

## OPINION

# The potential of genomics for restoring ecosystems and biodiversity

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**Abstract** | Billions of hectares of natural ecosystems have been degraded through human actions. The global community has agreed on targets to halt and reverse these declines, and the restoration sector faces the important but arduous task of implementing programmes to meet these objectives. Existing and emerging genomics tools offer the potential to improve the odds of achieving these targets. These tools include population genomics that can improve seed sourcing, meta-omics that can improve assessment and monitoring of restoration outcomes, and genome editing that can generate novel genotypes for restoring challenging environments. We identify barriers to adopting these tools in a restoration context and emphasize that regulatory and ethical frameworks are required to guide their use.

Destruction and degradation of landscapes and substantial losses of biodiversity are major global challenges. The current rate of species extinction is comparable with past mass-extinction events<sup>1</sup> and approximately one-third of the world's arable land is degraded<sup>2</sup>. The disciplines of conservation biology and restoration ecology are tasked with addressing these environmental challenges. The science and practice of restoration aim to reset the ecological trajectory of a degraded site towards a reference, functional or future-adapted state. Restoration requires that ecological stressors (such as deforestation and overgrazing) are identified and halted and that ecosystem components (such as native species) and processes are reinstated.

The restoration sector hopes to achieve ambitious targets in the coming decades. For example, more than 300 million hectares of degraded land are targeted for restoration by 2030 under *The Bonn Challenge* (BOX 1). Restoration activities offer the potential to return not only lost native biodiversity but also ecosystem services (such as pollination of crops, disease regulation, climate regulation and maintenance of fresh water)<sup>3</sup>, which, if done well, provide

a valuable service to society<sup>4</sup>. However, success in restoration practice is elusive<sup>5,6</sup> and restoration practitioners are struggling to keep pace with increased demand for their services<sup>7</sup>. Several unresolved factors are impeding the success of restoration at the scale required to meet its global targets, such as sourcing adequate and appropriate plants<sup>7,8</sup> and assessing and monitoring the success of restoration interventions<sup>6,9</sup>.

The field of restoration, like its sister discipline of conservation, has the opportunity to leverage new techniques and approaches, such as genomics, to achieve its targets<sup>10,11</sup>. Genomic technologies are becoming ever cheaper<sup>12</sup>, which has resulted in their increased application. Indeed, a host of conservation challenges have been met through the application of genomics<sup>13</sup>. Among the early applications, population genomics<sup>14</sup> offers conservation practitioners a detailed molecular picture of species lineages, even for non-model organisms<sup>15</sup>. This knowledge is central to precisely delineating conservation units and key to ex situ conservation management<sup>14,16</sup>. Genomic approaches have also been applied to detecting and monitoring species that are priorities for conservation<sup>17,18</sup>, and recent

work has investigated ways in which genome editing might help to manage invasive species<sup>19–21</sup>. Despite facing barriers<sup>13</sup> — as any innovation does — genomic tools provide many opportunities to complement existing conservation practices.

Restoration science has utilized genetics, for example, to inform seed sourcing<sup>22,23</sup>, however, the use of genomic tools in the practice of restoration ecology is nascent. In this Review, we evaluate the potential and importance of genomics to restoration and suggest areas in which it could greatly advance the science and practice of restoration. We draw on examples from conservation genomics to show that population genomics can provide high-resolution data to better plan for resilient restoration plantings in the face of a rapidly changing environment. We emphasize that meta-omics can aid the assessment and monitoring of restoration of biodiversity and biotic interactions. Further, we explore how genome-editing approaches could, in the future, help fast-track the generation of genotypes for restoring challenging environments (FIG. 1; TABLE 1). However, ecological restoration success relies on much more than just genomics, and for each of the genomic applications we discuss we also identify associated challenges and limitations. Nevertheless, we believe genomics can help the field of restoration to achieve its ambitious promise to return biodiversity and ecosystem services to unprecedentedly vast areas.

## Genomics for seed sourcing

A long-standing principle in ecological restoration is to use plants that are indigenous to the location being restored — that is, to use plants with a local provenance. However, where native plant populations are fragmented, they are likely to suffer from a decline in seed quality through erosion of genetic diversity<sup>24</sup> and increased inbreeding<sup>25</sup>. Furthermore, land use and climate change may have altered local environmental conditions such that local provenances that evolved in situ over hundreds of generations are no longer well adapted to local conditions. Consequently, many ecosystems are being pushed past their historic physiological thresholds, leading to shifts in entire biomes<sup>26</sup>. As a result,

**Box 1 | A new age dawns for restoration**

In 1996, when the field of restoration ecology was in its infancy, Richard Hobbs and David Norton — two doyens of today's discipline — presented a restoration roadmap<sup>146</sup>. The authors suggested that “to become a useful tool for combatting the continuous decline in production and conservation values across the globe, restoration ecology must also become a landscape-scale endeavour”<sup>146</sup>. Despite this call 22 years ago, approximately one-third of Earth's arable land surface is degraded, requiring a new era of landscape-scale ecological restoration.

