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Conserving intraspecific variation for nature's contributions to people

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The rapid loss of intraspecific variation is a hidden biodiversity crisis. Intraspecific variation, which includes the genomic and phenotypic diversity found within and among populations, is threatened by local extinctions, abundance declines, and anthropogenic selection. However, biodiversity assessments often fail to highlight this loss of diversity within species. We review the literature on how intraspecific variation supports critical ecological functions and nature's contributions to people (NCP). Results show that the main categories of NCP (material, non-material, and regulating) are supported by intraspecific variation. We highlight new strategies that are needed to further explore these connections and to make explicit the value of intraspecific variation for NCP. These strategies will require collaboration with local and Indigenous groups who possess critical knowledge on the relationships between intraspecific variation and ecosystem function. New genomic methods provide a promising set of tools to uncover hidden variation. Urgent action is needed to document, conserve, and restore the intraspecific variation that supports nature and people. Thus, we propose that the maintenance and restoration of intraspecific variation should be raised to a major global conservation objective.

The 2019 report by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) concluded that one million species are at risk of extinction[1,2]. While widespread extinctions will undoubtedly have dire consequences for human wellbeing, the report fails to highlight another equally important biodiversity crisis: the loss of biodiversity within species, termed 'intraspecific variation'. Intraspecific variation, which includes genetic and phenotypic diversity within and among populations of wild and domestic organisms, plays a critical role in regulating ecological processes[3] and provides important contributions to people, including food security and medicine, cultural value and inspiration, and ecosystem resiliency to climate change.

The rate of loss of intraspecific variation is many times that of species loss[4–7]; however, diversity below the species level remains severely under-evaluated by global surveys[8]. For instance, as of late 2020, only 1.1% (848) of species evaluated by the International Union for Conservation of Nature (IUCN) were assessed at the intraspecific level. Over half of this 1.1%, which includes 1,486 subspecies, 750 varieties, and 212 subpopulations (Fig. 1), are listed as threatened or worse[9]. As intraspecific variation provides important functions[3] for ecosystems and people (Fig. 2), this loss poses a threat to ecosystem health and human society that may exceed that of species extinctions.

Both the number of populations within species and the genetic variation within populations are declining due to human impacts[4,6,7,10–12]. Recent estimates show a 6% genetic diversity loss for wild animals since the Industrial Revolution (Fig. 3)[6] and a 60% decline in population sizes in the last 40 years[13]. Anthropogenic activity is the overwhelming cause of intraspecific declines[10–12]. Humans alter selective pressures on wild populations directly (for example, through selective harvest[14]) and indirectly (for example, through habitat modification[11,15], climate change[16], pollution[17], and species introductions[18]). Species-level extinctions are implicitly preceded by intraspecific diversity loss, whether through range contraction[7,19], genetic erosion[20,21], or population extirpation[7], and threatened species frequently show reduced genetic diversity compared with species of least concern[12]. In some cases, human activities can increase local diversity, for example, as species expand into human-modified habitats[22], are introduced as human-commensal species[23], or through hybridization[24]. While synthetic analyses have shown both increases and decreases in contemporary genetic diversity for particular populations[25], declines are more commonly observed[6,7,12,16,26].

A better understanding of intraspecific diversity declines can facilitate effective conservation strategies. Application of genomics in conservation enables rapid quantification of intraspecific genetic variation and detection of diversity loss over time[6] through estimates of genome-wide heterozygosity, allelic richness, gene flow, and changes in genetic isolation[5] (Fig. 3). These data can reveal genetic erosion, inbreeding, and accumulation of deleterious variation, any of which may precede local extirpation and species-wide extinction. Genomic data can also help identify populations at risk of entering an extinction vortex, whereby declines in abundance propel genetic diversity loss, thereby driving further declines in abundance due to genetic drift, loss of adaptive potential, and inbreeding depression (Fig. 4)[27].

We review the literature on how intraspecific variation supports essential ecological functions and NCP and highlight new strategies that can be used to test these connections. We emphasize the need for collaboration with local and Indigenous groups who have deep knowledge of the relationship between intraspecific variation and NCP. We advocate for immediate efforts to document, conserve, and restore intraspecific variation, which provides critical benefits for nature and people.

Nature's contributions to people

Beyond its importance for species-level conservation and shaping ecological processes, intraspecific biodiversity provides benefits to

