REVIEWS

The importance of genomic variation for biodiversity, ecosystems and people

Madlen Stange, Rowan D. H. Barrett and Andrew P. Hendry✉

Abstract | The 2019 United Nations Global assessment report on biodiversity and ecosystem services estimated that approximately 1 million species are at risk of extinction. This primarily human-driven loss of biodiversity has unprecedented negative consequences for ecosystems and people. Classic and emerging approaches in genetics and genomics have the potential to dramatically improve these outcomes. In particular, the study of interactions among genetic loci within and between species will play a critical role in understanding the adaptive potential of species and communities, and hence their direct and indirect effects on biodiversity, ecosystems and people. We explore these population and community genomic contexts in the hope of finding solutions for maintaining and improving ecosystem services and nature's contributions to people.

Intraspecific genetic variation
Variation in alleles of genes within and among populations of the same species.

Genetic diversity
Interspecific and intraspecific genetic variation.

Contemporary evolution
(Also known as rapid evolution). Natural selection that drives adaptive evolution in populations on timescales of less than a few hundred years.

Gene flow
Transfer of genetic variation from one population to another usually via migrating individuals.

Redpath Museum, McGill University, Montreal, QC, Canada.

✉*e-mail: andrew.hendry@mcgill.ca*

Humans are having a massive ecological impact on the world around us, leading to many immediate and long-term consequences for biodiversity, ecosystem function and people[1]. Indeed, several international programmes, assessments and goals have highlighted critical biodiversity losses, the human-mediated drivers of those losses and the immediate, often negative consequences for humans. High-profile examples of these initiatives include the United Nations Sustainable Development Goals, the Convention on Biological Diversity Aichi Biodiversity Targets and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) Global assessment report on biodiversity and ecosystem services. Such considerations of biodiversity losses, and their consequences for ecosystems and people, traditionally emphasize species identity (presence or absence of a given species), species diversity (number of species) and, increasingly, functional diversity (for example, phenotypic trait variation in a community)[2] or evolutionary diversity (for example, phylogenetic distance among species in a community)[3]. A more recently emphasized addition to these considerations is intraspecific genetic variation and its ecological consequences[4–8]. All these levels and forms of diversity (that is, species diversity, functional diversity, phenotypic diversity, evolutionary diversity, phylogenetic diversity and intraspecific genetic diversity) are currently declining across the globe, although at rates that differ dramatically among indices, taxa and geographical regions[9].

Increasing recognition of the importance of intraspecific genetic (henceforth, simply 'genetic') variation, as well as its contemporary evolution, has led to more frequent calls for its preservation[10] and also for direct actions to increase current levels of that variation in natural, captive and domesticated populations. Suggested direct actions include species translocations[11], assisted gene flow[12] and breeding programmes[13] that actively seek to maintain or increase genetic variation. Moreover, the number of proposals to manipulate genetic diversity using genetic engineering is increasing, for example, in 'de-extinction' efforts to restore long-extinct alleles in a population or even to resurrect extinct species[14]. Determining and implementing the most effective methods for monitoring and modifying genetic diversity will require a thorough understanding of not just allelic variation at specific loci but also epistatic interactions between loci and genome structure, as well as careful consideration of its population and community genomic context. The reason for this complexity is that the effects of a given genetic variant (allele, gene or structural variation) will depend on the frequencies of alleles at other loci in the individual, the frequencies of those alleles in the population and the patterns of spatio-temporal co-occurrence between alleles in interacting species. At present, however, such knowledge is lacking in most instances, with potentially damaging outcomes (TABLE 1).

Our aim in writing this Review is to pique the interest of geneticists and evolutionary biologists in applying their skills towards an improved understanding of how genetic variation influences the health and well-being of ecosystems and people. Such applications are already frequent in medicine and agriculture, as well as in some conservation and natural resource contexts[4,6,13,15,16]. We hope to expand the sphere of interest in these

Table 1 | **Unintentional effects of manipulations to intraspecific variation**

Modified organism	Effect on interspecific diversity	Refs
Petunia (*Petunia hybrids*)	Artificial insertion of a maize flower pigmentation gene caused its unintended silencing via hypermethylation of the promoter	136
Canola (*Brassica napus*)	Genetically engineered canola fields, engineered to resist herbicide treatment, had lower wild bee abundance, resulting in a pollination deficit	137
Bt aspen (*Populus* hybrids)	Insect-resistant *Bt* aspens caused a change in leaf litter decomposition that resulted in a shift in the aquatic insect community	138
Bt aspen (*Populus* hybrids)	Insect-resistant *Bt* aspens did not grow larger despite lesser leaf damage and were still targeted by one main pest	139
GH-transgenic coho salmon (*Oncorhynchus kisutch*)	GH-transgenic salmon, as compared with their non-transgenic half-siblings, showed more aggressive foraging behaviour, with differential effects on mortality and foraging success that were contingent on age	140,141

Bt, *Bacillus thuringiensis*; GH, growth hormone.

Mutation
Change in the DNA sequence.

Genetic drift
Stochastic process altering the genetic variation in a population, usually reducing genetic diversity.

Population genetics
The study of genetic variation and evolutionary history within species using single-gene markers (population genetics) and multigene markers up to full genomes for consideration of structural and epigenetic variation (population genomics).

Community genetics
A community is the sum of populations formed by different species within a particular geographical area. Community genetics and genomics studies the effects of interactions among genomic variation between interacting species. Such interactions are mediated through phenotypes that are determined by heritable genetic variation and environmental influences.

Extended phenotypes
Phenotypes that include effects of genes on the environment, such as an organism's behaviour or life history, or ecosystem.

Keystone species
A species with a disproportionate ecological effect in an ecosystem. Removal of that species would lead to a drastic change in the ecosystem.

applications to a wider community of policymakers, practitioners and conservation programme managers and that the researcher and policymaker communities will find reasons to value partnering together in the co-design of solutions for pressing environmental problems. This Review is divided into two main sections. In the first section, we provide the context for how biodiversity has been conceptualized in terms of its influences on humanity. In the second section, we describe major knowledge gaps with respect to the genetics and genomics of biodiversity and its contributions to people. These gaps provide logical targets for future research.

From genes to phenotypes to people

The benefits of nature (that is, biodiversity) to people are often conceptualized in terms of 'ecosystem services'[17] or 'nature's contributions to people' (NCP)[18] (BOX 1). In 2019, the seventh plenary of the IPBES defined 18 categories of NCP (TABLE 2); these NCP include ecosystem services, and so we will use the more inclusive term 'NCP' throughout this Review.

Genetic diversity influences biodiversity, and thus NCP, in two main ways: (1) through standing genetic variation (that is, the particular combination of genes and alleles present at a given time in a given place); and (2) through contemporary evolution (that is, ongoing evolutionary changes that affect the genetic variation in a given place at a given time). With respect to standing genetic variation, the underlying idea is that a particular mix of genetic variants will influence NCP — through the expressed phenotype — differently from some other mix of genetic variants. With respect to contemporary evolution, the basic idea is that natural selection and other evolutionary processes (such as gene flow, mutation and genetic drift) act on very short time scales to modify the mean and distribution (for example, variance) of genetically based (that is, heritable) traits that influence NCP.

At the outset of this discussion, it is important to note that genes interact with the environment through their influence on phenotypes — hence, phenotypes are the key link between genes and the environment[19]

(FIG. 1). The effect of an organism's phenotype extends to the population level via changes in the relative fitness of a given phenotype in that population. Subsequently, the population's phenotypic distribution influences community-level patterns and processes where those phenotypes interact with the distribution of phenotypes in other species. The effects of genetic variation on population demography are studied in population genetics, whereas the effects of phenotypes expressed from that genetic variation on interacting species within a community are studied in the fields of community genetics and community genomics. The expressed phenotypes at each of these levels can be summarized as population, community and ecosystem phenotypes (also known as 'extended phenotypes' in some phraseologies). For example, genetic changes in keystone species[20] can result in new community and ecosystem phenotypes that affect community structure, biodiversity and fundamental ecosystem processes. However, the genetics and genomics of NCP are not the same as the genetics and genomics of particular traits, because NCP are emergent properties of whole-organismal performance and the effects of many (often unknown) traits working in combination. Hence, this Review of the genetics and genomics of NCP is complementary to existing reviews on the genetics and genomics of specific phenotypic trait[21–23].

To make these points concrete, we start by highlighting five specific exemplars of NCP, describing one to two examples of how standing genetic variation and its contemporary evolution can influence each NCP, with further examples for all 18 NCP provided in TABLE 2. The examples are chosen on the basis of the inherent nature of a given NCP; for example, NCP 11 (energy) is more likely to contain examples from biotechnological applications, whereas NCP 16 (physical and experiential interactions with nature) is more likely to contain examples in which people interact with organisms in nature. We have deliberately chosen, and mixed, examples from a diversity of organism types to highlight how any one NCP can be influenced by many types of organisms and their interactions. Certain types of organisms (for example, abundant, large or migratory species) can have particularly large effects; indeed, such organisms are frequently mentioned. However, we have not attempted to link particular organism types to particular types and strengths of genetic effects on NCP, as it does not seem useful to here focus only on a subset of organism types. Some taxa (for example, migratory salmon) appear as examples in multiple places in this Review, thus making clear that a particular organism can have effects on several NCP. We anticipate that future expansions of our points will emphasize how particular organism types have particularly large effects on NCP and how some NCP are disproportionately influenced by certain types of organisms.

Habitat creation and maintenance (NCP 1)
Plants can possess tannins, which are polyphenolic biomolecules that aid in defence against herbivory and that influence people: for instance, tannins make some freshwater 'tea stained', they add astringency to tea and wine, and they are used in tanning animal hides. The levels of

these tannins can differ dramatically among individual plants within a species, leading to a host of ecological effects. As one example, the differential preference of beavers for certain tannin genotypes in *Populus* trees, a widespread and ecologically important North American tree species, has cascading effects on riparian ecosystems and their associated fauna[24] (FIG. 2). The key to this phenomenon lies in the role of beavers as an 'ecosystem engineer' and 'keystone species' coupled to their adaptive behaviour to forage first on the most easily digestible and nutritious *Populus* genotypes (that is, those with lower tannin levels). Due to the resulting selection against low-tannin *Populus* genotypes, a community of primarily high-tannin *Populus* genotypes can be established, which then has a variety of consequences for biological communities (for example, microorganisms and arthropods) and ecosystem functions (for example, decomposition rates)[25]. These large and diverse influences will surely cascade to affect people living nearby, although this last link has yet to be formally demonstrated.