Ambitious global ecological restoration targets have been established to combat this degradation and to restore ecosystems and biodiversity. [The Bonn Challenge](#) aspires to restore 350 million hectares by 2030, a goal set at the September 2014 United Nations Climate Summit in New York. The new restoration projects that contribute to [The Bonn Challenge](#) span geopolitical boundaries and biomes on a scale with no historical precedent. For example, the African Forest Landscape Restoration Initiative, [AFR100](#), aims to restore 100 million hectares across central Africa by 2030, and [Initiative 20×20](#) has pledged to restore 20 million hectares in Latin America and the Caribbean by 2020. Additional programmes with substantial ecological restoration targets include reducing deforestation and forest degradation and the sustainable management of forests and enhancement of forest carbon stocks in developing countries ([REDD+](#)) and the 2015 [UNFCCC Paris Agreement](#).

Despite their importance, restoration efforts may not achieve success, due in part to the complex biotic and abiotic interactions that occur in both natural and degraded ecosystems<sup>147</sup>. In addition, fundamental knowledge gaps in best-practice restoration remain and recently have been robustly debated in the literature<sup>10,148,149</sup>. However, to achieve future targets, restoration practices desperately need not only to be effective but also to be scaled-up. These challenges can be addressed in part by innovative solutions<sup>150</sup>, including the use of the genomics tools presented in this Review.

mixing provenances from within the native distribution of a species is increasingly considered an effective means of helping to conserve species gene pools and to increase resilience to current and future environments<sup>27,28</sup>. Restoration practitioners are beginning to adopt these interventions into plantings; however, many challenges remain in their uptake<sup>29</sup>, such as the need

to better understand the geographical extent of local provenances, the spatial patterns of adaptive variation among provenances and how far provenances can be transferred to minimize maladaptation.

Mixing provenances to facilitate adaptation to future environments is conceptually straightforward and much of our understanding of the relevant

evolutionary processes comes from long-term experimental field trials<sup>30</sup>. For example, experimental plantings can be used to develop species transfer functions by demonstrating how far provenances can be transferred over environmental gradients before maladaptation occurs<sup>31,32</sup>. However, it is rare for the required array of experimental plantings to be in place, especially for restoration species, and for longitudinal data sets to be available to accurately model these transfer functions. Indeed, there is often a time lag between establishing experimental plantings and the selection events that shape the transfer functions. Therefore, setting up new experimental plantings to inform seed sourcing may not be a time-effective way to inform the choice of well-adapted provenances. Time is especially important in considering the long-lived nature of many restoration species and the current velocity of climate change.

Population genomics can generate data that complement experimental plantings and help provide timely evidence-based recommendations for provenance transfer decisions to increase the resilience of restoration plantings. Population genomic methods that sequence a reduced representation of target genomes (for example, through digestion with restriction enzymes, target capture enrichment or transcriptome

**Glossary****Adaptive variation**

Genetic variation that increases the fitness of an organism.

**Alpha diversity**

The species diversity within a given sample or site.

**Beta diversity**

The turnover of species diversity across a landscape.

**CRISPR–Cas9 system**

A targeted genome-editing tool comprising two components: the programmable Cas9 endonuclease, which introduces double-strand breaks into the DNA; and a guide RNA, which targets the Cas9 nuclease to a specific DNA sequence.

**Effective population sizes**

The size of ideal breeding populations, which meet Hardy–Weinberg equilibrium assumptions, that would maintain the same allele frequencies as a census population.

**Environmental DNA or RNA**

DNA or RNA present in an environmental sample, such as water, soil and air.

**Gene flow**

The exchange of genetic material within or between populations as a result of the movement of gametes or individuals.

**Genetic drift**

The change in allele frequencies through generations of a population due to random sampling.

**Genotype-by-environment**

Differential trait responses (such as growth or survival) of genotypes grown in contrasting environments, resulting in a statistical genotype and environment interaction for traits.

**Guide RNA**

(gRNA). A small sequence of synthetic RNA (about 20 bases long) located within a longer RNA scaffold, which binds to DNA and directs the Cas9 endonuclease to the targeted genomic location.

**Metabarcoding**

A meta-omics approach that combines DNA identification and DNA sequencing, in which universal primers are used to amplify DNA barcodes from bulk samples, such as soil environmental DNA.

**Metabolomic turnover**

The change in metabolic molecules within cells, biofluids, tissues or organisms.

**Metagenomics**

A meta-omics approach similar to metabarcoding, but instead of using DNA barcodes it involves random sequencing of DNA from bulk samples.

**Metatranscriptomic**

Pertaining to a meta-omics approach similar to metagenomics, but instead of randomly sequencing DNA it randomly sequences transcriptomes or expressed genes.

**Meta-omics**

A collection of methods (including metabarcoding, metagenomics and metatranscriptomics) that use next-generation sequencing to characterize whole communities of organisms.

**Neutral variation**

Genetic variation that is not shaped by natural selection and does not directly impact the fitness of an organism.

**Population genetics**

The application of high-density, genome-wide molecular markers to the study of neutral and adaptive evolutionary processes occurring within species.