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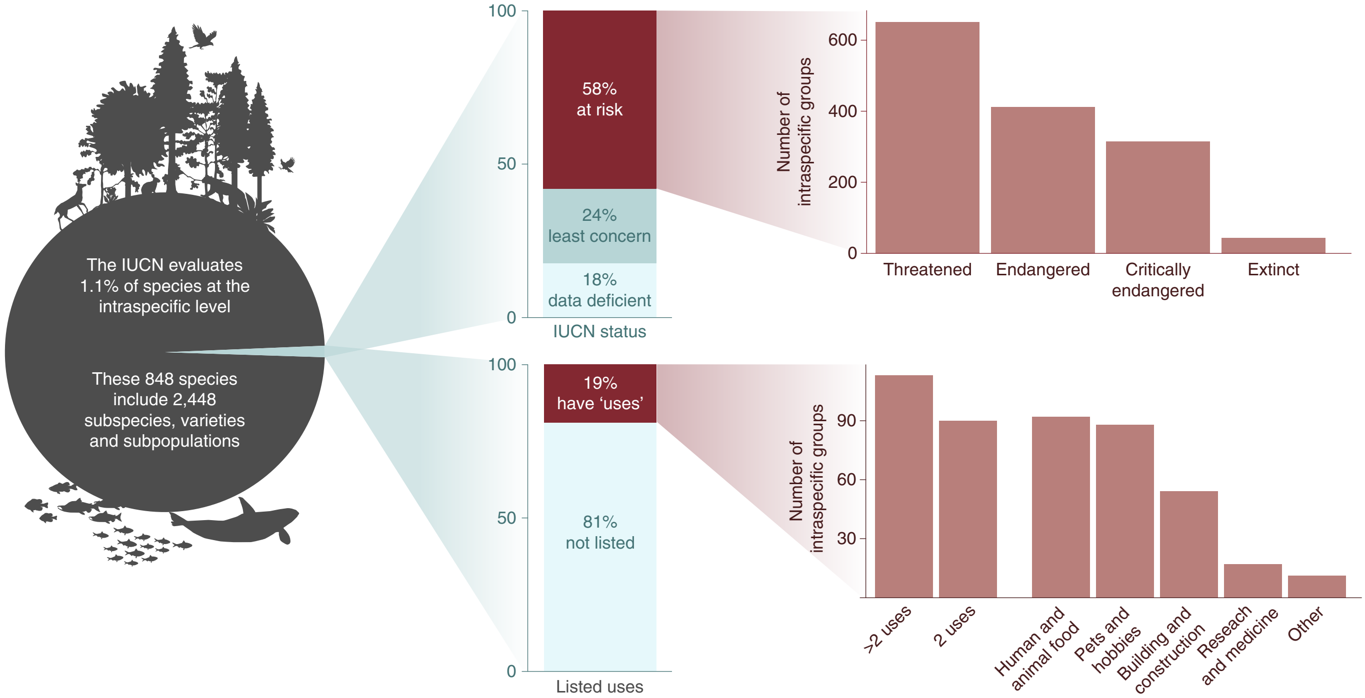

Fig. 1 | The IUCN provides foundational data for global conservation efforts but drastically under-quantifies and thus under-protects intraspecific variation. Only 1.1% of the species evaluated by the IUCN are done so below the species level. Where they are evaluated, these subspecies, varieties, and subpopulations are more likely than not to be at risk (ranked as 'threatened' or worse), a factor probably contributing to their increased attention. We lack understanding on the status of the bulk of intraspecific groups, either because they are unnamed and unclassified or because they have not been individually assessed. Intraspecific groups often have their own unique uses (19% have at least one use listed by the IUCN). In particular, diverse varieties and subspecies of animals kept as pets, and plants kept as ornamentals are often prized, collected, and bred for human enjoyment.

people. The IPBES framework for understanding the human benefits of biodiversity has expanded from economic evaluation of ecosystem services to explicit consideration of the role of human culture in shaping NCP[2]. This shift emphasizes the cultural underpinnings of nature's support of humankind, which have long been recognized by local communities and Indigenous people[28,29]. The NCP framework divides contributions into three principal categories: material, non-material, and regulating (Fig. 5). Material contributions are substances or products that sustain people directly, including food, energy, and building materials. Non-material contributions are psychological benefits that improve human quality of life, through aesthetic value and cultural significance. Regulating contributions include functional or structural aspects of biodiversity that support entire ecosystems. NCP can be direct, for example, plant genotypes that provide novel medicinal products, or indirect, such as the importance of population variation for stabilizing fisheries harvest. As we outline below, intraspecific variation can be an important component of all of these contributions, thus its rapid decline requires immediate focused attention in biodiversity assessments and conservation plans.

Review of literature on intraspecific variation and NCP. We performed a literature review of articles that mentioned intraspecific variation and contributions, services, or benefits toward people (search terms listed in Supplementary Information). Our survey initially produced 344 articles, 67 of which (20%) described primary research where the authors quantified, categorized, or identified intraspecific diversity, as a response, an explanatory variable, or both (Supplementary Table 1). Of these 67, two-thirds measured or described intraspecific variation (primarily genetic diversity) in a focal species for which contributions were recognized but not quantified. This left roughly one-third ($N=23$, Fig. 2) that quantified and depicted the relationship between intraspecific variation and what the authors considered to be contributions or services to people. These studies collectively examined 22 species, including plants, fishes, insects, and fungi, and found effects of intraspecific genetic, morphological, life history, and physiological diversity on material and regulating contributions.