Energy (NCP 11)

Human-directed evolution in yeast has improved xylose fermentation for biofuel production[26]. Biofuel production is based on the conversion of plant dry matter (lignocellulose) to bioethanol. The biochemical properties of lignocellulose make it difficult for microorganisms to break plant matter down into smaller biopolymers. For this reason, biotechnological efforts are focused on breaking down hemicellulose, which contains large fractions of xylose, a pentose polysaccharide. Lee and colleagues[26] modified a *Saccharomyces cerevisiae* strain to break down xylose via a pathway it does not naturally possess but which they inserted from *Scheffersomyces stipitis*. The result was the highest ethanol yield (45 g ethanol per gram of xylose) to date compared with other methods. Another directed evolution experiment led to the transformation of heterotrophic *Escherichia coli* to autotrophy, which enabled the bacterial strain to capture atmospheric carbon, representing a potential breakthrough for tackling the carbon emissions that contribute to climate change via carbon sequestration[27].

Food and feed (NCP 12)

Low genetic variation in crops can increase their susceptibility to disease. One example of this 'monoculture effect' comes from a field study comparing monocultured with genetically diversified rice crops attacked by a common disease, rice blast, in Yunnan province, China[28]. In that study, genetically heterogeneous plantings were 94% less affected by rice blast and had 89% higher yield[28]. Similar effects of genetic variation have been documented in disease resistance to other microparasites[29–32]. Furthermore, the importance of contemporary evolution for crop yields has been documented many times in relation to the evolution of pests and pathogens[33–35]. In another context, fishery-induced evolution is the impact that commercial fisheries have on the evolution of fish traits, especially age and size at maturity, often as a result of increased adult mortality and, especially, selective harvesting of larger fish[36,37]. Notably, increased adult mortality can also be caused by other factors, such as increased water temperatures, and therefore a similar process can affect species that are not targeted by fisheries[37]. The evolution of these traits then can reduce biomass, abundance and harvest levels, which can contribute to fishery collapses and thus have a major impact on food production, local economies and entire ecosystems[38]. Harvest-induced evolutionary effects on the benefits that people receive from natural resources

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Box 1 | Ecosystem services and NCP

To provide common ground for the discussion of the impact associated with biodiversity loss, the concept of ecosystem services was defined by the Millennium Ecosystem Assessment (MA)[17] (see the figure, left panel). Ecosystem services (ES) are the benefits that natural environments or ecosystems provide to people. More recently, the concept has been updated, refined and renamed — first as 'nature's benefits to people' at the second plenary (2013) (see the figure, middle panel) and then 'nature's contributions to people' (NCP; TABLE 2) at the fifth plenary (2017) (see the figure, right panel) of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)[18].

The emergent property of any ecosystem is the function of the entire system, thus including all interactions among individuals, populations, species and communities. Those properties, as initially considered ES under the MA, include 'supporting services', such as nutrient cycling and primary production; 'regulating services', such as carbon sequestration and climate regulation; 'cultural services', which can be recreational, ethical and spiritual, or educational; and 'provisioning services', such as water or food. In the above-noted process of restructuring, supporting ES were split and incorporated into regulating ES and 'nature' (IPBES 2013)[163]. Finally, in the IPBES 2017 framework, regulating ES were further distinguished as regulating NCP and non-material NCP. Also, cultural ES were first adopted by IPBES in 2013 but were then considered in 2017 to be an inherent property of the relationship between people and NCP and not an NCP themselves. Hence, they are represented as the 'cultural context' (dotted box outline for dropped ES concepts and orange box on the right-hand side for incorporation of cultural context as an inherent feature of all NCP in the IPBES 2017 framework). Green boxes indicate western science categories, and blue boxes indicate wording from other knowledge systems.
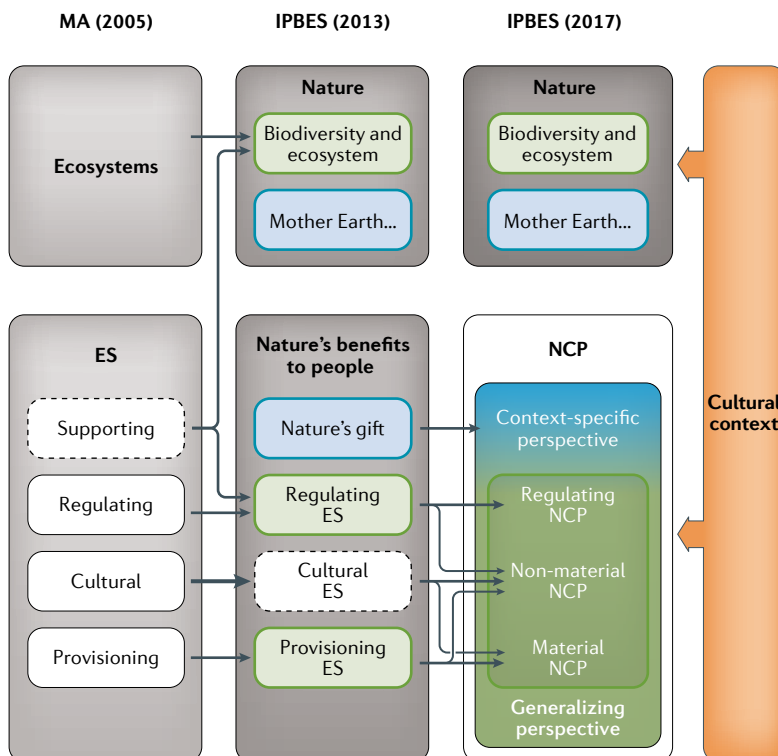

Figure adapted with permission from REF.[163], AAAS.

Table 2 | **Effects of genetic variation and contemporary evolution on NCP**

NCP		Roles of genetic variation and contemporary evolution
1	Habitat creation and maintenance	Genetic variation (and its evolution) in important (that is, keystone or foundation) plant species influences many community and ecosystem properties. For example, different cottonwood (*Populus* spp.) genotypes exhibit different tannin levels and influence the impact of ecosystem engineers, such as beavers, which forage for low-tannin variants[24,61,62]
		Evolution of (or caused by) ecosystem engineers can change how they shape the environment. For example, beavers show differential removal of *Populus* trees with different tannin genotypes, which has many cascading influences on riparian ecosystems[24]
2	Pollination and propagule dispersal	Rapid evolution of plant reproductive systems in response to pollinator decline increases plant fitness, as demonstrated in an experimental study with *Mimulus guttatus*[142]
		Rapid evolution of dispersal traits in response to habitat fragmentation. For example, urbanization leads to the evolution of reduced dispersal in *Crepis sancta*[143]
3	Regulation of air quality	The role of airborne microorganisms, as well as their evolution and genetic diversity, is currently underappreciated and understudied[144]
4	Regulation of climate	Rapid evolution of marine phytoplankton increases carbon uptake[145]
		Plants and soil microorganisms influence rates of weathering, which in turn controls CO_2 sequestration and lifetime of CO_2 fuel[146]
5	Regulation of ocean acidification	Rapid evolution of marine phytoplankton increases carbon uptake[145]
		Rapid evolution of many species facilitates persistence in the face of increasing acidification[147]
6	Regulation of freshwater quantity, location and timing	No known examples
7	Regulation of freshwater and coastal water quality	Rapid evolution of fish influences water clarity. For example, sticklebacks have recently undergone parallel diversification into limnetic and benthic types, ultimately leading to decreased algal biomass through trophic and non-trophic interactions[148]
		Zooplankton evolves increased ability to consume toxic cyanobacteria. For example, *Daphnia* 'resurrected' from sediments in Lake Constance showed increased resistance to ingested cyanobacteria with increasing eutrophication of the lake[149]
8	Formation, protection and decontamination of soils and sediments	Genetic variation in plant species influences decomposition rates and nutrient cycling in soils. For example, different *Populus* genotypes produce different amounts of tannins[61]
		Soil communities 'evolve' to local plant genotypes, which have positive feedback on plant growth[60]
		Metallophyte plants have adapted to highly toxic soils[150]
9	Regulation of the impacts of hazards and extreme events	Genetic variation within species enhances ecosystem recovery after extreme temperatures. For example, genetically diverse seagrass (*Zostera marina*) showed increased biomass production, plant density and faunal abundance during a European heat wave[151]
		Genetic variation within species makes them more resistant to biological invasions. For example, increased genetic variation within *Solidago* leads to increased stem density, which in turn limits invasions by alien species[152]
10	Pest, disease and stress regulation	Rapid evolution of resistance to herbicides, with reductions of productivity[33]
		Rapid evolution of resistance to diseases. For example brown rats (*Rattus norvegicus*) have evolved resistance to warfarin at least partly through pre-existing variants of the *Vkorc1* gene[153]
11	Energy	Rapid (human-directed) evolution can improve biofuel production, for example, xylose fermentation by yeast based on genetic engineering or atmospheric carbon capture by synthetically engineered autotrophic *Escherichia coli*[26,27]
12	Food and feed	Rapid evolution of harvested fish populations influences their productivity, resilience to exploitation and recovery following collapse[36]
		Use of refuge strategies to prevent (or slow) evolution of resistance to pesticides seems to be effective in reducing the evolution of resistance to *Bt* crops[126]
		Genetic variation in crops reduces susceptibility to disease. For example, genetically diversified rice crops attacked by rice blast were less affected by the disease and had higher yield[28]

Table 2 (cont.) | **Effects of genetic variation and contemporary evolution on NCP**