**Provenance**

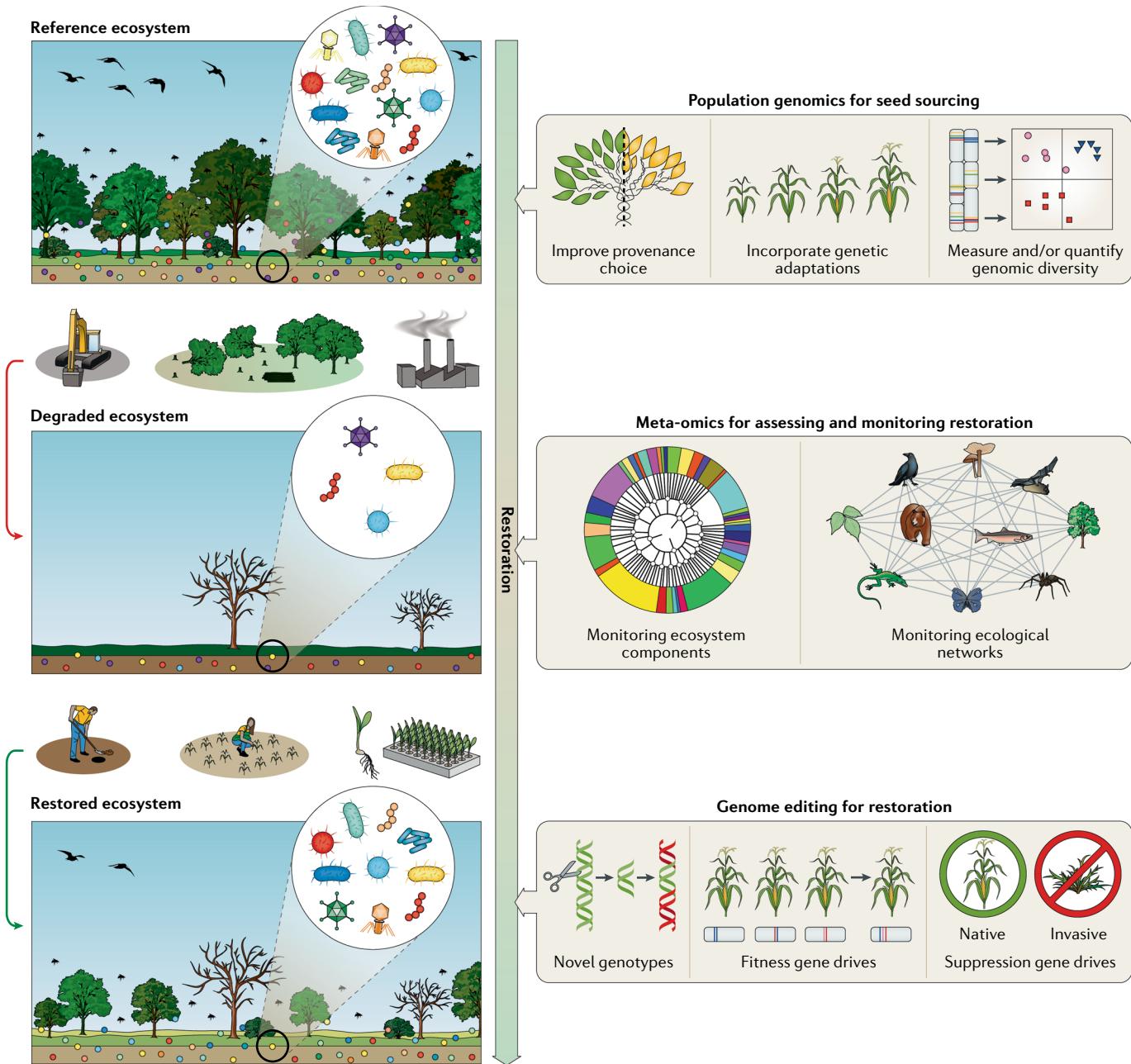
The geographical location of a plant population or seed source.

**Seed transfer zones**

The geographical regions over which seeds can be transferred with minimal maladaptive responses.

**Transfer functions**

The relationships between the performance of multiple plant populations within a test site and the environmental dissimilarity between the populations' home site and test site.



**Fig. 1 | Potential applications of genomics in restoration.** The ecosystems relevant to a restoration ecologist are shown in the left panels—reference, degraded and restored; each indicates the processes leading to these different states and some common and important taxonomic targets of restoration (such as birds, plants, insects and microorganisms (represented as coloured circles)). How and where genomics can be applied to restoration is shown on the right. Population genomics can be used to improve restoration inputs, such as enhancing plant provenance delineation and assessing how well restoration plantings capture genomic diversity (further detailed

in FIG. 2). Meta-omics can be used in numerous ways to improve restoration assessment and monitoring, including functional and often cryptic ecosystem components such as bacteria and insects and their interactions (further detailed in FIG. 4). CRISPR–Cas9-based genome-editing technologies may become useful in the future for recovery of severely degraded landscapes with appropriate attention to safety and risks, such as to develop novel genotypes to thrive under challenging conditions and gene drives to help control pest species (further detailed in FIG. 5); see also TABLE 1 for further information about each application.

sequencing<sup>33–35</sup>) can be used on non-model species as these methods can be applied without a reference genome. However, when genomic comparisons with model organisms are possible<sup>15</sup>, a reference genome can provide insights into the potential underlying mechanisms of adaptation.

For example, non-synonymous mutations in gene sequences can be linked to phenotypes through genome-wide association studies<sup>36</sup>. The following sections detail how population genomics can be applied in a restoration context by assessing neutral variation and adaptive variation to inform provenance

decisions and by evaluating the genomic diversity captured in restoration plantings.