Our review is limited to studies that labelled response variables as services or contributions to people. Other relevant studies missed by our review may not have referenced ecosystem services or NCP explicitly. Non-material contributions are particularly difficult to measure and as such are likely underrepresented in the primary literature. The paucity of references to non-material contributions reflects both an understatement of the cultural, educational, and psychological benefits in the ecosystem services framework and the logistical challenge (or ethical hesitation) that researchers face in quantifying these contributions[30,31]. The fact that there are few measured examples in the literature likely does not reflect a lack of relationship between intraspecific variation and NCP, but rather the absence of specific terminology or framing. Thus, there are ample opportunities to establish new links between intraspecific variation and NCP and to quantify known contributions to people. As an illustration, we describe several examples that reveal crucial ties between intraspecific variation and material, non-material, and regulating contributions.

Material contributions. Material contributions are the most direct and quantifiable benefits of intraspecific variation to people. Food security and the economic value of harvested species depend on intraspecific variation. For example, sockeye salmon (*Oncorhynchus nerka*) harvest in Bristol Bay, AK, USA, is maintained through subpopulations that are locally adapted to the conditions of different watersheds[32]. Over time, environmental fluctuations cause

	Intraspecific variation measured					Human interactions			Contributions to people										
									Regulating							Material			
	Genetic	Cultivar or population level	Life history or phenological	Physiological	Morphological	Farmed or cultivated	Harvested or hunted	Restored or managed	Habitat creation	Pollination	Climate control	Freshwater quantity	Coastal and freshwater quality	Sediment regulation	Pest and pathogen control	Energy and fuel	Food and feed	Materials and companionship	
Sockeye salmon	●	●	●	●	●		●	●									●		Freshwater et al. (2018) Griffiths et al. (2013) Larson et al. (2016)
Chinook salmon	●	●	●				●	●									●		Yamane et al. (2018)
Western honeybee	●					●				○					●		○		López-Uribe et al. (2017)
Buff-tailed honeybee		●				●	●			●							○		Trillo et al. (2019)
Common apple		●				●									●		○		Mody et al. (2017)
European aspen	●					●	●		●	○						○			Zhang et al. (2015)
Quaking aspen	●					●	●		●	○						○			Zhang et al. (2015)
Red maple		●		●	●	●	●				●				●			●	Lahr et al. (2020)
Norway spruce					●		●	●										●	Piermattei et al. (2020)
Common eelgrass	●							●	●				●	●					Reynolds et al. (2012)
Common reed		●		●				●					●						Song et al. (2020)
Catgrass	●	●				●								●	●		●		Poirier et al. (2012) Yoshihara and Isogai (2019)
Tall fescue		●				●								●					Poirier et al. (2012)
Perennial ryegrass		●	●	●											●		●		Lowry et al. (2020)
Soft rush	●	●		●	●									●					Born and Michalski (2017)
Common wheat	●	●				●									●		●		Dubs et al. (2018) Mansion-Vaquié et al. (2019)
Switchgrass	●					●									●	○	○		Schuh et al. (2019)
Rye		●		●	●	●								●			●		Bukovsky-Reyes et al. (2019)
Vase bromeliad									●										Zytynska et al. (2012)
Hairy vetch		●		●	●	●								●			●		Bukovsky-Reyes et al. (2019)
Common bean		●				●											●		Koskey et al. (2017)
Articulospora tetracladia	●	●										●	●						Duarte et al. (2019)

Fig. 2 | Few studies assess the relationship between NCP and intraspecific variation. This table summarizes studies that quantify this relationship, highlighting the type of intraspecific variation measured (left columns in teal), the relationship to humans (where specified in the original study; middle columns in orange), and the contributions measured (right columns in maroon) or mentioned (lighter maroon points). Literature review methodology and references for this table are available in the Supplementary Information. A list of all studies identified by the review, including those that did not quantify NCP, can be found in Supplementary Table 1.

declines in some subpopulations but increases in others, resulting in a stable aggregated population overall[33,34]. These portfolio effects reduce the frequency of fishery closure, increasing long-term commercial economic revenue and food security for subsistence fishing[35,36]. Portfolio effects in salmon are undermined by dams, which prevent subpopulation access to critical spawning habitat[37]. They can be further harmed when managers augment declining wild salmon populations with hatchery-reared individuals[38], a practice