NCP		Roles of genetic variation and contemporary evolution
13	Materials and assistance	Multiple uses of biomaterials in medicine and industry[154]
14	Medicinal, biochemical and genetic resources	Strategies are designed by managers to reduce the evolution of resistance in, for example, bacteria, viruses and cancer and to maintain genetic variation in pest species by retaining drug sanctuaries with sensitive and resistant variants in coexistence; for example, non-*Bt* maize refugia to deter pest resistance evolution[155,156]
15	Learning, artistic, scientific and technological inspiration	Rapid evolution of iconic study systems, for example, the evolution of beak morphology in response to environmental changes[157–159]
		Evolution of site-specific selfish genes inspires gene-editing tools for biological control[112]
		Art inspired by evolution[160]
16	Physical and experiential interactions with nature	Trophy hunting causes evolution of reduced trophy size or frequency, for example, reduced horn size in bighorn sheep due to selective harvest of individuals with the largest horns[42]
		Recreational fishing leads to the evolution of decreased catchability in largemouth bass via angling-driven selection against the most aggressive males[41]
17	Supporting identities: symbolic meaning, involving spiritual, religious and identity connections, social cohesion and cultural continuity	Evolution can influence the multiple organismal traits valued by indigenous communities. For example, evolution of reduced body size in harvested salmon reduces their value to north-temperate indigenous communities[85,161]
18	Maintenance of options	Maintenance of phylogenetic and hence genetic diversity retains and creates opportunities for pharmaceutical and nutritional use. For example, the Natura 2000 network of the European Union retains traditional knowledge of wild edible plants[49]

Bt, *Bacillus thuringiensis*; NCP, nature's contributions to people.

have also been documented for reptiles, mammals, plants and a variety of other organisms[39].

Interactions with nature (NCP 16)

Selective harvest of animals with desirable traits, such as large body size in recreational fisheries and large horns or tusks in trophy hunting, can have an evolutionary impact on those traits and hence the benefits that people seek from those species. For example, evolution towards tameness via angling-driven selection against the most aggressive males ultimately decreases the catchability of largemouth bass[40,41]. Similarly, average horn size in bighorn sheep has decreased because of hunting that targets individuals with larger horns[42]. In the case of bighorn sheep, populations have not regained previous horn sizes years after hunting was banned[42].

Maintenance of options (NCP 18)

NCP 18 represents the future importance to other categories of NCP (1–17) of genetic diversity both within species (phenotypic or genetic) and among species (often measured as phylogenetic diversity)[43]. In some conceptualizations, the importance of NCP 18 is discussed as having two functions: 'insurance' and 'options'. The insurance function of NCP 18 captures the role of evolutionary history and genetic diversity in maintaining NCP under changing future conditions. For instance, the adaptive potential of ecologically important species helps them to maintain their current abundance and ecological role in the face of changing environments[44,45]. Stated another way, genetic variation and its contemporary evolution can enhance the stability, resilience and

evolvability of populations, species and communities[46] and hence maintain current NCP even as environments change. The options function of NCP 18 captures the potential for current genetic variation to provide future benefits to people that are currently unknown, either because these benefits have not yet been discovered, they are not yet needed or they have not yet evolved. The options function of NCP 18 thus includes, as one example, opportunities for new pharmaceutical and nutritional discoveries, such as bioprospecting to identify and characterize new antimicrobial compounds[47,48]. This options function of NCP 18 is formally recognized in some initiatives, such as the EU biodiversity strategy Natura 2000, which established a network of protected areas specifically to facilitate future options for a diversity of edible plants[49].

Classic genetic methods to inform NCP

Genetic diversity can be measured using a number of marker genes or via broader genome-wide approaches[50,51]. Such analyses can yield 'proxies' for species' adaptive potential brought about by the varying phenotypes expressed by that genetic diversity. The vast majority of existing work that investigates genetic diversity and molecular mechanisms that influence biodiversity emphasizes simple summary measures of within-population or among-population single-locus variation (typically averaged across many loci), such as nucleotide diversity, heterozygosity, allelic richness, allele frequency differences and allele frequency variance[52]. Some additional work has focused on quantitative genetic measures of within-population

Evolvability
The ability to evolve (that is, to produce genetic diversity on which selection can act).

Heterozygosity
Proportion of sites on the chromosome at which two randomly chosen copies differ in DNA sequence.
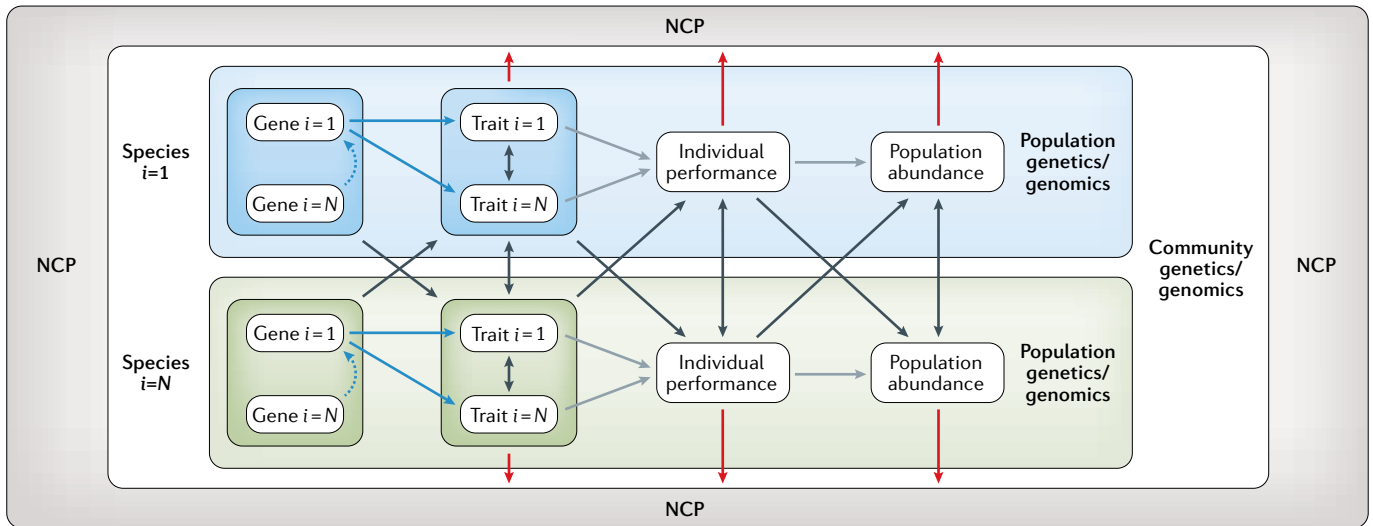
Fig. 1 | **Contributions of genetic and genomic effects to NCP.** Population genetic and genomic contributions are shown in each coloured box representing a given species ($i = 1 – N$ species). A given gene (and its alternative alleles) can influence multiple traits (pleiotropy; solid blue arrows) within an organism and multiple genes can interact (epistasis; dashed blue arrows) to influence a single trait within an organism. Those traits then influence nature's contributions to people (NCP) directly (red arrow) or indirectly (grey arrows) via the performance of individual organisms, which in turn influences NCP either directly (red arrows) or indirectly (grey arrows) by altering the population abundance of that species. Community genetic and genomic contributions are reflected in black arrows between species. That is, genetic variants in one species can — through phenotypic variation — interact with genetic variants in another species to shape trait variation in that species (interspecific epistasis). These effects can then resonate within and between species to individual performance and population abundance, thus shaping NCP through a variety of direct and indirect routes.

variation (for example, additive genetic variance) or among-population variation, such as Wright's F_{ST}. Similarly simple measures are used in analyses conducted at the among-species level, with examples including nucleotide divergence, fixed allele frequency differences and phylogenetic distance[53]. Such quantifications of genetic diversity are important as they can support policymakers and conservation programme managers in their efforts to understand, support and manage NCP. Furthermore, the genetics and genomics of NCP are in many instances the genetics and genomics of 'phenotypes', specifically the association of community and ecosystem genotypes with expressed community and ecosystem phenotypes (FIG. 3A) whenever these phenotypes have emergent effects on the environment. Various manifestations of this idea include extended phenotypes *sensu* Dawkins[20,54], genes to ecosystems[25] and interspecific indirect genetic effects[55]. In each instance the genetic variation at the individual, population or community level is cascading through the levels of biological organization as opposed to affecting 'just' individuals of the same population. Here, we illustrate how some classic genetic and genomic methods translate to NCP.

Heritability

Classic quantitative genetic approaches quantify the proportion of phenotypic variation in a population that is attributable to additive genetic variance, as this quantity indicates the expected relationship between the traits of parents and the average traits of their offspring[56]. At the ecological level, several authors have estimated community heritabilities[55] or ecological heritabilities[19], which are, in essence, the relationships between parents and offspring

of the communities of their associated organisms (for example, arthropods on individual trees)[55]. As such, one could quantify the 'heritability' of any community or ecosystem property emerging from phenotypes.

Line cross analyses

A classic quantitative genetic approach to identify the genetic basis of differences between populations involves generating pure types (non-segregating in the phenotype of interest and thus assumed to be homozygous for the underlying genes), hybrids and backcrosses, with the patterns then informing the extent to which trait differences are additive or subject to non-additive effects (that is, dominance or epistasis). We are not aware of any line cross analyses specifically for NCP. However, some studies have examined traits that could influence NCP; for instance, those involving invasive plants and phytophagous (that is, plant-eating) insects (FIG. 3B) or those that estimate the effect of within-host and between-host genetic variation on arthropod community structure[55].

Genotype comparisons

Classic genetic studies test for phenotypic differences between alternative genotypes at particular loci, an effort recently made much easier through gene editing technologies such as CRISPR–Cas9 (REFS[57,58]). In the context of NCP, such methods could be particularly useful for considering 'ecologically important genes', so-called keystone genes, foundation genes or ecosystem engineering genes (reviewed in REF.[59]). For example, different cottonwood (*Populus* spp.) genotypes exhibit different tannin levels (FIG. 3C), which has ecosystem-level effects by affecting soil microbiota[60], the arthropod community[61],

Additive genetic variance
The independent genetic effect of an allele on the phenotype of an individual organism resulting in deviation from the population mean phenotype. Additive genetic variance contributes to the evolvability of a population.