**Improved resolution and accuracy of provenance collections.** Delineating provenances is the first step in constructing seed transfer zones that can be used to

Table 1 | Potential applications of genomics to restoration

Genomics tool and role	Specific purposes	Requirements for greater application
<b>Currently available for restoration purposes</b>		
Population genetics for seed sourcing	Improving resolution and accuracy to delineate provenances by describing fine-scale historical demographic information between and within provenances (such as associating population structure with landscape features) that is not attainable using traditional population genetic methods <sup>37,47,151</sup>	<ul style="list-style-type: none"> <li>Building on the existing applications of restoration genetics</li> <li>Better integration of geographical data into bioinformatics pipelines</li> <li>Improved understanding of associations between neutral genomic variation and functional and fitness traits</li> </ul>
	Making predictive provenance decisions by identifying genetic adaptations that have the potential to increase resilience to future environmental change <sup>42,43,48</sup>	<ul style="list-style-type: none"> <li>Unified bioinformatics pipelines to confidently detect true genomic adaptations</li> <li>Greater validation of genomic adaptations via long-term field trials</li> </ul>
	Quantifying how well restoration plantings capture neutral and adaptive genomic diversity <sup>55</sup>	No impediments to wider use
Meta-omics for monitoring and assessment	Tracking the restoration of important functional, but often cryptic, ecological communities, including bacteria, archaea, fungi and insects <sup>56,66,67</sup>	<ul style="list-style-type: none"> <li>Greater understanding of functionally relevant approaches (such as metagenomics)</li> <li>Development of better methods to accurately describe or account for biological abundance</li> </ul>
	Monitoring and assessing interactions between organisms in restored ecological networks, such as mapping metabolic networks or plant–pollinator networks <sup>70</sup>	Development of more streamlined bioinformatic and analysis pipelines
<b>Potential for future application to restoration</b>		
Genome editing for restoration	Using CRISPR–Cas9 to develop novel genotypes suited to challenging new conditions, while retaining existing desirable traits and a local genetic background	<ul style="list-style-type: none"> <li>Development of technical, ethical and legislative framework</li> <li>Requires detailed information on species genetic architecture to understand the polygenic nature of traits of interest</li> </ul>
	Developing gene drives to target essential fitness genes of foundation or keystone restoration species	<ul style="list-style-type: none"> <li>Investment</li> <li>Development of technical, ethical and legislative framework</li> </ul>
	Developing suppression gene drives to target essential survival or reproduction genes of unwanted pest species (such as exotic weeds and herbivores)	<ul style="list-style-type: none"> <li>Investment</li> <li>Development of technical, ethical and legislative framework</li> </ul>

guide provenance mixing. However, a lack of understanding of how to incorporate the evolutionary processes of adaptation, gene flow and genetic drift is a hurdle to delineating provenances. A detailed understanding of these processes, which shape the genetic and functional diversity of wild populations, could improve provenance choices for restoration plantings by identifying genotypes that are already adapted to likely future environmental conditions — a key factor in the resilience of restoration plantings.

Population genetics typically samples thousands of molecular markers distributed across the genome of a species, providing increased resolution of genetic and functional diversity when compared with traditional population genetic approaches<sup>13,15</sup> [FIG. 2]. Indeed, putatively neutral genome-wide markers often outperform traditional microsatellite markers to map breaks in gene flow and migration routes, and to estimate effective population sizes<sup>13,15</sup>. Although caution must be applied when interpreting the ecological meaning of genomic variation associated with geographical distance,

an operational definition of a provenance can be derived from the autocorrelation of allele frequencies among individuals. For example, genome-wide single-nucleotide polymorphism variation was used in a generalized dissimilarity modelling framework to show that populations of *Eucalyptus melliodora* within 500 km of each other shared more genomic similarity than expected through chance alone, regardless of the proximity of the single-nucleotide polymorphism to functional genes<sup>37</sup>. Beyond 500 km there was no significant genetic similarity, likely reflecting the maintenance of large, continuous populations via gene flow. Thus, in this case, seeds could be collected within 500 km to represent the ‘local’ provenance of a restoration site. Although this broad delineation of a ‘local’ provenance is perhaps an extreme case (plant spatial genetic structure generally declines over a few to tens of kilometres, rather than hundreds of kilometres<sup>38,39</sup>), it nonetheless provides provenance delineation in a restoration context that accounts for genomic variation associated with geographical distance that can be used to guide seed sourcing.

**Predictive plant provenances based on genetic adaptations.** Typically, provenances are based on geographical distance<sup>29,40</sup>, as described above, but geographical distance can be a poor predictor of historical demography and fitness, particularly in complex landscapes<sup>41</sup>. A key advance enabled by population genetics is the ability to distinguish adaptive variation — that is, genomic regions that have fitness effects — from neutral variation. The interplay between natural selection, recombination, mutation and gene flow can result in the development of genetic adaptations to local environments. Adaptation is complex and involves shifts in frequencies of favourable alleles of genes, or combinations of genes, that contribute to adaptive phenotypes. Genomic indicators of adaptation can be derived from population genetics by associating variation in population-level allele frequencies with site-specific biotic (such as disease resistance) and abiotic (such as climate and soil chemistry) factors<sup>42,43</sup>, rather than using a candidate gene approach to identify adaptations. Detecting genomic signatures

of adaptation using these approaches can help identify the spatial arrangement of the main environmental drivers of adaptation in target restoration species (FIG. 2).