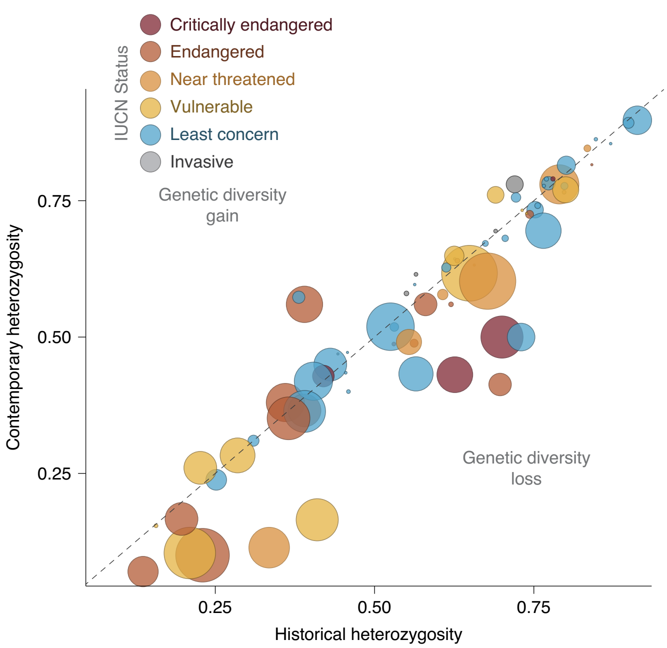

Fig. 3 | Genetic diversity within species shows drastic declines since the Industrial Revolution. A comparison between historical and contemporary estimates of heterozygosity shows that losses are much more common and dramatic than gains. These data, amalgamated from ref. [6], combine expected heterozygosity estimates from 88 studies quantifying changes in genetic variation between historical (from archival or ancient DNA specimens) and contemporary samples of 91 different species. Point size represents the amount of time between contemporary and historical measures of expected heterozygosity (an average of 27 generations). Point colour corresponds to the IUCN ranking of that species as of March 2020.

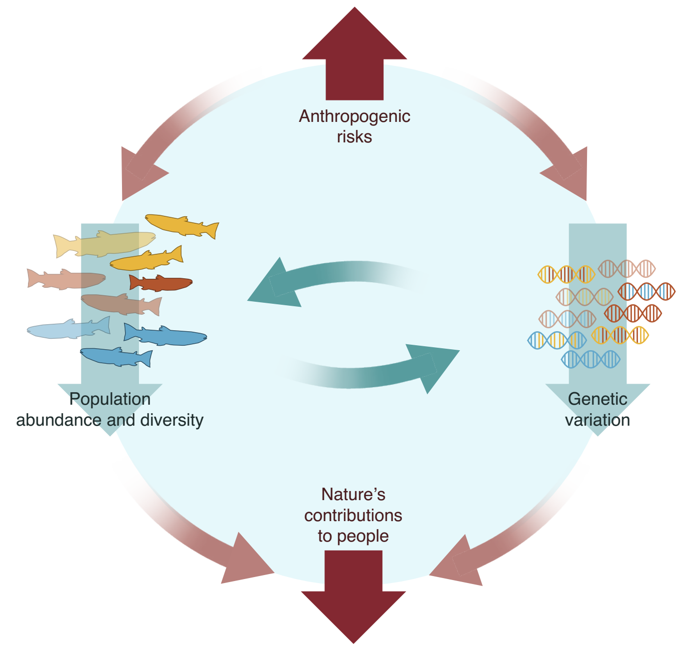

Fig. 4 | Intraspecific variation and its contributions to people are threatened by anthropogenic risks. These risks (habitat change and loss, pollution, invasive species, exploitation, and climate change) threaten intraspecific diversity by driving decreases in species' ranges and population sizes, and by causing decreases in genetic and phenotypic variation. These declines compound one another and can lead to decreases in material, non-material, and regulating contributions to people.

which reduces intraspecific diversity through genetic homogenization[39,40]. In California's Central Valley, for example, increased hatchery production has reduced genetic variation in Chinook salmon (*Oncorhynchus tshawytscha*)[38,41], causing boom–bust population cycles that are detrimental to the long-term value of the fishery[38,41]. In contrast, strategies that promote and restore diverse natural populations can increase abundance while also maintaining long-term harvest stability (Fig. 6).

Intraspecific biodiversity also provides material contributions in the form of natural medicinal products. Both traditional and Western medicine use biopharmaceuticals to diagnose, treat, and manage disease, infection, and biotoxin exposure. Naturally produced alkaloid compounds, for example, have substantial physiological effects on humans and have been important pharmacological products for centuries[42]. *Cinchona calisaya* bark, for example, was once the exclusive source of alkaloids used in the production of the antimalarial drugs quinine, quinidine, cinchonine, and cinchonidine, which target malarial plasmodia through alternate pathways[6]. Genetic diversity underlies considerable variation among alkaloids produced by different *C. calisaya* individuals[43]. Understanding and protecting intraspecific variation may therefore be critical for human health, particularly for the discovery of new drugs and to confront the threat of drug resistance[44]. To this end, recognition of the biochemical and economic potential of populations and genotypes is a major human health incentive.