Dominance
A genetic interaction between the two alleles at a locus, such that the phenotype of heterozygotes deviates from the average of the two homozygotes.

Epistasis
Non-additive gene–gene interaction. A given allele might function well in one genetic background but poorly in another genetic background. We also refer to interspecific epistasis, in which alleles in different species interact (for example, gene–gene interactions between a native host and a parasite perform differently from an invasive host and the parasite genotype).
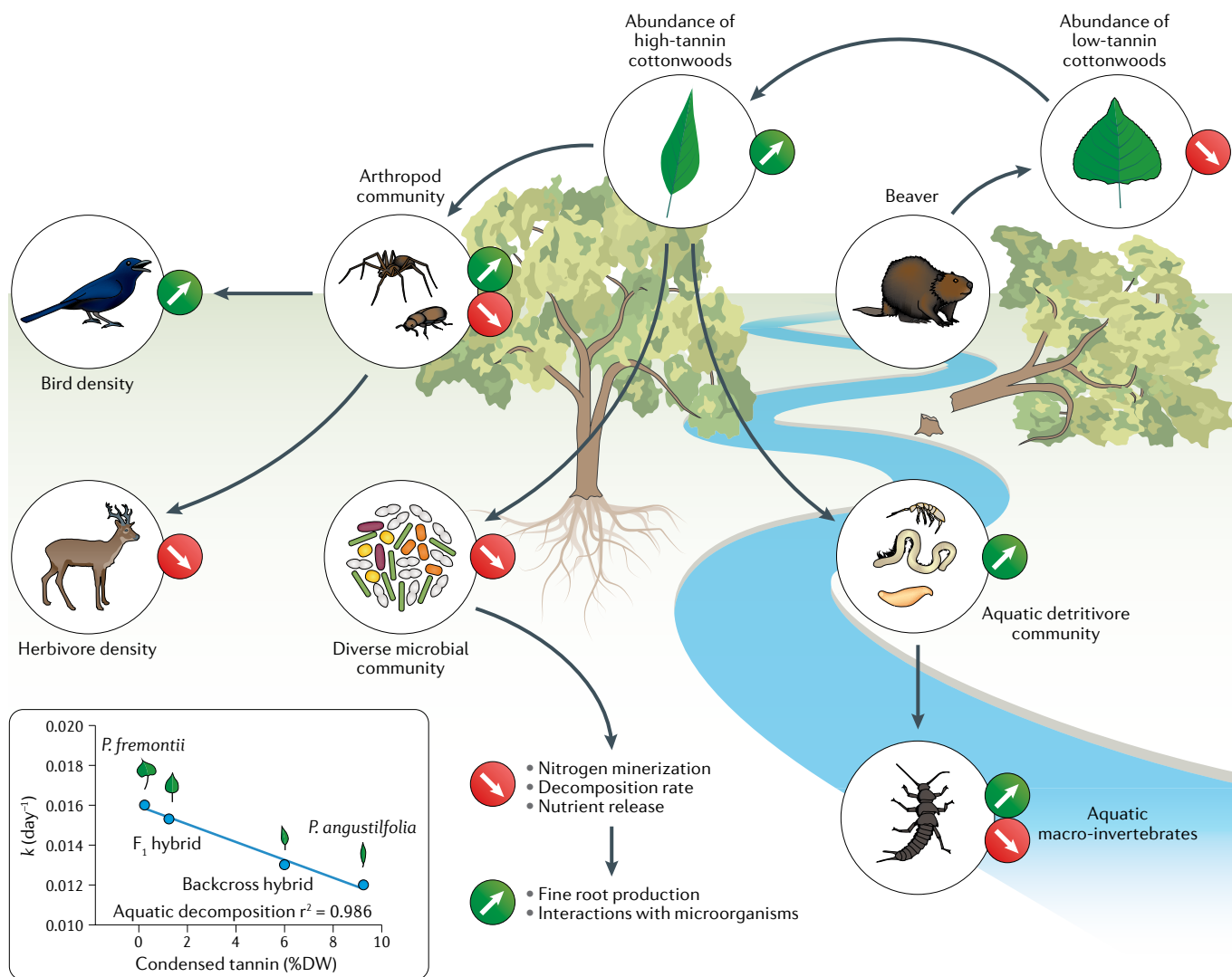
Fig. 2 | **Ecosystem-level effects of genetic variation in individual trees mediated through keystone species.** Beavers, as a keystone species, have disproportionally large effects on the ecosystem. Through their preferential harvesting of *Populus* (cottonwood) trees that produce low amounts of condensed tannins (*Populus fremontii*), enabling larger populations of high-tannin cottonwoods (*Populus angustifolia*), a number of communities are affected in the ecosystem. High-tannin and low-tannin cottonwoods support different arthropod communities. High-tannin cottonwoods have increased densities of aphids, which are predated by birds. High amounts of condensed tannins reduce mineralization and decomposition rates, hindering nutrient release for lower trophic levels and affecting soil microbial communities. DW, dry weight. Graph reprinted from REF.[162], Springer Nature Limited.

plant herbivory[62] and nutrient cycling (NCP 8); they also influence the impact of ecosystem engineers, such as beavers[24] (NCP 1) (FIG. 2). Another example is the evidence that particular genotypes influence the movement of organisms in ways that have cascading effects for ecosystems and people, such as genes influencing migration timing in salmonid fishes[63]. For example, wild chinook salmon from the Rogue River were shown to possess alternative alleles at the *GREB1L* locus that determine whether the individuals enter freshwater streams during the spring or the autumn. The allelic composition within these populations has been affected by anthropogenic disturbances, ultimately resulting in genetically impoverished populations that are less resistant to environmental variability and hence show reduced evolvability[63,64]. The absence of salmon that migrate

in spring most likely affects entire nutrient cycling pathways in freshwater streams[65].

