say, a physicist. In the Martin et al. 2012 meta-analysis of ecology study research sites, the team found that majority of studies were performed in “protected areas”, i.e., protected from humans, a choice that Inkpen argues probably comes from the idea that nonhuman environments “better represent ecological and evolutionary processes and are therefore better objects of study”. Laboratory experiments show a similar bias to field experiments in that experimental practice in the laboratory has been characterized as “unreal” or artificial, and the concept of “natural” experiments are defined as studies where biologists study perturbations that are not human-induced. In theory development and application, Inkpen gives the example of urban ecologists who lament that classical ecological models do not meet their needs because there is no account for a human-disturbed system (Collins 2000; Alberti 2003). Taken together, the evidence and discussion provided by Inkpen dispels the justification for treating humans as disturbing conditions, once again leaving us without a clear reason for considering humans, and their impact on other species (e.g., current mass extinction), as unnatural.

Adapting Ereshefsky’s 2007 Thesis to Biodiversity

The Ecological Framework

In a 2007 review on the human/nature topic in relation to ecological preservation, Ereshefsky states that the philosophical literature has two views on the division between humans and nature: one that highlights the distinctive nature of humans and suggests these differences make humans unnatural, and one that highlights what is distinctive about humans while still considering them as natural. I have discussed and dispelled the distinctive nature of humans during the brief literature review in this paper; however, it is worth considering the implications for decision making under the assumption made so often (but incorrectly) that humans *are* distinctive. Ereshefsky continues the conversation by asking: if humans are distinctive, does the distinction provide the basis for determining what to preserve? In other words, do unique human properties provide grounds for deciding what is natural, wild, or a candidate for preservation? Ereshefsky states (and I have discussed in this paper) that environmental philosophy emphasizes the unique features of humans: human's unique culture makes us unnatural, and human culture distinguishes us from what is wild and a candidate for preservation. Determining what to preserve thus "turns on deciding which effects on the environment we wish to avoid".

This leads to a convincing conclusion by Ereshefsky, one that can be directly applied to the Washington Post perspective piece and rebuttal. He writes that debating the definition of the word "natural", as well as whether humans are truly unique, doesn't make a case for protecting the environment or even add to the discussion. He suggests we change the focus of our questions to value and mechanism, namely, "which parts of the environment do we value?" and, "what is the best means for preserving those parts of the environment?" Answers to questions about the naturalness of humans do not get us any closer to answering these suggested questions, and value judgments are not determined by deciding what is unique or natural about humans. Leaving these discussions behind will, according to Erekshefsky, "clear the ground for stronger arguments for environmental preservation."

As Applied to Biodiversity

Regarding biodiversity, the same argument applies. If the goal is to preserve biodiversity, then we need to avoid the current mass extinction. This goal is put in place because of some value being placed on biodiversity, and neither the goal nor the value has anything to do with whether humans are natural or unique. We can still aim to preserve biodiversity because it is instrumentally useful or intrinsically valuable, but human uniqueness and what is natural does not pertain to either. Ereshefsky's thesis statement on environmental preservation applies so well to biodiversity conservation that the terms are replaceable in Ereshefsky's own thesis statement. The following is how his passage reads with the word "biodiversity" put in for "environment":

> "Debates over the definition of 'natural' or the uniqueness of humans do not further the case for protecting [biodiversity]. Instead we should focus on such questions as: Which parts of [biodiversity] do we value? And, what is the best means for preserving those parts of [biodiversity]? Answers to these questions do not hinge on deciding what is unique about humans, nor do they turn on deciding what is natural. By dropping discussions of human uniqueness and what is natural we clear the ground for stronger arguments for [biodiversity conservation]"

This similarity was not missed on Ereshefsky, who concluded his 2007 article by mentioning the application of this logic to biodiversity conservation. Humans are causing the loss of species on Earth, and these species are being negatively affected whether we consider ourselves a part of the natural world or not. Making the active choice to curb this loss of life on Earth will be based on values first, science second- namely, that empirical information will be crucial to attain our goals, but these goals ought to be decided on the basis of ethical reasoning.

Value-based conservation action is not necessarily always explicitly known or demonstrated, nor is it the full story. Emotional and ethical responses of humans to conflicts of morality and decency towards the other are deeply seated within values, but experienced more viscerally. Additionally, human communities that sustainably harvest and conserve resources might do so because of cultural practices and generational habits. These approaches to conversation occur without explicit statement of values, yet are grounded within values or have evolved from an internal or shared prioritization of care and concern for life on Earth.

Conclusions

The distinctness of humans is neither sufficient nor necessary to argue for the uniqueness of the current mass extinction in that uniqueness does not determine the establishment of conservation goals. I therefore argue that conservation biology professionals must give reasons for conserving biodiversity other than repeating the largely untrue and inoperable argument that humans are causing extinctions in a way that is unnatural. The current mass extinction is not unique or highly distinct from a scientific point of view in terms of the rate of extinction or involvement of humans, and that even if it were, this is not relevant to the choices conservation biologists make to conserve biodiversity. Rather, deciding why and how to go about biodiversity conservation is a value-based and ethical and/or cultural consideration that can and ought to be empirically informed once we decide what we value and why.

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Table 1. Top 20 words used in the rebuttal text and comment section. Bold/italics means shared between the two.

Google Doc Rebuttal Text	Pyron Perspective Comment Section
Biodiversity	***Humans***
Human	***Nature***
People	***Evolution***
Moral	***Human***
Natural	***Life***
Humans	***Future***
World	***Natural***
Loss	***Planet***

Value	***Need***
Life	***Time***
Evolution	***Biodiversity***
Future	***People***
Important	***Know***
Nature	Animals
Ecosystem	Survival
Need	Process
Time	Forests
Events	***World***
Know	Earth
Planet	Evolutionary

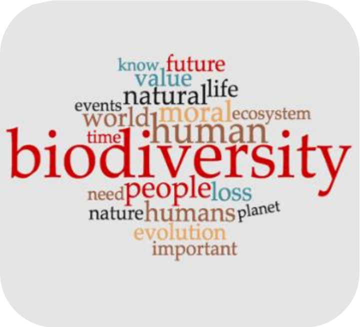

Figure 1. Word cloud representing 20 most common words appearing in the rebuttal text document.

Figure 2. Word cloud representing 20 most common words appearing in the Pyron article comment section.

Chapter 6: Anthropocene Conservation Media Products

Philosophy and Climate Change

This product is a five-part video mini-series on the intersection of philosophy in climate change, produced in collaboration with Gray O'Reilly, a M.A. student in environmental philosophy. Content breakdowns are as follows:

Episode 1: What is the Anthropocene?
Episode 2: The balance of nature
Episode 3: What's at stake with climate change
Episode 4: Climate models and robustness
Episode 5: The scicomm solution

Videos are available at youtube.com/natureleague under the Philosophy and Climate Change playlist

Nature League

Nature League is an ongoing YouTube channel since March of 2018 that explores life on Earth. Formats include field trips, lesson plans, chats with friends, formal interviews, livestreams, current events, and breakdowns of scientific literature.