Non-material contributions. Humans have an inherent appreciation and curiosity for biological variation, which is not limited to the species level[45]. Indeed, observations of intraspecific variation led to the insights by Charles Darwin[46] and Gregor Mendel[47] that founded modern evolutionary theory. Intraspecific variation is also a source of knowledge and culture for Indigenous people, as is reflected in language. For example, the Dene people in the Northwest Territories, Canada, have unique words distinguishing distinct groups of caribou (*Rangifer tarandus*) based on differences in morphology, behaviour, and habitat preferences, now supported by genetic analysis[28]. Rare colour and pattern polymorphisms within species have also captured the collective human psyche[48]. People travel to distant locations to glimpse unusual bird colour morphs[49] and preferentially collect highly polymorphic herpetofauna[50,51] and fishes[52,53]. These preferences even motivate official classification of subspecies and varieties: nearly 10% of the 2,288 subspecies and varieties assessed by the IUCN have listed uses as pets, display animals, and horticultural varieties and for sport hunting or specimen collection[9]. While some named intraspecific variants have boosted ecosystem conservation (for example, British Columbia's white spirit bear; *Ursus americanus kermodei*[54]), others have propelled poaching (for example, white Bengal tigers; *Panthera tigris tigris*[55]) and illegal collection (for example, Asian arowana; *Scleropages formosus*[53]). Thus, human fondness for rare variants has had mixed impacts on conservation, driving efforts for exploitation as well as protection.

Quantifying and understanding intraspecific variation at genetic and genomic levels has become increasingly important for conserving the threatened charismatic megafauna, such as tigers[55], giant pandas[56], hawksbill turtles[57] and whale sharks[58], that provide cultural meaning and inspiration. In the absence of genomic data, morphological and geographic variation has sometimes misled conservation. In tigers, for example, inappropriate subspecies delineation thwarted broad-scale reintroduction and breeding programmes that might have promoted genetic diversity and species recovery[59]. On the other hand, genetic information has been successfully used in reintroduction programmes to mitigate inbreeding depression. For example, augmentation of Florida panther (*Puma concolor*

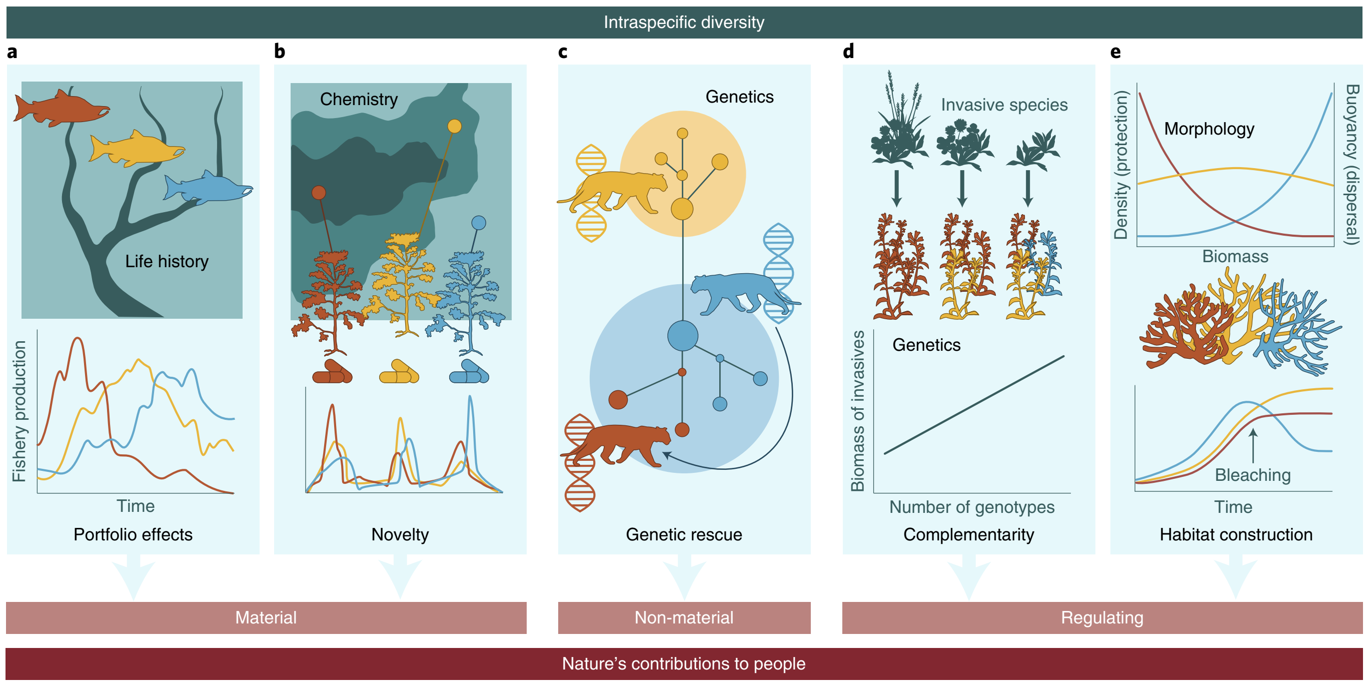

Fig. 5 | Intraspecific diversity provides material, non-material, and regulating contributions to people. **a**, Portfolio effects ensure stability of fisheries through time as production is shared across multiple subpopulations. **b**, Novelty in medicinal compounds varies across locations and promotes the discovery of new drugs. **c**, Genetic rescue of threatened populations using captive breeding and reintroduction can be used to help recovery efforts. **d**, Complementarity among diverse plant genotypes promotes more productive and invasion-resistant ecosystems. **e**, Habitat construction is supported by diversity among coral genotypes, with some clones being more resistant to bleaching, others supporting shoreline protection, and others promoting dispersal.

coryi) populations with Texas pumas (*Puma concolor stanleyana*)[60,61] helped increase genetic variation necessary for recovery.