Linking adaptive genomic data to current and predicted future environments can improve provenance decisions for restoration plantings under climate change<sup>44</sup>. By modelling the associations between adaptive genomic data and predicted future environments, it is possible to spatially visualize and predict genome–environment associations<sup>45,46</sup>. These predictive models can be used to identify and delineate provenances best suited for future climates<sup>47</sup>. Such an approach holds promise for guiding provenance decisions in response to global change<sup>48</sup>. For example, an ‘Aridity Index’ was derived that predicted the degree of genomic adaptation to aridity of populations of *Eucalyptus tricarpa*, a widespread and commonly-used non-model restoration species<sup>48</sup> (FIG. 3; Supplementary Methods). Modelling the Aridity Index shows that large components of the current species distribution are adapted to mesic climates (blue to yellow colours in FIG. 3a) and arid climates (yellow to red colours in FIG. 3a). Incorporating predicted future climatic variables into the spatial projection of the Aridity Index (FIG. 3b) reveals a clear shift across the species distribution towards the arid end of the adaptive genotypes. A large proportion of the predicted distribution is outside the current Aridity Index range (FIG. 3b) and, therefore, possibly outside the current adaptive capacity of the species. Because arid-adapted provenances grown in experimental plantings tend to outperform mesic provenances at an arid site<sup>48</sup>, these results suggest that restoration plantings with this species would benefit from the inclusion of arid-adapted seed from populations within the current north-western, arid-adapted gene pool. Examples such as this can help forecast the likely impacts of climate change on a species and can be incorporated into provenance decision tools that match standing genotypes to predicted future environments of a restoration site.

Additional complexity and limitations must be considered when applying population genomic approaches to provenance decision-making. For example, many adaptive phenotypes are likely to be polygenic, that is, they are affected by many genes potentially of small effect, and population genomic methods are generally not well suited to detecting the allelic variation involved<sup>49</sup>. Although inferring the genetic basis of

polygenic traits is difficult, an overall signal of genomic adaptation can be used to improve provenance decisions (FIG. 3), which accounts for the polygenic nature of phenotypes. By contrast, convergent adaptive phenotypes can derive from very different genomic backgrounds<sup>42</sup>, and these different evolutionary histories can increase uncertainty for provenance decisions based on these adaptive phenotypes. Furthermore, additional work is needed to better understand how variation in provenance performance translates to transfers across environmental gradients. In addition to the reciprocal field trials required to assess genotype-by-environment interactions, more research is needed on linking putatively adaptive loci with quantitative trait variation. Indeed, emerging evidence directly links the identification of adaptive loci via population genomics with quantitative trait loci and adaptive differences among populations<sup>50</sup>.

**Quantifying genomic diversity in restoration plantings.** It is important to verify whether restoration plantings capture the genomic variation of their native source populations because this provides insight into their future resilience and evolutionary potential. The processes of collecting and storing seeds, rearing seedlings and natural selection post-planting all have the potential to reduce the genetic diversity of these newly established plant populations. If seed collection greatly under-represents the standing genetic diversity of native populations, then the planted populations are likely to undergo genetic bottlenecks<sup>51</sup>. Bottlenecks can expose the plantings to the deleterious effects of reduced genetic diversity, including reduced evolutionary potential and increased inbreeding<sup>52</sup>. Compared with population genetic studies based on markers such as microsatellites, population genomics offers a much more detailed picture of the distribution of genome-wide variation within and between provenances<sup>53,54</sup>, as well as insight into how well neutral and adaptive genomic variation are represented in restoration plantings<sup>55</sup> (FIG. 2). Although implementation has been limited, its value has been demonstrated in experiments that compared genome-wide patterns of diversity in *Eucalyptus microcarpa* restoration plantings and their source provenances<sup>55</sup>. Overall, these restoration plantings reflected the genome-wide patterns of standing diversity of wild *E. microcarpa* populations. However, the levels and patterns of diversity across individual

chromosomes differed substantially and were associated with the degree of habitat fragmentation of the sampled populations. The long-term ecological and evolutionary implications of such chromosomal variation are unknown; however, it is possible that the variation may relate to adaptive differences, with corresponding effects on restoration plantings.