Channel available at youtube.com/natureleague

Nature Insight: Speed Dating with the Future

Nature Insight is a six-episode podcast produced in collaboration with IPBES, the United Nations-adjacent Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Content breakdowns are as follows:

Episode 1: Dr. Peter Daszak: Disease X
Episode 2: Billy Offland, Dr. Anne Poelina: Wake up the Snake
Episode 3: Professor Kai Chan: Choose Your Own Adventure
Episode 4: Dr. David Obura: The New Natural
Episode 5: Samata, Marie-Claire Daveu: Bending the Curve with Business
Episode 6: Brigitte Baptiste: Show Me the Value(s)!

Podcast available at: https://ipbes.net/podcast

Lessons Learned

Throughout my exploration of scicomm as a means of public engagement with biodiversity conservation and general biology, I've been most humbled by the necessary isolation of what I *don't know*. Reducing obscenely complex topics and nuances into digestible media formats requires a synthesis, distillation, and reworking of almost every presented fact, with constant consideration of audience, length, format, and areas of potential *mis*communication. Going through these processes on a regular basis has kept me open to recognizing my own gaps in knowledge and challenged me to hone my own understanding in order to elucidate concepts for others.

I've also been struck by the sheer power of collaboration in these projects and more. For Nature League, I worked closely with non-scientists like graphic designers, video producers, cinematographers, and directors. I relied on them for their individual expertise outside of my own, and also for feedback about the accessibility of my content and the language I would use during episodes (e.g., jargon, vocabulary, etc.). For the IPBES podcast, I was not only working with a professional audio company located abroad, but the interviewees were from a massively varied assortment of backgrounds, cultures, specialties, and languages. I had to learn about the political nature of being attached to global NGOs operating alongside the United Nation, and constantly check in with my team about appropriateness of narrative and communication efficacy, as well as branding. I've come away from all of these projects with a renewed initiative to be open to myself, to others, and to the world around me, while learning about all three along the way.

Science and the Ghost Light: Theatrical Hope in the Time of COVID-19

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Overview

In this chapter, I will present, detail, and analyze the intersection of science and musical theatre during an unprecedented era of modern human history using two full-length musical theatre productions presented in Missoula during the COVID-19 pandemic. In this, I argue that scientific thought, process, and implementation was key to production success and artistic and audience fulfillment in two shows with deep dramaturgical ties to connectedness. By considering one in-person and one pre-recorded musical production, I leave the long-standing academic discourse regarding liveness and theatre (Phelan 1993; Auslander 1997) out of the main exploration, and instead consider the procedures and experiences of how science mediates connectedness in an isolating age, and worked to conserve the performing arts in the face of extinction due to COVID-19.

The Beginning of the End

On March 12th, 2020 at around 9:30 PM, I took my final bow for *The Spitfire Grill* at the Missoula Community Theatre- a bow that should have been repeated for another week, but was prematurely finalized as the town of Missoula, Montana shut down due to the COVID-19 pandemic (Figure 1).

Figure 1. Final bows of MCT's "The Spitfire Grill". Credit: Joseph Martinez

Unfortunately, this experience was not unique to me or my community- as the COVID-19 virus spread globally, myriad performances of all kinds were postponed, canceled, or prematurely closed. At the time, there was the constant question of when the performing arts would come back; as I write this 15 months later, Broadway remains closed, but is scheduled to reopen in the fall of 2021.

COVID-19 and the Performing Arts

COVID-19 has ravaged the performing arts world in an extensive and ongoing way. While many, if not all, job and social sectors have been impacted by this pandemic, the reliance of the performing arts on physical proximity has resulted in longer lasting problems within this community (Guibert and Hyde, 2021). As of May 2021, the financial losses to nonprofit arts and culture organizations in the U.S. were estimated at $16.5 billion to date (AftA, 2021). In the same research update, artists and creatives were among the most severely affected sectors of the American workforce, with average losses of $34,000 each since the start of the pandemic. In fact, nonprofit arts organizations suffered job losses of ~28% as of April 2021, which is four times the average losses across the American nonprofit sector (Johns Hopkins University, 2021). As for lasting impact, the U.S. Census Bureau (2021) notes that arts, entertainment, and recreation businesses are among the most likely sectors to take more than six months to recover from the pandemic.

The losses experienced went beyond those of the economic and personal finance realms. Performing artists face high work demands, insecurity, and short-lived careers even in the best of circumstances, yet the social aspects of these lines of work contribute to wellbeing, demonstrated in both musicians (Ascenso et al., 2017) and dancers (Cahalan and O'Sullivan, 2013). As such, the significant reduction in work and performance impacted health and wellbeing outcomes for performing artists. Spiro et al. (2021) surveyed psychological patterns among performing arts professionals in the U.K. between April and June of 2020. In the survey, 63% of participants reported increased loneliness, 85% reported increased anxiousness, and 69% could be categorized as depressed, with the most frequently cited challenge being the loss of work and performing activities. An intense sense of loss permeated this community, myself included. In the words of one respondent:

"I am also in a kind of mourning for the industry which I know will never be the same. And there is a huge sense of grief and foreboding for all of my peers and the many wonderful organizations that I work with." (Spiro et al., 2021)

Incredibly, the impact of humans on their environment and other species has contributed to the outbreak of this novel virus, and much like with biodiversity conservation in the Anthropocene, science and technology were posed to lead the way in preventing the extinction of the performing arts during COVID-19.

The Show Must Go On

While unique to our current life spans and experiences, humanity and the performing arts have always been persisting and adapting to contagious diseases. In the 14th century, the Black Death was ravaging the human population across Europe; and yet, the Renaissance still succeeded, and artists and patrons alike adapted to and persisted through the challenges of communicable disease (Florida and Seman, 2020). During the influenza pandemic of 1918, Broadway itself remained open to patrons with the likes of Harry Houdini, Will Rogers, and W.C. Fields gracing stages despite the U.S. surgeon general urging the closures of theatres across the country (Collins-Hughes 2020).

While theatres in 2020 adhered more closely to urgings of medical professionals, the show must, and did, go on. Theatrical productions still occurred across the world. Unable to perform in person, many performing arts venues began to reimagine their productions as online experiences (Bonotti and Zech, 2021). Unlike during the Black Death or even Spanish Flu of the early 20th century, scientific and technological advancements made available an entire suite of digital tools and spaces. While some venues toward the beginning of the pandemic chose to adapt indoor spaces for more physical distancing or move productions outside, the majority of performing arts organizations began to transition their programming online (Guibert and Hyde, 2021).

Figure 2. Still frame from San Francisco Ballet's "Dance of Dreams". Credit: San Francisco Ballet

Full-length Shakespeare plays were performed for audiences via Zoom by independent theatre companies (Wright 2020), while The Guardian and Shakepeare's Globe presented a solo video series of famous speeches performed by both theatre professionals and fans (Wiegand 2020). The San Francisco Ballet created and shared a short film as an homage to its hometown and the "beauty of connectivity during a time full of fear and isolation" (Runyan, 2020; Figure 2). Storytelling boundaries began to get pushed with virtual actors and audiences, while practitioners and producers noted the benefits of increased accessibility and an expansion of viewership demographics with both pre-recorded and live-streamed productions (Jacobson, 2020). Techniques used in live theatre to break the fourth wall and increase audience connectivity were adapted to digital platforms as performing artists strived to maintain the intimacy of the theatre, that most intimate of art forms (Marks, 2020). As Gordon Cox noted in a November, 2020 piece in Variety, “all arts organizations are media companies now”.

What Am I Watching Anyways?