Genome-wide association studies

Genome-wide analyses seek associations between specific alleles at particular loci, or multilocus combinations thereof, and qualitative or quantitative phenotypic differences. These methods could be used to inform NCP if the 'phenotypes' of traditional analyses are replaced with the ecological effects of organisms. As one example, Crutsinger et al.[66] used thousands of SNPs to test for the genetic basis of the ecological effects (for example, nutrient dynamics in aquatic habitats) of individual genotypes of riparian trees (FIG. 3D). They found that variation in riparian black cottonwood (*Populus trichocarpa*) genotypes from phenotypically divergent
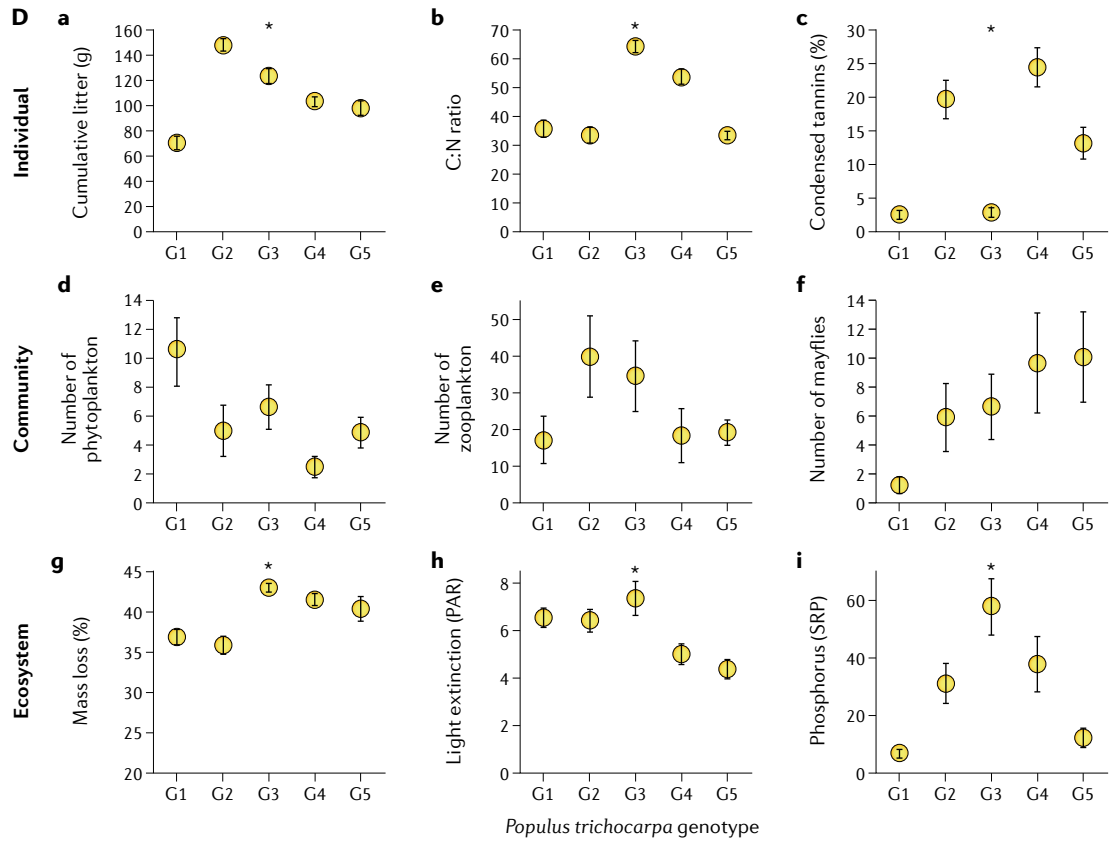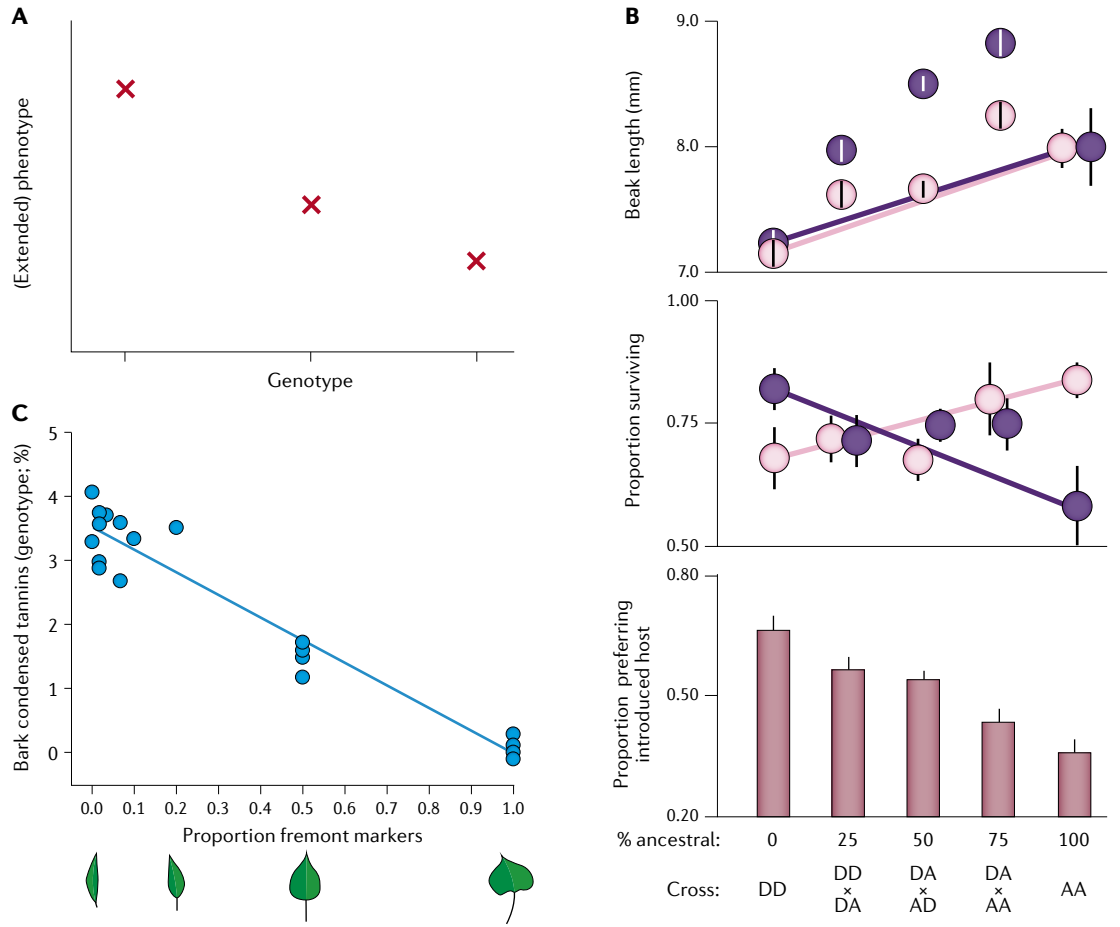
Fig. 3 | **Classic genetic methods can inform NCP. A** | The association between genotype and phenotype (individual phenotype as in classic genotype comparisons or genome-wide association studies, or extended phenotype as in community or ecosystem phenotype). **B** | Line cross analyses were used to show that the length of the beak of native North American soapberry bugs evolving to feed on the non-native golden rain tree occurred mostly through large epistatic effects. Soapberry bug beak length increased when soapberry bugs were reared on the seeds of the introduced host (golden rain tree, dark circles), and derived individuals (genotype DD) had increased survival and preferences for the introduced host, when compared with rearing of soapberry bugs on the native host (light circles) and ancestral individuals (AA). **C** | Different genotypes of cotton-woods exhibit different levels of condensed tannins. *Populus angustifolia* (right) has low amounts of condensed tannins, which makes it a preferred food source of beavers; *Populus fremontii* and hybrids have high amounts of condensed tannins, which creates a feedback loop within the ecosystem. **D** | Individual, community and ecosystem responses to five different genotypes (accessions) of black cottonwood (*Populus trichocarpa*). PAR, photo-synthetically active radiation; SRP soluble reactive phosphorus. Part **B** republished with permission of The Royal Society, from Rapid appearance of epistasis during adaptive divergence following colonization, Carroll, S. P., Dingle, H. & Famula, T. R., **270** (Suppl. 1), 2003, REF.[70]; permission conveyed through Copyright Clearance Center, Inc. Part **C** reprinted with permission from REF.[24], Wiley. Part **D** reprinted with permission from REF.[66], Wiley.

Biocontrol agent
In contrast to chemical control agents, biocontrol agents are natural predators or parasites of a pest.

populations results in variable ecosystem traits such as leaf litter production. This variation in turn affects phytoplankton abundances and nutrient dynamics, which then affects light availability in neighbouring aquatic habitats. Less light in aquatic habitats negatively feeds back on phytoplankton and zooplankton abundance, which has large ecological effects up and down the trophic chain to the predators and prey of the phytoplankton and zooplankton. Other possibilities could be association mapping of the diets of keystone species or the behaviours of ecosystem engineers.

Genomics for biodiversity

In the rest of this Review, we advocate moving beyond the above indices towards the consideration of the genomic context for genetic variation and its influence on NCP. The following sections outline what amounts to genetic and genomic assessment and monitoring, which then could inform any number of manipulations aimed at altering NCP, such as selective breeding or assisted gene flow (FIG. 4).

Population genomics

"Even if it were possible to randomize the alleles at a single locus with respect to the rest of the genome … it would be a useless occupation. Genes in populations do not exist in random combinations with other genes. … context and interaction are not simply second-order effects… [they] are of the essence."[67] In 1974, the evolutionary biologist Richard Lewontin presciently anticipated the importance of genetic and genomic interactions such as dominance, epistasis, linkage, structural genomic variation (for example, inversions) and regulatory variation. That is, for a given level and type of genetic variation at a single locus, interactions among loci (for example, epistasis), patterns of inheritance (for example, physical linkage), epigenetic influences and many other factors will play a critical role in phenotypic effects[68]. The upshot of this genomic complexity is that the phenotypes and adaptive potential of species — and hence their direct and indirect effects on NCP — will require an understanding not just of genetic variation

but also its genomic context. We therefore now highlight how knowledge of these genomic contexts is essential for understanding the adaptive potential of organisms and their likely effects on communities, ecosystems and NCP.

Epistasis. Epistasis can be critically important in the process of adaptation, with particularly clear examples coming from new associations evolving between plants and phytophagous insects[69–71]. For instance, native soapberry bugs in North America evolved a new 'host race' on an introduced non-native plant, the golden rain tree. Many traits of these bugs have shown adaptive contemporary evolution on the new host plant; and one of the most ecologically important traits — the length of the beak through which the bugs feed on the tree's seeds — is strongly affected by epistatic effects, as determined by line cross analysis[70]. This epistasis could play an important role in NCP 10 (pests and diseases) because the evolution of soapberry bugs, and native phytophagous insects in general, has been suggested as a potential biocontrol agent against detrimental invasive plants[71]. In short, interactions between alleles at different loci could be a critical component of the biocontrol of invasive species and hence the costs and benefits that humans incur. However, genetic details of the epistatic interactions that shape the role of phytophagous insects in biocontrol, or other organisms having effects on other categories of NCP, are typically not known and require further research. By contrast, epistasis has been argued not to have played a major role in phenotypic evolution during domestication of many crops[72] (NCP 12). Hence, one cannot simply assume that epistasis is or is not important in some new context; rather it needs to be assessed in that new context.

Structural genomic variation. Structural genomic variation can manifest itself as regions of DNA that show variation in copy number (deletions, insertions and duplications), orientation (inversions) or chromosomal location (translocations and fusions). This variation can play a key role during local adaptation and speciation[73] and hence can alter the contributions of organisms to NCP and biodiversity. For example, desiccation tolerance in the malaria-transmitting mosquito *Anopheles gambiae* is facilitated by an inversion that contains polymorphisms in several genes that encode ion channels and related functions[74]. Mosquitos with this inversion exhibit increased tolerance to desiccation and thus have a fitness advantage in dry regions of the world (NCP 10 — pests and diseases). Another example comes from East African honeybees, in which inversions facilitate local adaptation to high altitudes, potentially through the *foxo* gene (also known as LOC727091)[75]. Honeybees, as an important pollinator, affect several NCP, including NCP 12 (food and feed), NCP 14 (medicinal resources) and NCP 17 (symbolic meaning). Yet another example involves an inversion in Atlantic cod associated with migratory behaviour which causes substantial population structuring[76,77]. Similar to the previous example in chinook salmon where the *GREB1L* gene variant defined whether an individual migrates upstream in spring or autumn[63], genes captured in an inversion in linkage