Regulating contributions. Humans benefit from the regulating contributions of ecosystems supported by intraspecific biodiversity, which serve to increase ecosystem resilience to threats such as invasive species[62], pathogens[63–65], pollution[66], and climate change[67] (Fig. 2). In particular, genetically diverse plant populations partition resources such as light and nutrients more efficiently compared with monoclonal stands[68]. For example, diverse populations of goldenrod (*Solidago altissima*), a dominant North American plant, have increased stem density and are less susceptible to invasion by exotic plants than less diverse populations[62]. Plots of mixed goldenrod genotypes also experience reduced insect herbivory because genetically dissimilar individuals are less likely to be susceptible to the same natural enemies[62,69]. The resistance benefits of intraspecific genetic diversity extend to crop species, which are often planted in monoclonal stands[70–72]. Croplands with natural genetic diversity decrease the need for pesticides[72,73], both conferring financial incentives for farmers and benefitting nearby ecosystems.

Intraspecific variation in the traits of foundation species, such as reef-building corals, seagrasses, and mangroves, can have widespread effects on the regulating contributions of ecosystems. For example, phenotypic diversity in growth and branching patterns of the reef-forming staghorn coral (*Acropora cervicornis*) ensures long-term stability of the communities they support[74,75]. Trade-offs between branch density and growth rate in staghorn coral influence resistance to breakage, an important determinant of the reef's ability to buffer storm surges[76]. Using heat-resistant corals in restoration projects may increase the ability of reefs to cope with climate change[77], but such approaches must be managed carefully to avoid genetic homogenization that could have detrimental long-term ecosystem effects. Similarly, intraspecific variation in species that interact with foundation species can have important effects on ecosystem processes. For example, populations of dogwhelks (*Nucella ostrina*) differ in their predatory effects on foundational habitat-building mussels[78], and individual variation in several fish species contributes to nutrient recycling in Bahamian mangrove estuaries[79].

The importance of local and Indigenous ecological knowledge. The importance of intraspecific variation to local and Indigenous people is reflected within languages and cultural practices[28,29]. This local knowledge (also called 'traditional ecological knowledge') often implicitly recognizes intraspecific variation and its importance for NCP. Many important intraspecific differences relate to variation in behaviour, habitat use, timing of reproduction, and other traits recognized only through consistent long-term observation. For example, in the remote northern Lake Mistassini (Quebec, Canada), First Nations Cree fishers recognize lake trout (*Salvelinus namaycush*) forms based on morphology, habitat preferences, seasonal movements, spawning locations, and reproductive timing[29]. Lake trout are an important food resource, and this intraspecific diversity is critical to local food security. Further, in agroecosystems, local knowledge about intraspecific plant traits supports sustainable harvests. Traditional coffee (*Coffea arabica*) farmers in Costa Rica predict functional traits from leaf features and use this knowledge to determine ideal shade and nutrient levels[80]. The same deep understanding of relationships between plant traits and ecological function exists for wild harvested species. In the Peruvian Amazon, traditional harvesters' estimates of nut production by individual Brazil nut trees (*Bertholletia excelsa*) closely reflect results of scientific surveys[81]. Collaboration with local communities can inform scientific understanding of the ecosystem processes that provide such important non-timber forest products for local people.

The intimate familiarity of local and Indigenous people with intraspecific biodiversity makes their active involvement in conservation efforts crucial. Because many of these societies rely on intraspecific diversity, they are likely to know when certain variants or