The evolution of recording and streaming capabilities has spurred deep reflection and analysis of what theatre and “liveness” really is, both by scholars and practitioners. It should be noted that my purpose here is not to give a comprehensive review of the liveness and theatre debate, but rather summarize key findings within the debate that apply to the evolution of performance via science and technology during the COVID-19 pandemic. While the conversation predates the modern era (Balme, 2008), two seminal works from the 1990’s laid the groundwork for much of the current conversation around these definitions. Phelan (1993) characterized liveness as dependent upon living bodies being able to share both time and space, going further to state that once a performance is recorded or represented in some other form it fails to continue existence as a performance. The benefits of this sort of live performance include feedback loops between performer and audience (Neuringer and Willis, 1987), as well as distinct cognitive and communicative values, modes of audience attention, and a heightened sense of being (Reason, 2004; Dixon, 2007; Shrader, 2015).

On the other side of the original debate was Auslander, who in 1999 considered the mediatization of live events and concluded that these can have the same ontological characteristics as live performance. In later reflections, Auslander expounded upon his original arguments and added that the real-time interactions, connections, and feedback of classic live performance are possible through mediated experiences, and the most important factor in experiencing liveness is the conscious act of the audience to consider virtual entities as “live in response to the claims they make on us” (Auslander, 2006; Auslander, 2012). As time went on, the literature on the subject began to coalesce into an understanding of technology and mediatization being inescapable, though definitionally intriguing. After all, theatre has always been a hybrid form of sorts (Kumar, 2013), and in our age of digital ability, the physical environment of the “theatre” is made accessible by technological networks with technology playing a mediating role (Rosenberger, 2012; Nedelkopoulou, 2016). We experience digital media in multiple lived ways (Irwin, 2016), and “the relationship between the live and the mediated is far less confrontational in artistic practice than it is in academic discourse” (Balme, 2008).

Some have gone so far as to argue that practitioners and audiences alike must completely dismantle the idea that live theatre is some unreproducible event, and allow it to escape the realm of elitism and restriction (Billington, 2014). In practice, theatres have found distinct demographic differences in audiences when considering streamed performances. In a 2016 survey by AEA Consulting for Arts Council England, UK Theatre, and Society of London Theatre, significantly younger and more diverse audiences attend streamed performances, with a significant correlation between increasing streaming and decreasing household income. In terms of audience sentiment, they found that audiences generally believed that streamed theatre was a distinct experience but that "liveness" didn't greatly influence the quality of the audience experience. In fact, only 9% of streamers ranked the factor of "liveness" as "very important" to their overall theatre experience.

It Was This or Nothing At All

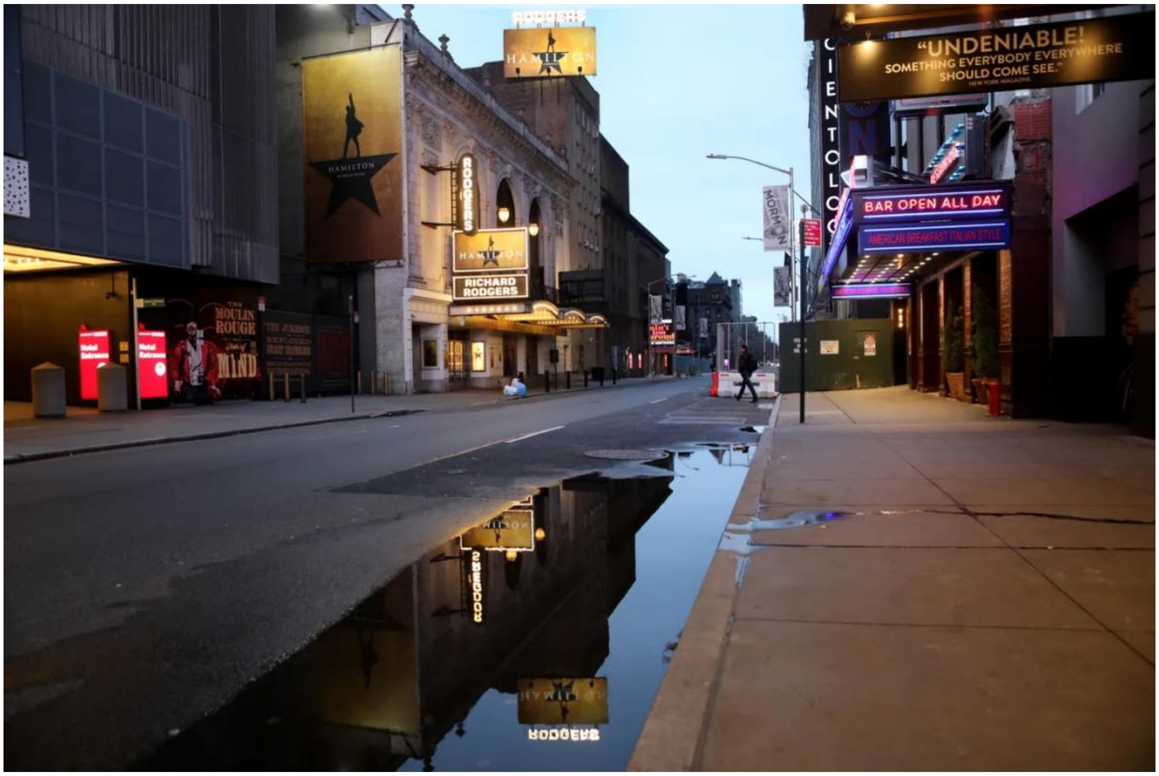


Figure 3. The closed streets of Broadway in 2020: Kevin Wexler, NorthJersey.com-USA TODAY NETWORK

Unlike the optional explorations of technological use in the theatre and the academic deconstructions of technology incorporation, the COVID-19 pandemic created a legally and socially forced movement of theatre into digital spaces. Instead of considering whether or not mediatized theatre *should* count as "theatre", we instead had to realize that it was our *only option* in most cases. The pandemic removed the digital space as a creative option and instead placed it in a space of necessity and survival. Phelan and Auslander's arguments become near obsolete: there was no choice in going digital, so we have to remove it from the consideration of the art form. Following Phelan's definitions of liveness would have literally caused death in some cases, an irony not lost of current literature (Timplalexi, 2020). If mediatized and adapted performance is all we've got, the problem at hand is not defining what we have, but rather making it as connective as possible given the forced constraints.

In literature published during the COVID-19 pandemic, researchers found that connectivity is what mattered most to streaming audiences, even more than any excitement about liveness (Sullivan, 2020). This same desire emerged as a key concern for theatre practitioners and theorists as the pandemic shut down in-person events, and yet the history and precedent of remote viewing and livestreaming pre-pandemic offered optimism in this time of darkness (Starner, 2020). Groups began to understand mediatization as a sort of resilience within the theatre sector, and adapted to the circumstances by finding ways to create a sense of an "event", e.g., by making materials ephemerally accessible, or "redefining the sense of hic et nunc" (Gemini, 2020). While some questions might remain, Timplalexi succinctly summarized the state of the theatre in 2020 as such:

"...theatre first has to acknowledge that the arbitrary privilege of its ontology over mediated performance, supported by theorists like Phelan, can remain intact neither now nor after the current crisis any more"

Science and Theatre Connectivity

How, then, can we achieve what Larson described in *RENT* as "connection in an isolating age"? There is no one answer, nor is any solution able to completely encompass the needs of every member of every audience. However, by briefly exploring the digital theatre options proffered by technology and science both before and during the COVID-19 pandemic, it becomes reasonable to argue that these fields have mechanically facilitated the continuation of theatre in *some form*. In addition to these logistical considerations, science offers human connectivity on a *conceptual plane* when presented theatrically: perhaps science can play a thematically connective role in addition to its mechanical one.