a Species translocation

Environment gradient

Translocated population

b Assisted gene flow

c Breeding programmes

Breeding pair   A   B   C   D

Generation 1

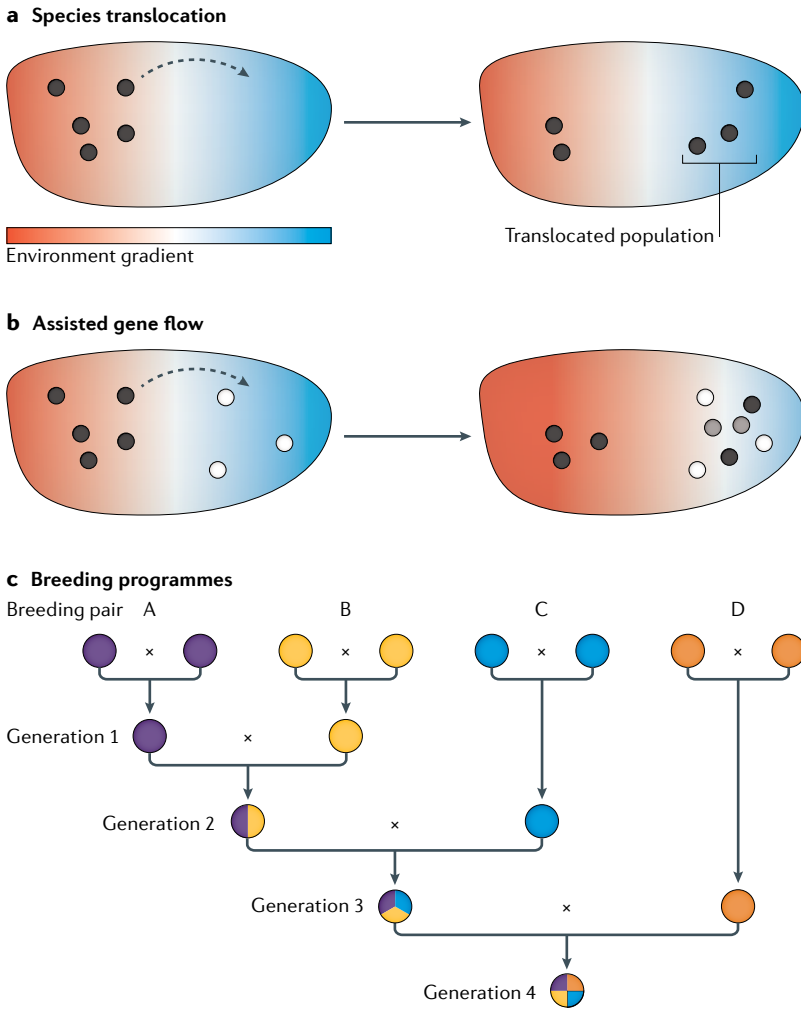Generation 2

Generation 3

Generation 4

Fig. 4 | **Some current approaches to preserve or increase intraspecific genetic variation. a** | Species translocation (or assisted colonization) is the human-mediated intentional movement of individuals or populations to a geographical locality inside or outside its historic species' range. Individuals are translocated to a locality that contains suitable environmental conditions (symbolized in the blue or the right edge of the species range). The source population (left) might undergo decimation or extirpation following environmental change (indicated by red colour), whereas environmental conditions in the target locality match that of the initial conditions (blue) of the source locality. **b** | Assisted gene flow is the human-mediated intentional translocation of individuals or their gametes within a species range to facilitate rapid adaptation in a target population experiencing environmental change. To provide a target population with genetic resources that potentially carry advantageous alleles in the case of environmental change, individuals of the source population (black circles) can be mixed within the target population (white) to form hybrids (grey). **c** | Breeding programmes are applied for endangered species to maintain intraspecific genetic variation, usually in captivity (ex situ). The offspring of breeding pair A is paired with the offspring of breeding pair B to form a hybrid generation (generation 2). This hybrid offspring will be paired with offspring C, to form generation 3, now carrying alleles from three different lines (A, B and C). In this example, the fourth generation contains a genetic mix of four lines (A, B, C and D).

Epialleles
Alternative chromatin states at a given locus, defined with respect to individuals in the population for a given time point and tissue type.

group 1 in Atlantic cod contribute to whether or not an individual migrates. This migration-associated inversion is exclusive to the northern cod population found around Canada and acts as a 'supergene'. The number of individuals homozygous for the inversion has been declining since the onset of industrial fishing. As a result, overharvesting of the northern cod population led to its collapse, which resulted in reduced genetic variability

and population structure in Atlantic cod as a whole and had many consequences for ecosystems and people such as the reorganization of coastal shelf ecosystems[78]. Thus, the spatial distribution of a species important for NCP 12 (food and feed) and NCP 16 (physical and experiential interactions with nature) is shaped not just by particular alleles and their frequencies but also by their presence in genomic regions of reduced recombination. As a final example, gene copy number variation has been shown to affect phenological and ecophysiological traits in *Populus* trees via selection for resistance to disease in the south versus abiotic stress in the north[79], which has implications for forestry (NCP 1 — habitat creation and maintenance).

Epigenetics. Epigenetic changes, defined as mitotically and/or meiotically heritable changes in gene function that cannot be explained by changes in gene sequence[80], likely influence many NCP. Some of these contributions are established for NCP 12 (food and feed) via effects on growth, viability and reproduction of animal and plant agricultural species. For instance, naturally occurring epialleles of *Oryza sativa SPL14* (also known as LOC4345998), a gene that regulates rice plant architecture, increase yield[81]. In the oil palm, the *Bad Karma* epiallele in *Elaeis guineensis DEFICIENS*, a gene that regulates floral architecture, produces an unwanted phenotype with lower yield, which has enabled screening for suitable clones as *Bad Karma* exhibits hypomethylation at the *Karma* splice site[82]. In coho salmon, reduced fitness of hatchery-origin fish following their release into the wild for the purpose of enhancing salmon abundance is influenced by epigenetic variation that is caused by rearing environment (that is, in captivity as opposed to in the wild)[83]. Panmictic wild and captive-bred individuals showed distinct DNA methylation patterns, despite having no significant genetic differentiation. Reduced fitness in the hatchery-origin salmon is related to deficient ion homeostasis and hence reduced saltwater acclimation, which is important for the anadromous life cycle of salmon, as well as altered neuromuscular communication possibly causing reduced swimming performance[84]. Given the importance of salmon for ecosystems and people[85], such epigenetic variation could have influences that span many different NCP (NCP 1 — habitat creation and maintenance; NCP 12 — food and feed; NCP 16 — physical and experiential interactions with nature; NCP 17 — symbolic meaning).

Community genomics

The population dynamics of species, and their effects on NCP, depend not only on their own genomes (as above) but also on interactions with the genomes of other species. The frequency, nature and magnitude of these interactions will depend on the frequencies of the various alleles in each species combined with the spatial and temporal patterns of co-occurrence of alleles across the different species. Thus, a robust understanding of the effects of genetic variation on NCP will require spatio-temporally explicit multispecies genomics.

Existing studies that consider the effects of genetic or genomic variation on NCP typically emphasize

the effects of specific focal species, as evinced by the preceding examples. That is, relevant studies focus on how the genetic variation found in a particular ecologically important (for example, 'keystone' or 'foundation') species can influence communities, ecosystems, and NCP[6]. Such studies are typical in cases where individual species provide important NCP by themselves, such as a tree species harvested for wood products, a fish species harvested for consumption or a key nitrogen-fixing plant used for restoration. However, many NCP ultimately are the shared product of multiple species in a community, such as effects on water clarity in lakes, carbon sequestration in the ocean or decomposition in the soil. Such community-level NCP cannot be extrapolated from an additive summation of the individual contributions of each species to that NCP. That is, NCP provided by a community of species will inevitably involve non-additive interactions among multiple species that will generate and reflect various synergistic, compensatory or redundant effects.

One established multispecies genetic approach to NCP asks how phylogenetic diversity among the species in a community influences community and ecosystem properties[86,87]. For example, productivity in experimental plant mixtures is often better predicted by phylogenetic diversity than by species diversity[88], and the effectiveness of 'green roofs' can depend on the phylogenetic diversity of the plants used[89]. Importantly, these associations between diversity and NCP are highly non-linear[90], reinforcing the point made earlier that the effects of all species in a community are not simply the additive sum of their individual effects. These non-additive interactions among species presumably depend on genetic variation within those species, as has been shown in goldenrod (*Solidago altissima*), and they also depend on interspecific interactions between genes and alleles[91]. For example, grassland plant species, consisting of grasses, small and tall herbs and legumes grown together, were shown to evolve trait complementarity through increased niche differentiation via character displacement, such that the combination of genotypes evolving together generated higher productivity than those evolving separately[92,93].

In short, the ecological effect of a particular genetic variant within one species (and its genomic context, as discussed above) will reflect an interaction with the genetic variants (and their genomic context) in other species in the community. We highlight here these effects in three contexts: (1) interactions between alleles in different species (interspecific epistasis), (2) spatio-temporal patterns of co-occurrence among species, and (3) interspecific epigenetic interactions.

Interspecific epistasis. Interspecific epistasis occurs when alleles at loci in different species interact to shape the phenotypes, fitness or ecological effects of those species[94]. Such interactions have been revealed through studies of 'community genetics'[66,91,95,96] and they seem likely to have strong influences on several NCP. For example, garlic mustard (*Alliaria petiolata*) is an invasive species that now occupies forest understories in many areas of North America and — through the production of an allelopathic compound — has negative effects on

mycorrhizal fungal communities and native plant communities by reducing phylogenetic and species diversity in arbuscular mycorrhizal fungus–plant interactions (that is, the number of species that are interaction partners)[97]. Populations at the expanding margins (that is, the invasion front) of this species have high investment in these compounds to decrease competition from native plants, such as clearweed (*Pilea pumila*), sedges (*Carex*) and violets (*Viola*), and therefore these invasion front genotypes have the greatest negative effect on native arbuscular mycorrhizal fungus–plant communities[98]. When native communities of fungi and plants decline as a result, reduced allelopathy evolves in garlic mustard behind the invasion front as a function of evolutionary changes in both the invader and the native fungi and plants[99]. This co-evolution then alters mycorrhizal fungal communities[100]. This case study provides an example that merits further genomic study to identify the particular allelic combinations of invaders (invasion front individuals expressing allelopathic compound producing genes versus trailing individuals expressing alleles causing reduced allelopathy) and natives (evolving to new mycorrhizal fungus diversity and interaction partners) that jointly and non-additively determine soil properties and plant communities. These community changes likely affect a number of NCP, such as NCP 1 (habitat creation and maintenance), NCP 8 (formation of soils) and NCP 12 (food and feed), although NCP-focused research has yet to be conducted in this system.