## Meta-omics for monitoring

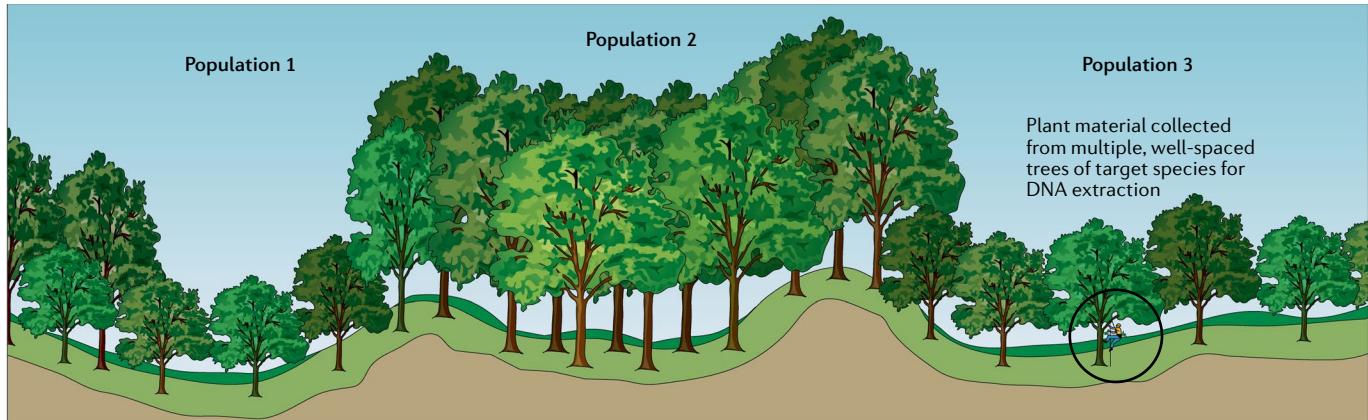
**Assessing and monitoring functional and cryptic ecosystem components.** Ecological restoration projects are justified because they return not only native biodiversity but also ecosystem functions (such as plant–microorganism and plant–insect symbioses, nitrogen or carbon nutrient cycling and soil and substrate formation). In turn, the restored biodiversity and ecosystem functions have the potential to provide ecosystem services, such as crop pollination, nutrient availability, soil stabilization, water purification and disease regulation<sup>3</sup>. As such, the biological components of ecosystems that provide these services should be the targets of restoration monitoring and assessment to ensure the ongoing success of restoration efforts<sup>9</sup>.

Many biotic components of ecosystems (such as bacterial, fungal and insect communities) are either difficult or impossible to survey using field-based restoration monitoring and assessment approaches. Field-based methods, such as sweep netting and/or blue-vane traps for flying insects, require taxonomic expertise and can be strongly biased in terms of which species are detected. By contrast, genomic and, in particular, meta-omic approaches enable these functional and diverse taxonomic groups to be accurately and rapidly characterized and quantified by sequencing bulk environmental DNA or RNA (FIG. 4). Meta-omic methods can be used to monitor eukaryotes<sup>56,57</sup>, but they are particularly useful when applied to prokaryotes. It was believed that the culture-dependent methods used to characterize prokaryotes could be applied to approximately 5% of taxa. Meta-omic applications have subsequently demonstrated that Earth is vastly richer in microbiota than previously thought and that only ~1% of it is culturable<sup>58,59</sup>.

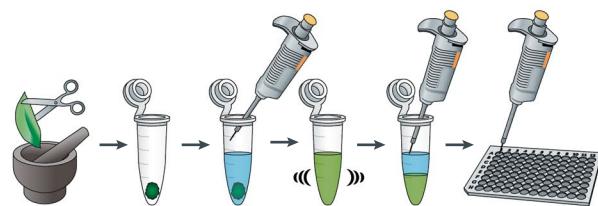
Environmental microbiota (that is, the community of microorganisms in a defined environment) are important for successful restoration of healthy ecosystems; they mediate many ecosystem functions and services that are important targets of restoration activities, including

# PERSPECTIVES

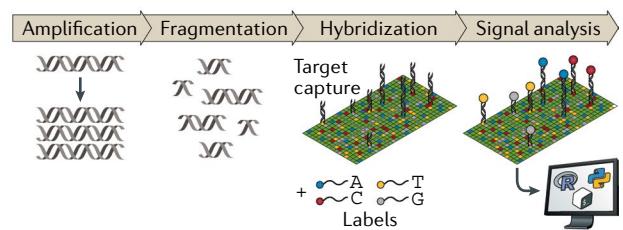
## a Population sampling



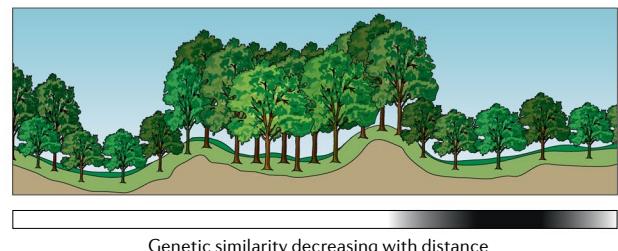
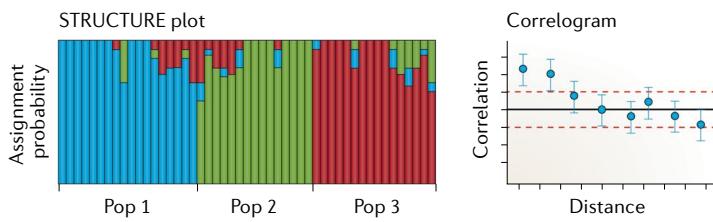
## b Genomic DNA preparation