Science has featured as a theatrical subject matter since at least the 1600's (e.g., Marlowe's *Dr. Faustus* in 1604), but has itself evolved as a topic on the stage. With the advent of nuclear power and the consequences of World War II, pieces like Brecht's *Life of Galileo* (1939 and 1947) changed the focus from the scientist to the dangers and implications of science itself. In 1998, Michael Frayn's *Copenhagen* pushed the science play into its next stage of development by seamlessly integrating drama and hard science. With many examples in between, the incorporation of science concepts, narratives, and people into theatrical works allows the playwright to explain important ideas in our daily lives and lead us to question both truth and reality (Yas et al., 2016). Science and theatre work synergistically and are mutualistic: the theatre brings the stories to life in a way that makes the science accessible, and the science brings the intimacy of the theatre alive by getting the audience to consider their place in the universe and similar conceptual frameworks. In the last decade, there has been significant growth in the types of science communication being utilized and the incorporation of science into media. With science moving deeper and deeper into the pop culture sector of humanity, the benefits of conceptual connectivity are seen more and more; ultimately, scientifically invested plays can succeed if they work at the human level (Djerassi, 2002; Carpineti, 2011; Figure 4).

Figure 4. Science and theatre project *Pale Blue Dot*. Credit: Jet Propulsion Theatre

Science in the theatre has provided audiences and theatre practitioners alike the opportunity for existential reflection: not simply offering content, but generating questions as well regarding the meaning of the world, life, and death (Barbacci, 2002; Brunello et al., 2019). In 2004, Barbacci presented a framework for categorizing performances that combine science and theatre. In this, they note the differences between theatre with pedagogical purpose and theatre using motifs inspired by science. In the former, the strengths of theatre enhance the learning process via emotional and sensory communication, a practice utilized in more formal settings like museums and institutions. In Barbacci's category of inspiration from science there are plays dealing with specific ethical dilemmas in relation to scientific pursuit and discovery, plays that are self-contained biographies of a famous scientist, and even theatrical activities and training exercises that draw from sciences like anatomy and physiology. Barbacci claims that the most interesting form of scientific theatre is that in which the performance maintains and uses its artistry to enhance the image of science as a human activity. In a time of desperate need for connectedness, the scientific advancements that allowed theatre to continue and the scientific concepts that created a deeper, more reflective space both provided light and hope for our community during COVID-19.

Local Solutions

As the fall of 2020 approached in Missoula, Montana, our performing arts community was acutely feeling the loss of performance opportunities due to the ongoing COVID-19 pandemic. Despite the size of our town, Missoula ranked in the top 40 of all U.S. cities in the 2019 Arts Vibrancy Index published by Southern Methodist University, taking the #4 spot for medium-sized cities. Missoula prides itself on its culture and communities of art cultivated with care over many years and many organizations; as such, our town understood that despite the COVID-19 pandemic, there were ways to adapt to the circumstances and produce performance projects in a safe and meaningful way. There were two full-length musical theatre productions put on in the fall of 2020 in Missoula: *Theory of Relativity* (TOR) at the University of Montana (UM), and *tick, tick...BOOM!* (TTB) presented by Cadmium Company (CadCo). I was directly involved in both of them, as were scientific concepts and implementations. In TOR, technology enabled an audience to safely view the production virtually, and scientific dramaturgy enabled a deeper connection to the audience via science themes despite the virtual, non-live production. In TTB, epidemiology research and CDC recommendations were implemented throughout the production process, allowing the only live, licensed musical theatre production in Missoula between March of 2020 and March of 2021.

Case Study 1: *The Theory of Relativity*

In accordance with Montana state, Missoula county, and University of Montana regulations, the UM School of Theatre and Dance changed their 2020/2021 season into an entirely virtual one. From October 28 to November 8, 2020, the UM School of Theatre and Dance and UM School of Music co-presented the 2015 Bartram and Hill's *The Theory of Relativity*, a song cycle about human connection (Figure 5). This choice of show was somehow simultaneously ironic and yet perfectly appropriate- a group of students would be performing pieces about connectivity while separated in physical space and time, yet the concepts and themes were genuinely craved by the entire production team. As music director and MFA student Jane Best put it, "Musical theatre is a medium that brings people together, and it has been a challenge to figure out what that means when we're not able to physically gather...what does it mean to sing together … separately? This show, with its theme about searching for connection, hits even harder now, and real life imitates art as we search for connection within our socially distanced rehearsals, Zoom coachings and solo recording sessions."

Figure 5. Still frame from UM’s *The Theory of Relativity*. Credit: https://www.umt.edu/news/2020/10/102220thry.php

The usage of science and technology was central to the *mechanical* success of presenting the musical as a pre-recorded video for audiences to stream. Both video and audio had to be synced between performers, musicians, and direction, and multiple devices and programs were used to create the final video product. However, science is also at the *conceptual* heart of a successful TOR production, and this creative team incorporated two separate science outreach sessions into the rehearsal process. In these, I used what I’ll call science dramaturgy as a means to enrich the connections between the performers and the material, as well as the performers to each other and their audience given the pandemic and virtual circumstances. As previously reviewed, presenting science as an ultimately human endeavor and one that literally and figuratively connects us all can strengthen the overall theatrical experience. In the UM production of TOR, the science concepts woven throughout the written materials were identified, clarified, and communicated as a facilitating force for theatre in that specific moment and environment.

In our first science session, we went through the show song by song and found lyrics and musical themes that related or represented scientific thought, process, or concepts as factors of connection (Table 1).

Table 1. *Theory of Relativity* within-script science and human connection relationships. The notation of [Full piece/thematic] denotes no specific lyrics being referenced for the reflection but rather the motifs and concepts expressed throughout the song as a whole.

Song/Scene	**Excerpt**	**Connection**
Person A	"How fast does B perceive A to be walking?" "A body...will remain in that state of motion unless an external force is applied to it." "...and how will the path of each person be altered by that contact?" "I exist only if observed." "I am nothing without you."	With discordant jolts from the orchestration and abrupt changes in tempo, the characters' lines quickly cross paths until a final line delivered by the full company as one. In the lead up to this thesis statement, there are constant scientific reminders (e.g., Newton's laws of physics and Heisenberg's quantum work) of how each character can and does impact the others.
Relativity	"I am energy. I am mass. I am light." "...light as it speeds..." "And it's you, on this marble...I see myself in your eyes." "And there's you."	Here, Einstein's famous $E=mc^2$ equation describing the relationship between energy, mass, and the speed of light is used literally and figuratively as an anchor point throughout the lyrics. As the song progresses, the pronouns evolve from first person singular to second person singular to first person plural (i.e., I, you, we) which allows the audience and other cast members to