Spatio-temporal co-occurrence. The spatio-temporal co-occurrence of interacting alleles in different species will dictate their joint effects on NCP. In other words, alleles in different species that come into contact more frequently are likely to be more important in shaping their joint dynamics and contributions to NCP. Thus, in addition to understanding how alleles in different species could interact when brought together, it is essential to determine how often and where they are brought together, which can be done by documenting the times and places and frequencies with which various alleles come into contact. These patterns of co-occurrence will be dictated by the properties of organisms (life histories, abundances, migration patterns and habitat preferences) and environments (habitat patches, connectivity and disturbances). A clear example of the highly non-random spatio-temporal co-occurrence of different species comes from microbiomes within hosts, where genetic interactions will be much more common within hosts than between them[101]. Another example comes from alleles that influence the migratory patterns of keystone organisms. For instance, in steelhead and rainbow trout (both are *Oncorhynchus mykiss*), different alleles in a single genomic region, chromosome 5, strongly influence whether individuals migrate (steelhead) to the ocean or do not migrate (rainbow trout)[102]. Moreover, it was shown in a congener that the presence or absence of migratory individuals, in this case chinook salmon (*Oncorhynchus tshawytscha*) has cascading effects on ecosystems[85]. The presence of salmon in an ecosystem, which depends on the season, increases fungal biomass and macroinvertebrate structure through nutrient

influx (that is, carcasses), which in turn increases leaf litter decomposition rates and contributes to accelerated decomposition of tannins and lignin[65], contributing to habitat creation and maintenance (NCP 1). Similarly, different alleles of the gene *GREB1L* in chinook salmon and steelhead determine whether individuals migrate in the spring or in the autumn[63,64,103,104]. Given that the prevalence of predators and parasites in and around aquatic ecosystems varies across time, allelic variation in such species that determines the place and time of their presence could interact with genomic variation in other species to shape freshwater ecosystems and the benefits that salmon provide to people in the form of food (NCP 12) and cultural values (NCP 17).

Interspecific epigenetic interactions. Given that epigenetic effects at the intraspecific level have been well characterized only in the past decade[105], interspecific epigenetic interactions have not yet received much study. Yet, rapid, environmentally responsive epigenetic changes that permit beneficial changes to the phenotype in multi-species communities could be advantageous in highly variable environments[106] or in species that cannot avoid biotic and abiotic disturbances by temporal or geographical avoidance strategies. For instance, research on plant–herbivore interactions indicates that browsed plants modulate antiherbivory strategies via DNA methylation[107]. Currently, however, research that addresses the epigenetic variation of interacting species, such as herbivores, is lacking. It seems plausible that such interactions could potentially result in Red Queen dynamics, that is, the evolution in one species necessitating co-evolution in interacting species (competitors or predators). Therefore, we speculate that interspecific epigenetic interactions must also be important for NCP — at least when they involve species that have large effects on NCP. Much more should soon be known about this topic given that several large projects are currently exploring various aspects of community-level epigenetics, such as in the EpiDiverse European Training Network, which is investigating epigenetic variation in natural plant communities.

Genetic engineering for biodiversity

Increasingly, direct manipulations that involve genetic engineering are being contemplated to preserve and perhaps even 'improve' biodiversity, ecosystems and outcomes for people. In the ~50 years since publication of the recombinant DNA technique[108] that laid the foundation for genetic engineering, different methods have been developed that can generate DNA insertions or deletions, and mediate gene silencing or repression. For instance, zinc-finger nucleases[109,110] and transcription activator-like effector nucleases[111] have been successfully applied in model organisms. The development of CRISPR–Cas systems greatly increased the simplicity and ease of targeted gene editing[57]. This technology, which is under constant development to increase specificity, renders genetic manipulations feasible in many non-model systems, including wild populations[57,112].

Genetic engineering — increasingly CRISPR–Cas — is being applied to numerous issues related to NCP.

Examples from controlled settings include new biotechnological tools for energy generation[26,27] (NCP 11), new and more resistant or resilient crops and breeds[113] (NCP 12), new biomaterials (NCP 13) such as modified silk with specific features[114], and improved decontamination of polluted soils and water via engineered microorganisms and plants[115] (NCP 7 and 8). Examples from more natural settings include the application of CRISPR–Cas to gene drives, for example, so-called rescue drives[116,117], which introduce beneficial mutations into threatened populations to alter resistance genes in populations susceptible to particular stressors, or that remove deleterious alleles from the population that might cause diseases. Potential applications have been discussed for species conservation[117] but are currently not used due to safety (introgression into non-target species) and ethical concerns[118]. CRISPR–Cas can also facilitate eradication or suppression drives, which introduce deleterious alleles in the hope of eradicating vector-borne diseases and invasive species[117]. For instance, an eradication drive is currently being used in a commercial genetic engineering project that targets disease vectors, specifically by releasing genetically engineered *Aedes aegypti* mosquitoes, which can transmit infectious diseases such as malaria, into wild populations[119]; plans are under way for their release in the USA (Pesticide Experimental Use Permit 93167-EUP-E). The eradication option of CRISPR–Cas gene drives is also being considered for use on invasive rodents (*Rattus rattus*, *Rattus norvegicus*, *Rattus exulans* and *Mus musculus*) that threaten the native fauna on islands (for example, the Galápagos Islands) by the Genetic Biocontrol of Invasive Rodents (GBIRd) programme[120]. The gene drive option could replace the application of rodenticides, avoiding their impact on non-target species.

The use of genetic engineering to aid de-extinction efforts, which aim to revive previously extinct species, has been contemplated since 2013 (REFS[14,121]). This is possible in cases where genetic material of the extinct species is available and closely related species are still extant, as, for example, in the North American passenger pigeon (*Ectopistes migratorius*), a species that went extinct in 1914 and that had large effects on ecosystems as an ecosystem engineer[14]. In many of these 'revive and restore' projects, such as for woolly mammoths and heath hens, de-extinction efforts for ecosystem-relevant species attempt to restore ecosystem functions of now disturbed ecosystems and NCP.

Genetic engineering to enhance NCP typically focuses on understanding how a particular genetic perturbation, such as the insertion of a gene or the alteration of an allele, influences phenotypic traits on a specific genomic background in a particular species. However, the success of this genetic engineering can benefit from, and perhaps often requires, a consideration of variation within a population genomic context as outlined earlier. The reason is that the effect of a genetic manipulation will depend on allele frequencies at the focal gene but also on alleles present at other genes in the genome. For example, studies are increasingly demonstrating that multiple CRISPR–Cas manipulations of a single genome are characterized
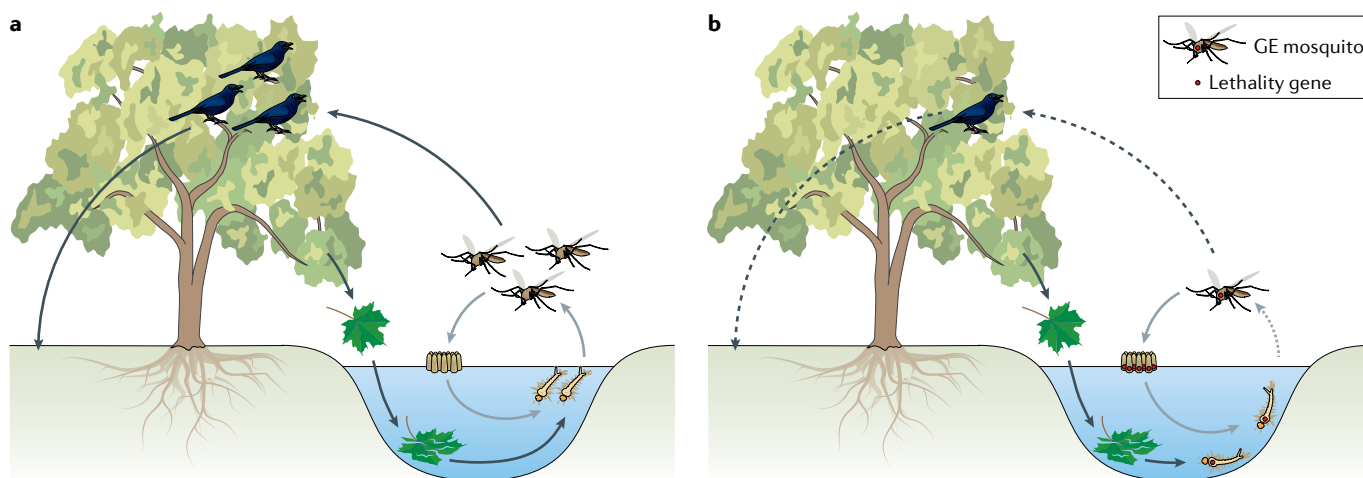
Fig. 5 | **Potential impact of genomic engineering on biodiversity and ecosystems. a** | Mosquitos are important distributors of aquatic and terrestrially derived carbon. As aquatic larval insects, they start their life cycle as eggs in pools of water, and as larvae they feed on detritus, such as microorganisms on decaying leaves. When they emerge as adults and are preyed on by terrestrial animals such as birds, spiders and bats, they distribute energy that was derived from aquatic and terrestrial carbon sources. **b** | Genetically engineered (GE) mosquitoes have been modified using the *tTAV* (tetracycline-repressible transcriptional activator) method, in which *tTAV* acts as a lethality gene. Without tetracycline all offspring overexpress tTAV protein, causing a positive feedback loop in which the transcription machinery becomes saturated and blocked by tTAV protein, ultimately causing death. This has two potential consequences: the eradication of the disease vector and the impairment of the carbon flux from the aquatic habitat to the terrestrial habitat, potentially reducing the abundance of species that prey on mosquitoes.

by strong epistasis (that is, one manipulation might increase fitness on its own but decrease fitness in combination with other manipulations)[122]. Beyond consideration of variation in genomic background, genetic engineering can also directly modify aspects of that background. For instance, structural genomic variation has been generated in vivo with the use of CRISPR–Cas in model organisms such as mice[123], although it has not yet been applied in natural populations. Moreover, epigenome editing tools that alter DNA methylation or chromatin states can be used to generate opportunities for novel epiallelic variants[124]. For example, alteration of methylation in *Arabidopsis thaliana* has been used to generate individuals with mosaic methylomes that in some cases led to novel (not derived from parental methylomes) methylation polymorphisms, revealing untapped sources of epigenetic variation present in the genome[125].