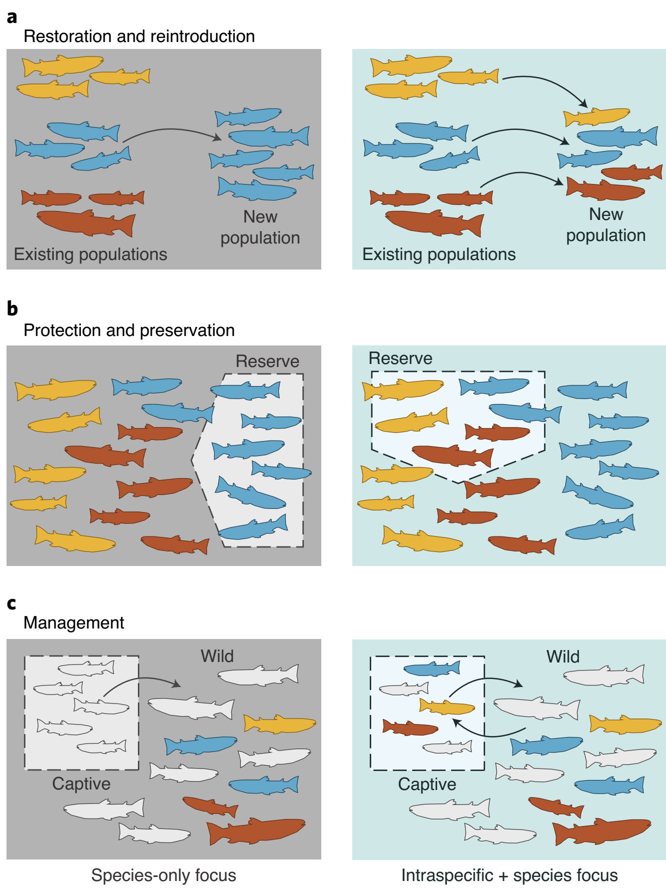

Fig. 6 | Opposite extremes of conservation strategies that ignore intraspecific variation, only focusing on species (left panel in grey) versus those that explicitly focus on preserving intraspecific variation (right panel in teal). a–c, To help protect NCP, successful conservation methods can use restoration (**a**), preservation (**b**), and management strategies that consider intraspecific diversity rather than just number of individuals (and species) (**c**). These tactics will help maintain the stability and persistence of species, and therefore the continuance of their contributions, into the future.

populations are disappearing or changing. For example, Cree fishers of Lake Mistassini in Quebec, Canada, were the first to document changes in lake trout spawning time and locations, declining body size, and morphological and behavioural changes[29]. These fishers identified how observed trait changes might be linked to threats posed by new fishing practices and which conservation measures could preserve lake trout diversity.

Local and Indigenous ecological knowledge can inform hypotheses about the relationships between intraspecific variation and NCP. Integration of this knowledge with Western science should be performed in close partnership with local and Indigenous people in order to generate effective conservation outcomes in ways that are respectful to other knowledge systems[28].

Conserving intraspecific variation for NCP

Intraspecific variation provides critical contributions to both nature and people and thus deserves much greater attention from conservation practitioners and policymakers. First, we encourage research that will help us understand and quantify intraspecific variation, its change through time, and its contributions to people. Second, we implore policymakers to better incorporate intraspecific variation into biodiversity assessments, such as those produced by the IPBES, IUCN, and US Endangered Species Act. Third, we suggest basic tactics for conserving intraspecific variation in the restoration, protection, and management of species. We outline these three steps below.

Understanding and documenting intraspecific variation and its contributions to people. To better understand intraspecific variation, its drivers, and its consequences for ecosystems and humans, we need to make use of novel approaches to efficiently gather quantitative and qualitative information. As DNA sequencing becomes less expensive, genome-wide association studies (GWAS) that link variation in phenotypic traits to genomic data are newly possible for many non-model species[82,83]. GWAS, which have traditionally been used to understand the genetic basis of intraspecific trait divergence, can be extended to explore the links among genetic variation, ecological functions, and NCP. Additionally, macrogenetics[84,85], which attempts to describe broad-scale patterns of genetic variation at large spatial and temporal scales and across taxa, can facilitate the understanding of changing patterns of intraspecific variation, especially for widely distributed species[86]. These methods and frameworks can be employed by consortia such as the Earth Biogenome Project[87] to rapidly approximate the true extent of intraspecific diversity loss and facilitate decision-making by conservation practitioners.

While genetic data can help to reveal quantifiable benefits of intraspecific variation, some functions and services provided by intraspecific variation are not easily measured. Non-material contributions, including those that foster and support education, conservation, and culture, might be better understood through local and Indigenous ecological knowledge[2]. As a result, documentation of intraspecific variation must include collaboration with local communities and Indigenous people. Community science (also known as citizen or participatory science)[81,88,89] takes advantage of people's inherent captivation with natural diversity and thus can help to record and showcase intraspecific variation. For example, community science groups detected differences in snail colour and pattern polymorphism in urban heat islands in the Netherlands[89] and birdwatchers recorded differences in sparrow song throughout North America[90]. Broader programmes and platforms such as the Breeding Bird Survey[91] and iNaturalist[92] can record intraspecific variation ranging from colour polymorphisms to phenological differences[89]. These efforts raise broader awareness and appreciation for all forms of biological diversity, helping prioritize its equitable conservation through public action[93].

Incorporating intraspecific variation and its contributions to people into biodiversity assessments. The incorporation of intraspecific variation into biodiversity assessments should build on existing frameworks to evaluate species, subspecies, varieties, and subpopulations. Genomic methods that measure genetic diversity are already used to infer population susceptibility to inbreeding depression, drift, and extirpation[94]. Biodiversity assessments should work towards standardizing genetic diversity evaluations, including for species of low concern[86]. These methods can improve identification of evolutionarily significant units (that is, reproductively distinct populations[95] that demonstrate significant divergence[96] from other groups as reflected by molecular data[97]) below the species level. In some cases, molecular data can reveal cryptic population structure and variation, encouraging the 'splitting' of existing conservation units into smaller groups for independent assessment and protection[98]. Molecular data can also uncover relatedness among populations and help determine suitability for translocation and genetic rescue[99]. Rapid decreases in the cost of whole-genome sequencing and advances in population genomic approaches[100] have the potential to accelerate and standardize intraspecific biodiversity assessments.