	“And we’re all on this marble…” “...but with someone beside me to measure my pace, somehow I’m not quite so meek.” “We are energy. We are mass. We are light.”	strengthen their bonds between and among themselves. We again get the theme of measurement and observation as key to a sort of existence and significance.
Allergic to Cats	[Full piece/thematic]	While allergies are presented here in a comedic fashion with several points of emotional reflection within fermatas and accelerandos, allergic reactions themselves are in response to some stimulus. The sort of inflammatory response to allergens that the character experiences is parallel to the “inflammatory” response of being in love with a partner who happens to love the thing which causes his inflammation (thereby providing a feedback loop of connectedness).
Cake (Parts 1-3)	[Full piece/thematic]	Similar to allergies, anxiety and other mental conditions are typically triggered by a stimulus of some sort. For this character, that trigger is the physical connection of others to objects that she must in turn engage with. Due to chemical similarities, her anxiety is able to turn into excitement at the idea of the physical connection when it’s enveloped within affection and care from the other.
Pi (Parts 1-3)	“The ratio of the circumference of a circle to its diameter is known as pi.” “Numbers are perfect...numbers are certain…”	The tempo marking is ¾, which numerically connects to the digits we encounter at the beginning of pi. At the top of the number, the character gives the definition of pi, which itself is a relationship; namely, the one between the circumference of a circle and its diameter. Through this three-part number, we find the character exploring

	“Chaos and order can never combine. It’s far too risky when lives intertwine.” “And could it be relationships between two things are more than ratios?”	in real-time the facade that is perfection within mathematics, and finds something even more “certain” in connection with another instead. Musically, the entirety of notes remain on the same pitch throughout parts 1 and 2, with a breakthrough in octaves as the singer engages with his other senses within the lyrics.
End of the Line	“I’m Jenny. I’m Sara. She’s Sara. She’s Jen.” “‘Cause you always looked good next to me.” “We were contrary forces who somehow combine.” “If two equal but opposing forces are applied to person C, one external and one internal...which one will he succumb to?”	This song utilizes both music and lyrics to represent Newton’s 3rd law of motion- an equal and opposite existence of forces exerted on each other. We also get relativity presented thematically with the idea of visual and social comparison- one character places themselves next to the other in order to appear better than she could on her own. In the last part of the song, the characters switch social tiers, again representing a balance of forces- while one is up, the other must be down (i.e., equal and opposite). In the text after the playoff, one character explicitly connects this law of motion to the internal conflict of decision-making.
Great Expectations	“...won for me, no struggle I see. “...is light years away from the life that I want.” “...don’t want the dream I was given. I want the dream that I dreamed.”	In a song about legacy, there are references to literal bloodlines as well as multi-generational cause and effect. Here is another example of opposing forces, in this case the hard work put in for the future vs being given the fruits of others’ labors. The reference to light years is interesting in that this is a unit of distance, not time, so the characters are discussing differences in the present instead of generationally.
Footprint	“They’re frozen in your head the way they were.” “And it’s hard to believe that months have come and gone.”	This piece details connectivity across physical and temporal distances, a theme particularly relevant to pandemic society. Memories and mental images are frozen because without an observer to note the change, it’s as if it doesn’t happen. Time itself is relative to the

	“...the foundation you’ve been rooted to so long is somehow less dependable, is suddenly less strong.” “You see that footprints don’t belong in just one place.” “And the universe gets larger, and the cosmos will expand.”	character as the observer. With the added physical distance between family members during COVID-19, footprints and foundations erode when external, so they must be created internally to have lasting effect. At the very end, the concept of external eternity coupled with internal presentness is cemented with the astrophysical reference to expansion and entropy.
Lipstick	[Full piece/thematic]	Here, Newton’s laws of motion combine with generic particle physics to display a kind of impact and connectedness not present in the rest of the show except for the very top (“Person A”). The particles (people) interact even if they don’t want to, because such a choice affects the other passively just as well as actively. Upon touching, we enter a fantasy space of manipulated motion within connection, but then return to particle physics.
Apples and Oranges	“I guess that I was simply born this way.” “And I learned there with Mike that you like what you like.”	While using food as a metaphor for sexual orientation, we get a light-hearted glimpse at versions of reality that are relative to shared experiences and core, rooted identity.
Me and Ricky; Promise Me This	“To prove that he was here, Ricky left a souvenir, a little gift that can’t be returned. For once I was clever, got rid of him forever. Lesson painfully learned.” “One simple procedure, and now that mem’ry’s erased.” ______________ “I was an only child. See, Mom had lost three others	These two consecutive songs each work as an equal and opposite force for the other in a conceptual framework. In “Me and Ricky”, there is an allusion to a series of actions that led to an abortion by the main character, who is utterly devastated by her connection to a single man. “Promise Me This” comes right after the ending of “Me and Ricky”, with an abrupt shift in chordal structure, musical tone, and tempo. Thematically, we get the beginning of new life- a baby whose mom considers them a miracle

	before it clicked with me. She called me her miracle. Mira, for short." "And my miracle will never fade away."	after having previous miscarriages. If viewed in this light of loss and life being directly exchanged between the songs, we get a transformation of Newton's laws of motion into emotion.
Julie's Song	"He may sniffle a lot. He may break out in hives. But like it or not he's now part of your lives. In spite of all obstacles true love survives…"	The connectivity of characters deepens by continuing the story from much earlier in the show, thus using references to allergic reactions to push the categorical boundaries of the material out of the song cycle realm and into a fully formed and connected musical.
Relative Pitch	[Full piece/thematic]	This piece has no written material included, however the stage directions imply that the actors should express sounds and aural themes that are "gradually picked up by the rest of the company...". There is freedom in how this is staged, and in the UM production there was an emphasis on percussion and shared but distanced physical space, which allowed a heightened sense of togetherness as intended while the show intensified towards its conclusion.
You Will Never Know	"You the subject. Me the observer. Me enthralled. You blissfully blind." "You changed me. But you will never know." "I'm diff'rent. But you will never know."	With venettes overlapping through music we get a sense of tangential connection, while the lyrics remind us of existing only because of being observed, i.e., reliance on the other. We are changed by others just as we change others.
Person A (Reprise)	"Their paths do not intersect. Nonetheless, does B change A's trajectory?" "I see myself in your eyes."	This brief text and musical coalescence uses references to quantum mechanics to take us into the monologue which completes the connecting strands between every cast member and narrative that's been shared.
Manicure	"...light's coming at us at one hundred and eighty-six	In this monologue, the character represents the observer- a single entity

	thousand miles per second. It should hit you first, right?...Wrong! It'll hit both of us at the same time." "The speed of life. Whether you're running from it or toward it, it hits you at the same time."	that by connecting to the rest of the show allows the actions and characters to exist. As originally demonstrated by Young and later considered by Heisenberg, it's possible that reality itself doesn't exist until observed. In a seemingly humorous and light-hearted monologue, we get the personification of the observer effect in physics as well as Einstein's relativity delivered via human connectedness and impact.
Nothing Without You	"...I am nothing without you." "You're a reflection of me. I reverberate. You reply. If I have a purpose, if I count at all, you are why." "You measure, compare, you make me aware that I'm neither small nor obscure." "I'm alive. You make sure." "And I hope it's true that you're nothing too without me."	In the final piece, the thesis statement is given explicitly in both lyrics and music. With the exception of a few harmonic hums, the entire first half of the song is sung in unison without deviation in pitch despite the gospel and modern underpinnings that denote changes to the musicality. There is an almost constant crescendo for the entire piece, with the crux- "I'm alive. You make sure."- building into a key change to solidify the significance of the connections between the characters, actors, and audience. The reference to measurement is taken directly from quantum physics, yet as applied to the characters here it feels as human as can be. The gospel styling allows the formality of the lyrics and scientific concepts to feel heartfelt and deeply soulful.