Yet, the situation is even more complicated because the effect of genetic engineering in one species depends not only on the population genomic context of that species but also on the community genomic context of other species in the community. A classic example comes from *Bt* crops, where the efficacy of pest control depends on the particular spatial distribution of *Bt* crops versus non-*Bt* refuges, as well as the specific resistance alleles present in the pests and their pattern of allelic dominance[126]. Additional effects will accompany the cascading consequences of how a genetic manipulation influences the spatio-temporal co-occurrence of species, such as when eradication or suppression drives reduce the abundance of the engineered species. In genetically engineered mosquitoes, for example, interspecific epistatic effects owing to altered abundance can

be expected across many levels of the ecosystem. That is, reductions in mosquito abundance owing to genetic engineering will influence genotype frequencies of detritus-associated microorganisms with which mosquito larvae compete for food[127]. Mosquito reductions will also influence the transport of recycled terrestrial carbon to predators such as birds, therefore acting as an important distributer of energy fluxes[128] (FIG. 5).

In short, the efficacy of genetic engineering for NCP is certain to be highly contingent on a clear understanding of the population genomic and community genomic context. That is, it is not sufficient to examine the effect of a single allele change at a single locus on a single genomic background in the laboratory. Rather, the effects of a given allele change need to be assessed on multiple genomic backgrounds and in the presence of realistic genomic variation in species with which the focal organism is likely to interact. Such an undertaking is obviously a tall order — but it will be necessary if we are to achieve desired outcomes without unforeseen negative consequences (TABLE 1).

Moving forward

The major goal of this Review has been to demonstrate and exemplify how genetic and genomic research on ecosystem-relevant species (for example, beavers, phytophagous insects, *Populus* trees and salmon) can be important to biodiversity, ecosystems and people, and especially how such research can be expanded to a community context (FIG. 6 sketches one route to such expansion). Our hope is to motivate geneticists to turn their expertise and tools to the study of NCP, and to convince stakeholders (for example, decision-makers, programme managers, NGOs and conservation practitioners) of the
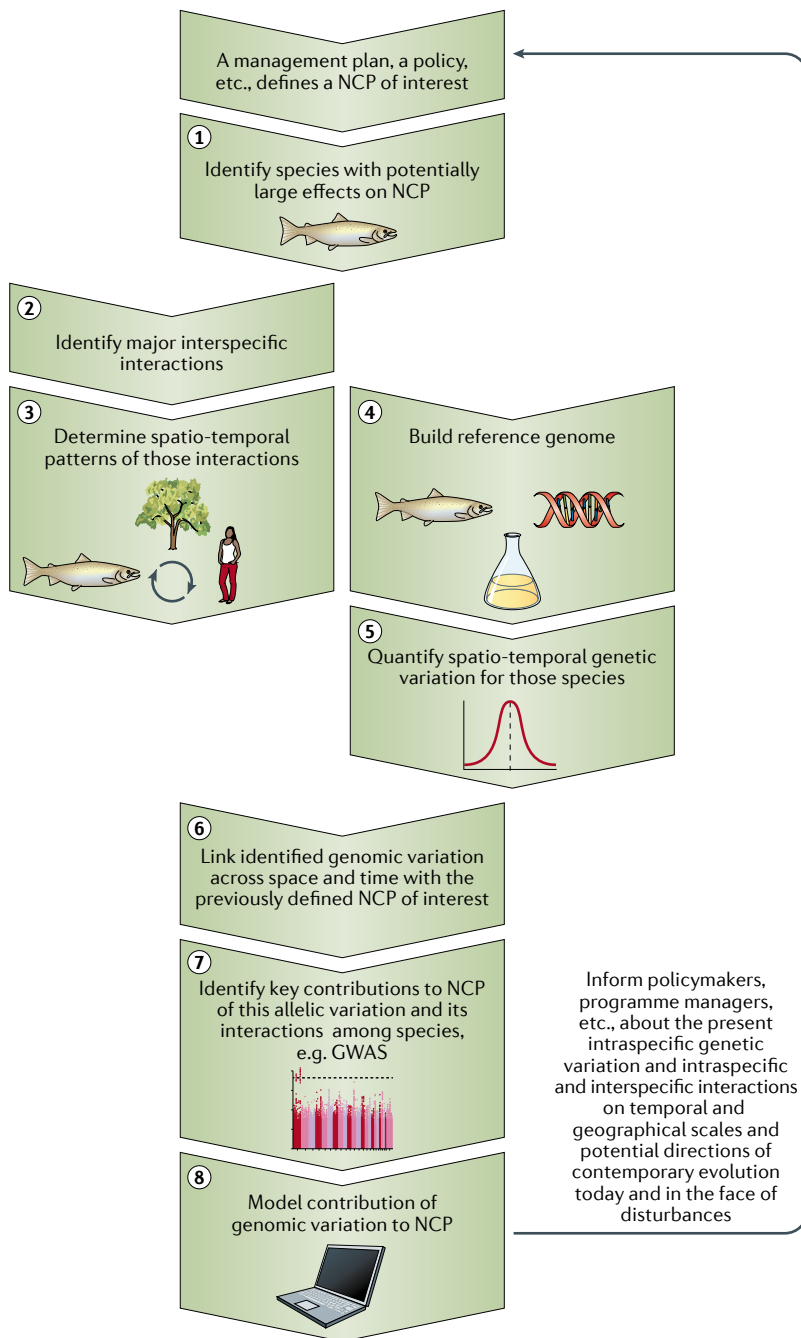
Fig. 6 | **Incorporating population and community genomics into NCP studies.** A hypothetical set of steps by which research could take us towards a strong understanding of the population and community genomics underlying nature's contributions to people (NCP). We emphasize that this sequence is an idealized scenario that will be hard to achieve in its full form — at least at present. Importantly, however, the steps outlined are each useful by themselves, and the full outline shows how they fit together in a larger aspirational framework. For a given geographical location of interest, such as that defined by a particular management plan, researchers could first identify a set of species important for the NCP of interest, with likely examples being keystone species, foundation species, ecosystem engineers, commercially or recreationally important species and critical pathogens (step 1). Identify the major interactions that occur among those species (host–parasite, predator–prey, competitor) (step 2). Determine the spatio-temporal patterns of co-occurrences of these species with each other and with people (step 3). Build a reference genome for each of these species (step 4). Quantify the corresponding spatio-temporal genetic variation for those species, including allele frequencies, genomic structure and epigenetic variation (step 5). Link the identified genomic variation across space and time with the previously defined NCP of interest. For instance, what is the allelic variation present in salmon and its key interacting species (parasites, bears, beavers and sea lions) leading up to its harvest by local people at a location of interest? Or, what is the allelic variation among *Anopheles* mosquitoes, the malaria-causing *Plasmodium* spp. and humans? (step 6). Identify key contributions to NCP of this allelic variation and its interactions among species, such as through genome-wide association studies (GWAS) of the ecological effects (standing in for phenotypes in the classical approach) of individuals or through manipulative experiments in controlled settings (step 7). Model the contribution of genetic and genomic variation, and its contemporary evolution, to NCP across time and space, including in the face of environmental change (step 8).

limiting step has perhaps now shifted to computational challenges; yet, these challenges will also lessen with advances in machine learning, computing power and algorithm speeds. We especially point out the likely importance of machine learning, which is being applied in population genomics to calculate population genetic parameters (selection and demography) from genomic data (first application in REF.[129] and reviewed in REF.[130]). Machine learning, especially deep learning, similarly has great potential in computational ecology (reviewed in REF.[131]), where it has recently been applied to predict species interactions[132] and community assemblies[133].

It has not escaped our notice — nor the attention of referees of this Review — that past calls for monitoring and incorporating genetic variation have, in a number of cases, met with only tepid responses from funding bodies, management agencies, governments and the general public[134,135]. Yet, we note that the situation has come far in the past few decades: many new and continuing monitoring programmes and decision frameworks now explicitly call for, and fund, the monitoring of genetic variation and its injection into the decision-making process (for example, IPBES and Group on Earth

importance of such approaches for understanding the outcomes of biodiversity-relevant decisions.

We recognize the ambitious — perhaps currently unrealistic — nature of our most expansive suggestions, in particular fully formed community genomics (FIG. 6). For instance, predicting the effects on NCP of genetic and genomic variation in natural populations and engineered organisms, as well as the epistatic interactions within and between individuals, populations and communities, will require the extensive production of whole-genome data. Fortunately, continual reductions in cost and time requirements have enabled, and will continue to accelerate, relevant genomic initiatives, such as the Earth BioGenome Project, the Vertebrate Genomes Project and the Genome 10K Project. Indeed, the major

Deep learning
A subdiscipline of machine learning, with the difference that no training data set is needed. The artificial neural network recognizes patterns from coarse to fine scale in multiple steps, so-called hidden layers, which compute increasingly more complex features by taking the results of preceding operations as input.

Observations Biodiversity Observation Networks). An excellent example is the work of the National Oceanic and Atmospheric Administration in the USA on the monitoring and management of salmon populations[64]. We are optimistic that such efforts will spread to additional systems and agencies, and also expand to include genomic, rather than just genetic, information and analysis. In short, historical calls for considering genetic variation[134] were not necessarily ignored or forgotten; they were simply slow to be implemented, making future expansion to more universal and sophisticated monitoring hopefully a quicker and simpler process — or at least an ever-improving process. These efforts take time, and our hope is to provide some motivation, encouragement and guidelines at this early stage.

Humanity faces many challenges — now and in the years to come — and our personal and societal responses to those challenges will be a primary determinant of the futures of biodiversity, ecosystems and people. One set of responses is sure to revolve around the assessment, monitoring and manipulation of genetic variation, for two major reasons. First, genetic variation, and the resultant phenotypic variation, shapes the interactions between organisms and their environments, hence being a primary determinant of organismal responses to future conditions and the role they will play in shaping future ecological dynamics and NCP. Second, science has reached a watershed moment where the ability to quantify genomic variation will soon become nearly unlimited. We now need to merge these realizations and abilities with a more holistic view of how nature interacts with people. The definition of NCP by the IPBES has provided us with unified and well-defined targets, and a common vocabulary for decision-makers and researchers to identify research targets. To synergize these efforts to maintain biodiversity, we call for creative collaboration among geneticists, ecologists, evolutionary biologists, social scientists and bioinformaticians. The future is not set.

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