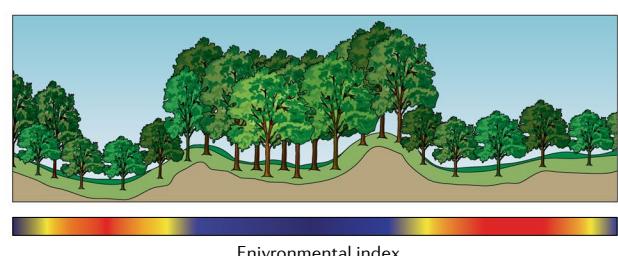
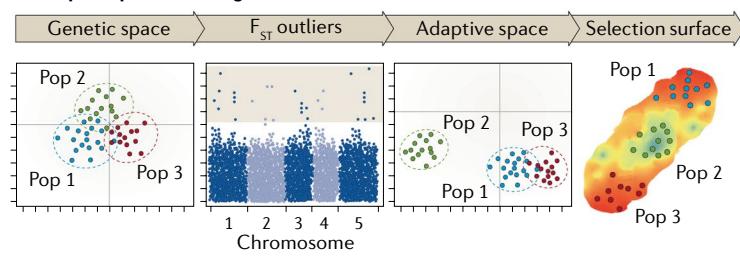
## c Identifying polymorphisms and bioinformatics



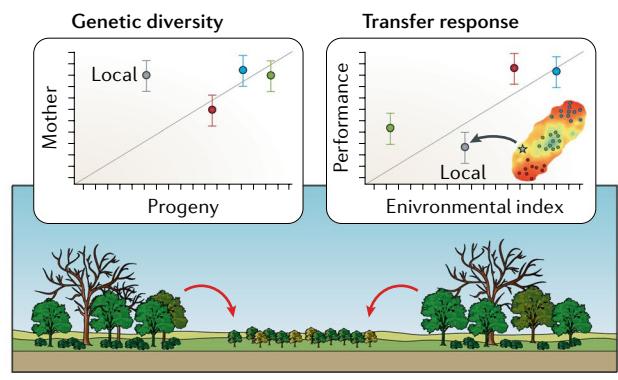
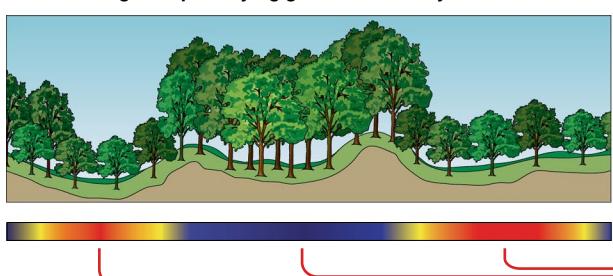
## d Provenance delineation



## e Adaptive provenancing



## f Monitoring and quantifying genomic diversity



◀ Fig. 2 | Potential applications of population genomics to ecological restoration. **a** | To demonstrate the procedure from DNA to ecological restoration application, we use a hypothetical species consisting of three sampled populations distributed across a frost-prone and drought-prone site (Population (Pop) 1), a mesic site (Pop 2) and an arid site (Pop 3). **b** | High-quality DNA or RNA is extracted from leaf material collected from each sampled population. **c** | DNA polymorphisms are identified by sequencing a reduced representation of individual genomes (methods include restriction enzyme digests, target capture enrichment and transcriptome sequencing). **d** | Genotyping is achieved with bioinformatics. Genotypic data inform provenance delineation through Bayesian approaches such as STRUCTURE or by modelling the decline in genetic similarity with geographical distance (for example, using correlograms). In our example, the grey colour bar shows the decline in genetic similarity (black to white) between Pop 3 and all others. **e** | Genomic diversity measures can be incorporated into restoration management through, for example, genomics-informed climate-adjusted provenancing. Here, both neutral and adaptive genetic variation is used to define seed transfer zones. Putatively adaptive markers are identified (for example, by genome-environment associations or genetic differentiation ( $F_{ST}$ ) outlier analyses) to derive an adaptively enriched genetic space, where provenances are aligned along the environmental axes that best describe the adaptive differences among them. The model describing the adaptive genome–environment association is interpolated spatially to produce a ‘selection surface’ that encompasses the geographical range of the species, including proposed restoration sites. In our hypothetical species, Pop 1 and Pop 3 have similar adaptive genomic profiles that differ from that of Pop 2, reflecting a putatively adaptive genomic response to aridity. **f** | Population genomics can also assess in detail the genomic diversity captured in restoration plantings by comparing the diversity of ‘donor’ provenances and restoration plantings.

nutrient cycling<sup>60</sup>, obligate and facultative symbioses<sup>61</sup>, carbon sequestration<sup>62</sup> and human health<sup>63–66</sup>. As such, quantification and characterization of these microbiota using meta-omics tools can be used to assess and monitor the success of ecological restoration. For example, recovery of soil fungi and bacteria following a restoration intervention in a post-agricultural context can be assessed using metabarcoding, which measures alpha diversity and beta diversity<sup>56,67</sup> and derives restoration indicator taxa<sup>66</sup> from DNA sequence abundances of marker genes. Metagenomics can be used to characterize functional gene abundances of soil microbiota along a nitrogen gradient to assess whether soil fertilization shifts the structure of the microbial communities to one dominated by microbiota that thrive in soils high in organic matter<sup>68</sup>. This approach to monitoring could be particularly useful in situations that demand a detailed understanding of nutrient changes with restoration, such as in post-agricultural settings where restoration activities often aim to reduce the soil fertility legacy of agricultural fertilizer use. Metatranscriptomic analysis of environmental RNA has been used to reveal the activity of functional genes and the role of rare microorganisms in nitrogen fixation and sulfur oxidation in acid mine drainage<sup>69</sup>. This approach holds promise for evaluating the recovery of such microbiota in the restoration of contaminated land, such as post-mining sites, and in turn the recovery potential of entire ecosystems.