The existing NCP framework provides a set of specific contributions that can be evaluated in the context of intraspecific variation.

Although some examples exist (Fig. 4), more systematic research is needed to explore how intraspecific variation affects these contributions across regions and organisms. Current methods for quantifying and attributing NCP (even at the species level) are idiosyncratic and not standardized across organisms or contribution types. While non-material and regulating contributions may often require detailed study of people and ecosystems through novel socio-ecological studies[101], standardized assessments of material contributions (for example, of costs and yield) are well within reach. If the compilation of this information is prioritized, assignment of material contributions using standardized criteria could be implemented quickly and at relatively low cost. Concerns about the cost of implementation are likely more than counter-balanced by the potential costs of losing intraspecific variants that provide critical NCP.

Conserving intraspecific variation and its contributions to people. Existing conservation efforts that restore, protect, and manage species and populations often focus on the number of individuals, ignoring genetic, phenotypic, and functional variation among those individuals—an approach that has several weaknesses. For example, low trait variation in dominant, foundation, and keystone species often supports less diverse ecosystems, ultimately leading to suppressed ecosystem function and reduced contributions to people. Reintroduced species that have smaller population sizes, and thus low genetic variation, are also subject to genetic drift and might be less capable of adapting to future conditions. To address these concerns, restoration efforts should incorporate genetic and phenotypic diversity into reintroduction plans. When appropriate, reintroduction projects should consider introducing genetically and phenotypically heterogeneous individuals[102] (Fig. 6a), although we note the risk of introducing maladaptive variation. Rather than focusing on species diversity alone, reserves should aim to protect genetic and phenotypic diversity within species[103]. Similarly, frozen zoos, seed banks, and gene banks should house genetically diverse samples when possible (Fig. 6b). Captive propagation efforts should aim to infuse genetic diversity from wild stocks to minimize selection for captive genotypes and phenotypes[39] and simultaneously pursue habitat restoration efforts to re-establish wild populations. Finally, harvest should be spread over multiple populations, ages, and size classes whenever possible to preserve portfolio effects[14,32,79] (Fig. 6c).

Additional contributions of intraspecific variation

The NCP framework is intended to demonstrate how biodiversity in all forms, including below the species level, benefits people. However, intraspecific genetic variation has important additional roles that the NCP framework does not address explicitly. Intraspecific variation underlies the temporal persistence and demographic stability of populations and their contributions. Populations threatened by the interdependent processes of demographic stochasticity and genetic drift are often caught in a vortex of declining genetic variation, ultimately leading to inbreeding depression[104] and loss of adaptive potential[105]. Because genetic variation is the raw material on which natural selection acts, it is essential for preserving the capacity for populations to adapt and persist (for example, through evolutionary rescue[106]). A better understanding of this variation will not only assist the preservation of populations and species through time, but also help predict how service-providing species could evolve in response to global change[107], for example, through decreases in body size[108].

Many species face disproportionate exploitation through harvest and hunting that can deplete intraspecific variation and reduce NCP. For example, oyster harvest causes genetic diversity declines, threatening the persistence and abundance of harvested wild populations. Oysters also provide ecological services such as cycling nutrients, reducing turbidity and improving overall water quality[109]. Thus, the decline in intraspecific variation from disproportionate exploitation can cause collateral damage to a great number of ecological processes that are beneficial to humans. This cascade of declines in NCP caused by exploitative intraspecific variation loss is evident in many species, including migratory fish that transport nutrients[110] and forest trees that act as carbon sinks and regulate climate[111].

Conclusions

The IPBES and other biodiversity assessments historically under-value variation below the species level. Though the 2019 IPBES report mentions the importance of genetic variation[1], it fails to highlight nature's contributions that are specifically supported by intraspecific variation as a whole. Intraspecific variation is especially reduced in threatened and exploited species[12] but can also be low in species that are abundant. As a result, we might experience declines in intraspecific variation and NCP even for species of low conservation concern. Further, because declines in intraspecific variation implicitly precede species extinction[21,27], NCP can be lost long before the extinction of the species themselves. We therefore encourage biodiversity assessments to more systematically evaluate and incorporate NCP that are tied to intraspecific variation. This task will require active engagement with community scientists, local and Indigenous communities, policymakers, managers, and scientists.

In a rapidly changing world, perhaps one of the most overarching benefits of intraspecific diversity is the maintenance of future options. Though rarely mentioned in the context of NCP, intraspecific variation inherently provides the raw material of adaptive evolution and thus supports the persistence of species, promotes ecosystem resilience, and offers novel contributions to people. Thus, the greatest value of intraspecific diversity may be in response to challenges that we have not yet perceived.

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Author contributions

S.D., L.H.P. and E.P.P. conceived the original idea for the manuscript. S.D. completed the literature review portion and the visualizations. S.D., L.H.P., B.S. and E.P.P. contributed to writing and revising the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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