In our second science session, I focused on summarizing and exploring Einstein's theories of special and general relativity from both scientific and theatrical perspectives with a goal of improving actor familiarity with the subject and improving feelings of connectedness based on the theories themselves. The sort of connections and impacts we understand through Einstein's theories of relativity can provide lasting and reaching impacts, even across virtual space. With Einstein's Special Theory of Relativity, we discussed the continuum and meshing of space and time with an emphasis on the constancy of the speed of light and relative experiences based on perspective. With the General Theory of Relativity, we focused on how the warping of space by mass is parallel to our interactions with each other, and how even through a screen we are still affecting each other's space in significant ways, visible or not. These concepts were especially relevant in the virtual space, not only in terms of emotional and mental connectivity, but in understanding and adapting to lag times in post-production created by the speed at which data travel through the internet (never at the speed of light, hence latency; Rofe and Reuben, 2017). I also answered actor-specific questions regarding scientific references in the material that were still unclear, particularly with the actor doing the "Manicure" scene and the concept of light and constant velocity.

Once the production had closed, I administered an optional survey to the cast members to informally gauge their experience with the science sessions (Figure 6). Overall, the students felt that the science sessions were not only very relevant to TOR as a production, but were generally enjoyable and useful in their character and acting journeys. Recognizing and understanding the underlying scientific themes and concepts throughout TOR not only strengthened the core thesis of the show as written, but provided conceptual and emotional connection among the actors despite the virtual circumstances forced by the COVID-19 pandemic.

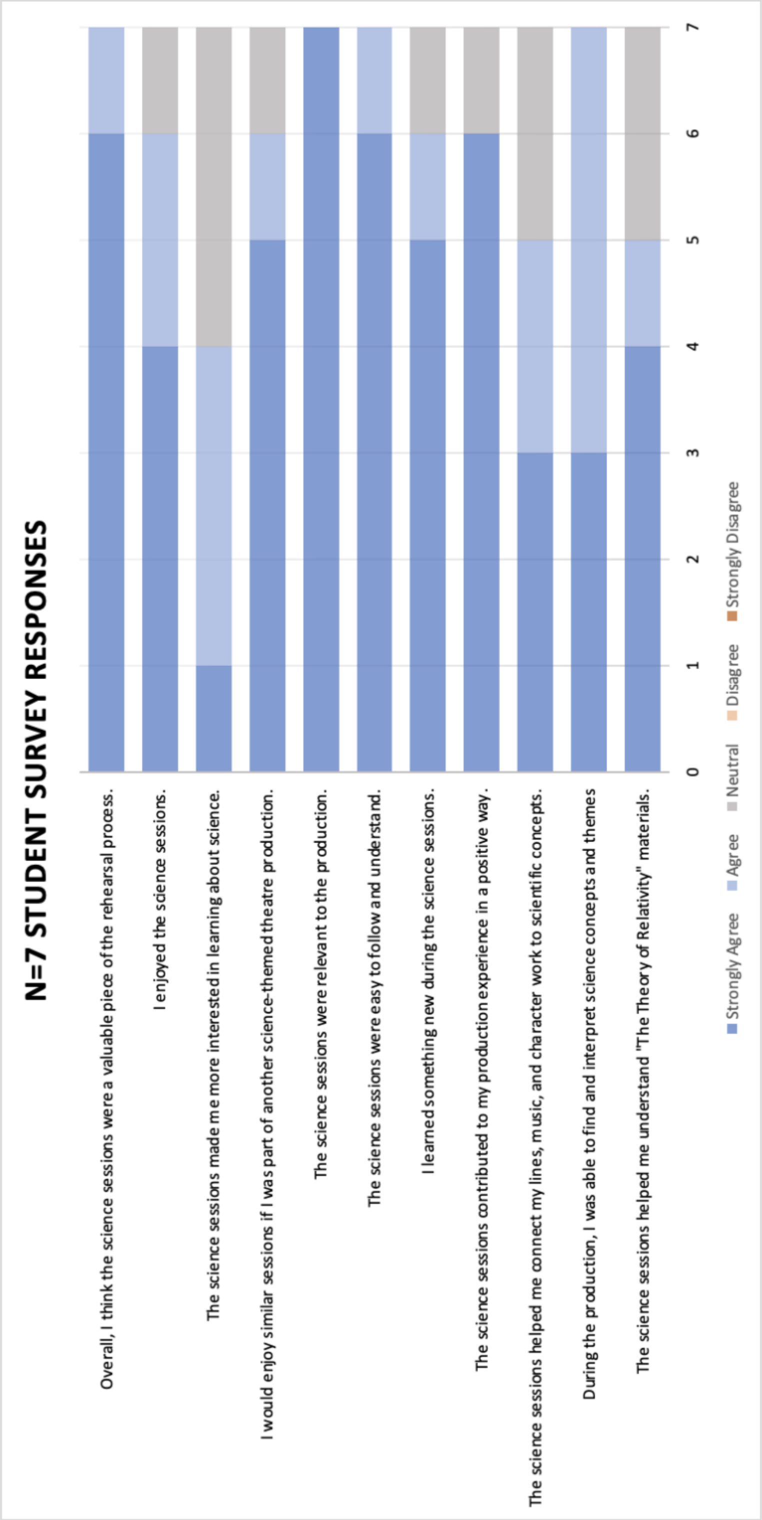


Figure 6. Student survey responses for questions regarding the rehearsal science session extensions.

Case Study 2: *tick, tick...BOOM!*

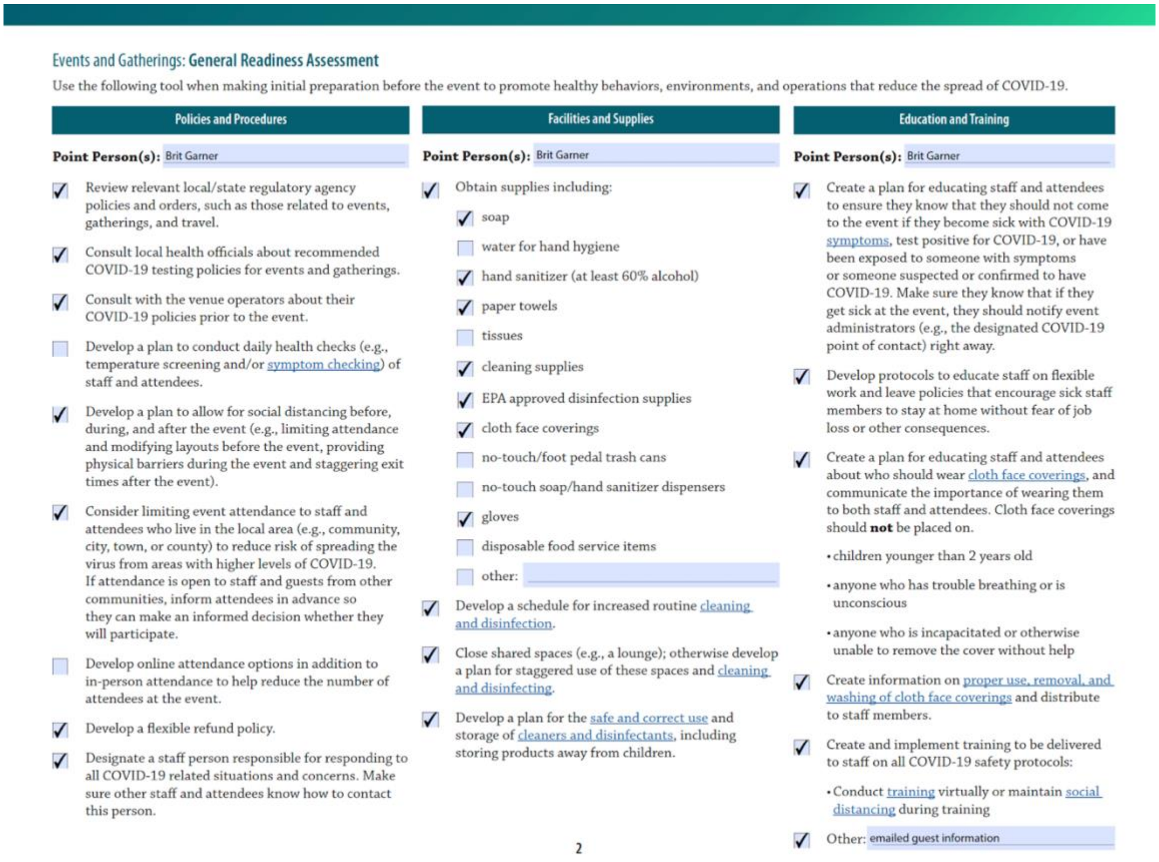
In the early fall of 2020, my personal household was experiencing acute feelings of anxiety and longing for performing arts opportunities. Myself, my partner (Thain Bertin), and another roommate (Andy Nelson) typically participate in musical theatre productions throughout the year, sometimes back-to-back depending on the season. My partner was feeling an additional load of existential ennui as he faced his 30th birthday on September 6th, 2020. On top of the sorts of reflective crises one faces while looking down a 30th birthday, these were combined with his being an actor in the middle of a pandemic with no end in sight or return to performance imminent. As I thought of what to get him and how to celebrate this birthday, a trip through history had another 30 year old artist come to mind- one who had greatly influenced our lives as performers and humans.

On September 6th, 1990, Jonathan Larson opened a four-night performance of what he called a “rock monologue” at Second Stage in New York City. That night, as my partner celebrated the start of his first year on Earth, Larson poured his soul into and out of his keyboard in an attempt to grapple with the 30th year of his own. Originally billed as *Boho Days*, Larson’s rock monologue would later be renamed *tick, tick...BOOM!* during subsequent developments (Jones, 2001; Figure 7). Originally, the show featured Jonathan Larson (plus band) doing autobiographical monologues and songs all about turning 30 in 1990 and the anxieties that came with it: everything from the typical long-term relationship drama to the more unique pressure of desperately wanting to change the face of American musical theatre forever. All of this, plus the raging AIDS epidemic affecting those in Larson's closest circles, including an HIV-positive diagnosis of his closest friend.

Figure 7. Still frame from video of Larson's *tick, tick...BOOM!*.
Credit: broderickjc https://www.youtube.com/watch?v=d-Fp-G6foGc&t=1s

Fans and practitioners of musical theatre know what happened next. In the years that followed, Larson would go on to do exactly what he'd dreamed of but been so afraid of failing to do on his 30th birthday. He would write and create *RENT*, a rock opera that moved to Broadway in 1996 and changed the canon of musical theatre forever. Those familiar with his story also know that he died of an undiagnosed aortic dissection the morning of *RENT's* first Off-Broadway preview performance- despite achieving his dreams, he never actually saw them come true in his own lifetime. In 2001, five years after his unexpected death, David Auburn's (playwright of *Proof*) three-person adaptation of Larson's *tick, tick...BOOM!* (TTB) premiered Off-Broadway, and afterwards became available for independent licensing. My historical Larson trip ended with a conviction to pull off one of the greatest birthdays ever- one that would span 60 years between two men, two pandemics, and three COVID-quarantined Missoula roommates.

Much like UM's *The Theory of Relativity* that would take place six weeks after our production of TTB, science would serve as the conduit for this performance, though in a less technological and conceptual way. Due to non-available streaming rights at the time, we decided to move ahead with an in-person production- the first in our town since March of 2020. We didn't know it at the time, but our Cadmium Company production of TTB, directed by Joseph Martinez with music direction by Scott Koljonen, would be the only fully licensed musical theatre production in Missoula between March of 2020 to May of 2021, making it seem almost Herculean in hindsight. With an in-person show planned for September 3-6 of 2020, our production tied itself to the best possible science, evidence, and adaptive planning available from the CDC, WHO, Missoula County Health Department, Montana state guidelines, and peer-reviewed epidemiological literature on COVID-19 (Figure 8).



Events and Gatherings: **General Readiness Assessment**

Use the following tool when making initial preparation before the event to promote healthy behaviors, environments, and operations that reduce the spread of COVID-19.

Policies and Procedures

Point Person(s): Brit Garner

- ☑ Review relevant local/state regulatory agency policies and orders, such as those related to events, gatherings, and travel.
- ☑ Consult local health officials about recommended COVID-19 testing policies for events and gatherings.
- ☑ Consult with the venue operators about their COVID-19 policies prior to the event.
- ☐ Develop a plan to conduct daily health checks (e.g., temperature screening and/or symptom checking) of staff and attendees.
- ☑ Develop a plan to allow for social distancing before, during, and after the event (e.g., limiting attendance and modifying layouts before the event, providing physical barriers during the event and staggering exit times after the event).
- ☑ Consider limiting event attendance to staff and attendees who live in the local area (e.g., community, city, town, or county) to reduce risk of spreading the virus from areas with higher levels of COVID-19. If attendance is open to staff and guests from other communities, inform attendees in advance so they can make an informed decision whether they will participate.
- ☐ Develop online attendance options in addition to in-person attendance to help reduce the number of attendees at the event.
- ☑ Develop a flexible refund policy.
- ☑ Designate a staff person responsible for responding to all COVID-19 related situations and concerns. Make sure other staff and attendees know how to contact this person.

Facilities and Supplies

Point Person(s): Brit Garner

- ☑ Obtain supplies including:
  - ☑ soap
  - ☐ water for hand hygiene
  - ☑ hand sanitizer (at least 60% alcohol)
  - ☑ paper towels
  - ☐ tissues
  - ☑ cleaning supplies
  - ☑ EPA approved disinfection supplies
  - ☑ cloth face coverings
  - ☐ no-touch/foot pedal trash cans
  - ☐ no-touch soap/hand sanitizer dispensers
  - ☑ gloves
  - ☐ disposable food service items
  - ☐ other:
- ☑ Develop a schedule for increased routine cleaning and disinfection.
- ☑ Close shared spaces (e.g., a lounge); otherwise develop a plan for staggered use of these spaces and cleaning and disinfecting.
- ☑ Develop a plan for the safe and correct use and storage of cleaners and disinfectants, including storing products away from children.

Education and Training

Point Person(s): Brit Garner

- ☑ Create a plan for educating staff and attendees to ensure they know that they should not come to the event if they become sick with COVID-19 symptoms, test positive for COVID-19, or have been exposed to someone with symptoms or someone suspected or confirmed to have COVID-19. Make sure they know that if they get sick at the event, they should notify event administrators (e.g., the designated COVID-19 point of contact) right away.
- ☑ Develop protocols to educate staff on flexible work and leave policies that encourage sick staff members to stay at home without fear of job loss or other consequences.
- ☑ Create a plan for educating staff and attendees about who should wear cloth face coverings, and communicate the importance of wearing them to both staff and attendees. Cloth face coverings should **not** be placed on.
  - children younger than 2 years old
  - anyone who has trouble breathing or is unconscious
  - anyone who is incapacitated or otherwise unable to remove the cover without help
- ☑ Create information on proper use, removal, and washing of cloth face coverings and distribute to staff members.
- ☑ Create and implement training to be delivered to staff on all COVID-19 safety protocols:
  - Conduct training virtually or maintain social distancing during training
- ☑ Other: emailed guest information

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Figure 8. Production-specific COVID-19 planning document adapted from the CDC (2020)

A complete musical theatre production overhaul with reference to health guidelines and epidemiology best practices took place in the first weeks before the rehearsal process began (CDC, 2020). We casted ourselves (three roommates) as the three characters in the show in order to remain within quarantine social bubbles. I did music direction at the house with the three of us for the first two weeks, then we added blocking rehearsals with a director in town but outside of our house's circle. Rehearsals with our director took place outside in our yard with scrap materials to replicate general boundaries of our actual location. Masks were worn while outside in order to minimize any potential spread between our household and our director, according to what was known about the virus at the time (Morawska et al., 2020). A remote pianist recorded backing tracks for use during rehearsals to keep the number of participants as low as possible at any given time, and a group of three musicians were chosen to round out the band based on existing social groupings- they were actively playing in a band together in August of 2020 and were part of a quarantine circle. Materials were dropped off to the musicians for distance learning, and our out-of-town pianist moved into a camper in our backyard for the two weeks leading up to the show so that he could safely return home to his household with older parents. All band members were required to wear a mask while rehearsing and during the performances, and individual practice was encouraged when possible instead of group meetings. We brought on only two additional members- one for sound, and one for venue management before, during, and after performances.

The venue and audience considerations for the actual performances were a separate but equally challenging logistical series (Figure 9). We went with a private residence just outside of town to reduce the chances of curious on-lookers gathering without precaution and directions, and reduced the run of the show to four performances with audience numbers reduced enough to allow a radius of ten feet per person under the scenario of all single-ticket purchases (i.e., no groups of people within quarantine bubbles). Masks were worn inside by both house residents and performers/musicians except for in one ventilated and separated part of the house used as a green room/stage entrance. All ticketing was done via email and payment was done online or at a contactless drop-box on-site. Audience members were given detailed rules, regulations, and directions at the time of ticket reservations and the day of the performance. Masks were mandatory, and audience members brought their own chairs/blankets/seating arrangements in with them to reduce as much surface contact as possible. Spacing was self-directed and then monitored/adjusted by the house manager, and entrances and exits were one way with guidance and signage. An outdoor restroom was available with increased availability of disinfectants, air flow, and with masks required for use- there were no concessions of exchanging of physical items between members of separate groups.

Figure 9. Outdoor performance venue, audience perspective (left). Original planning schematic for space utilization (right).

Part of post-show etiquette at some venues includes mingling and visiting with the cast after final bows. In order to dissuade this during our performance, the actors were removed immediately from the stage after the curtain call. To make up this connective opportunity, we created a process video including a thank you and sent it via YouTube link while encouraging the audience to use the comment section on the video in lieu of a lobby greeting (video available here: https://youtu.be/3NqHTj1CbSQ). In terms of other post-show considerations, we met as a team to discuss any necessary changes after every show and in collaboration with audience feedback. Contact tracing was made possible if necessary by tracking contact information and attendance at front of house and online. This list is not exhaustive, but gives a general picture of the breadth and depth of considerations made on the production side of this particular show. Since September of 2020, the world and our knowledge of COVID-19 has drastically changed, but the precautions and guidelines that we enacted followed the best science available at the time and remained open to adjustment through the entire process.

While we originally chose TTB because of the birthday and original performance connection and because of its small cast requirement, we began to note thematic connections to our current situation within the script. With our entire worlds seemingly moved into digital space for leisure, work, school, and more, some of Larson’s forebodings and themes on virtual life became more present than they’d ever been before. In *RENT*, the character of Maureen does an entire protest speech toward the end of Act 1 centered on a place called “Cyber Land”, where true art and human connection had been replaced by virtual life, money, and yes, even Diet Coke. In the second half of TTB, a character playing an actor in Jonathan's new musical sings about the vacuous nature of virtual spaces vs human sense and connection:

"Come to your senses/ Suspense is fine/ If you're just an empty image emanating out of a screen"

Despite being written decades before the time of COVID-19, this entire number felt eerily timely as we left our Zoom meetings to gather in our outdoor theatre, where simply seeing another person in real life from 20 feet away felt like a magical moment. Disease itself, particularly of the communicable variety, was readily apparent in both "Rent" and TTB, as well as our hourly lives before, during, and after our production. In both musicals, Larson writes deeply about the loss of friends to the growing AIDS epidemic in New York City and elsewhere in the late 1980's and early 1990's- the thematic connection between those times of intimacy being equated with death and the COVID-19 pandemic were undeniable, and connected us to our storytelling in ways we never expected. In TTB, Larson wrote autobiographically about a sort of existential threat that was caving in on him as he approached his 30th birthday, particularly in regards to not making it as an artist. During COVID-19, that existential threat has loomed over the entire performing arts sector of society as we continue to grapple with theatre closures and wonder if we'll ever truly come back from the utter devastation of 2020. On our closing night, September 6th, 2020, exactly 30 years since Larson opened the show and my partner was born, the candles were extinguished on his prop as well as real birthday cake as we toasted to love, loss, and the meaning of pursuing a dream.

It would be a wild understatement to say that performing TTB in-person with a live audience during COVID-19 was an overwhelming experience for our creative team, but also the audience. Our community, like so many countless others, was in mourning and craving connectivity, not to mention harboring a specific sort of grief for the loss of live performance. During the run, I'd been so focused on the organization, stakes, and safety of the live audience that I hadn't considered all of the *good* that we were able to inspire for those who shared that space with us. In several instances, audience members reached out to give their thanks; not just for a *show*, but for a *reminder*- a reminder that we are strong, have stories to tell, are capable of pragmatism, and most importantly, that our community was still alive. By detailing the process and production considerations implemented during our production of TTB, I hope that this document may not only serve as a reminder of resilience in seemingly impossible times, but as a template for the survival of live theatre during those unforeseen but inevitable conditions we'll face in the future (Figure 10).


Figure 10. View from the audience. Credit: Lauryn Windham

Connection in an Isolating Age

While TOR and TTB share little to nothing in the way of music, script, or themes, these two musicals represented the surviving and thriving of the Missoula performing arts community in the fall of 2020. Science and theatre are both methods of human storytelling and exploration- when combined, audiences and theatre practitioners alike can engage with deeper philosophical questions and connections. In the time of the COVID-19 pandemic, science not only exerted an influence on conceptual connectivity, but provided a mechanical means of connection via technology in the case of digital performance. While the performing arts world awaits extinguishing the ghost light, we find hope in the tools of humanity for resilience and connection in performance spaces, live and virtual.

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