Other than these examples, scalable and high-resolution meta-omic approaches to microbial monitoring and assessment

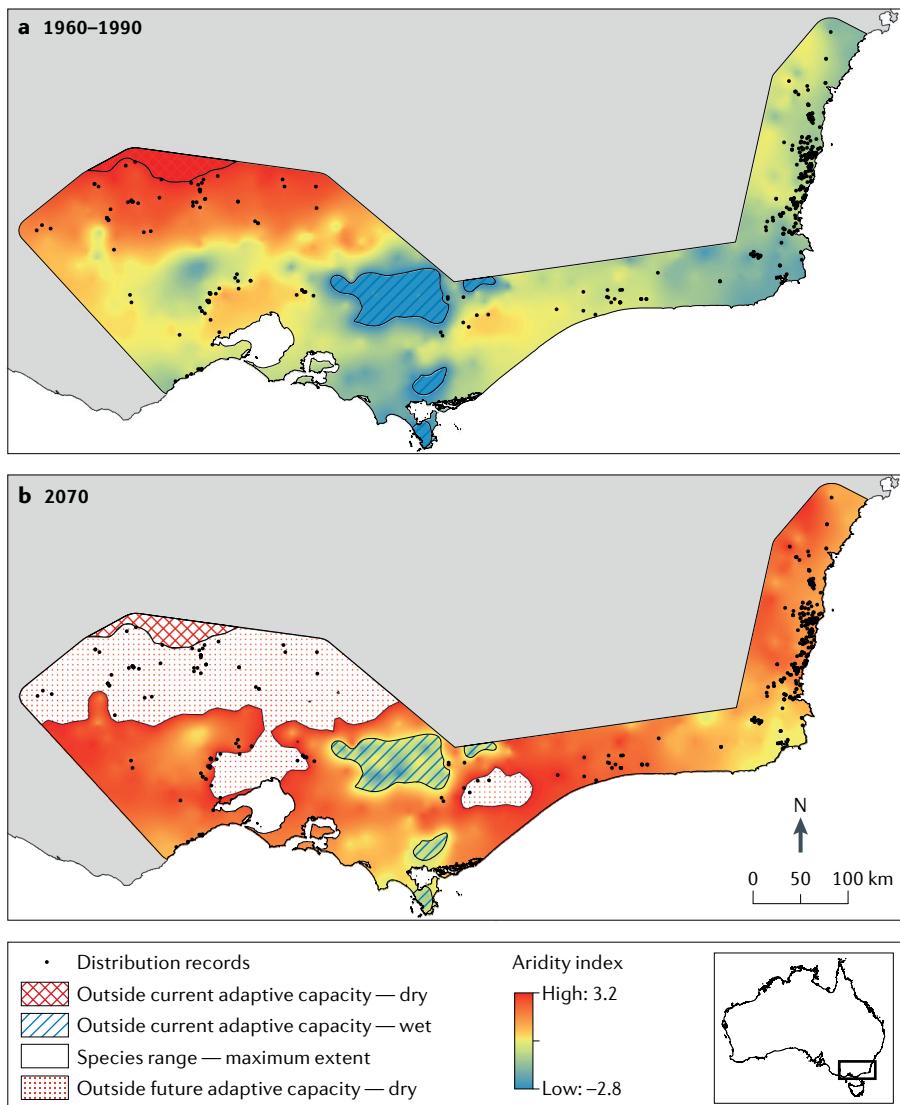
are largely absent in a restoration context. Although research into environmental microbiota is increasing, this field is still in its infancy — particularly in restoration ecology — with most studies being observational. Many knowledge gaps still need to be filled, such as defining the functional and ecological roles that microbiota have in reference, degraded and restored ecosystems. One of the most comprehensive environmental microbiota initiatives is the [Earth Microbiome Project](#), which aims to establish a global taxonomic and functional understanding of environmental microbiota. If taxon-specific functional activities are identified during such research efforts, the monitoring and assessment of microbial communities during restoration could be greatly improved.

**Assessing and monitoring interactions in restored ecological networks.** The interactions between organisms, rather than simply species diversity, are central to the successful restoration of functional ecosystems. Accurately reconstructing these interactions allows quantification of network properties and the establishment of clear restoration targets. For example, food webs are controlled by fluxes of organic and inorganic nutrients (such as the nitrogen cycle), which are vital for many types of organisms used in restoration, including plants<sup>70</sup>. Nutrient and energy fluxes reflect ecosystem inputs of the metabolic activity of microbiota. By quantifying and mapping these complex metabolic interactions with meta-omics, a metabolic network could be reconstructed that enables key metabolic processes and interactions to be

assessed and targeted by restoration actions. Furthermore, the effect of the restoration project can be quantified using meta-omics to evaluate the biological interactions involved in nutrient cycling before, during and after restoration activities (FIG. 4). For example, meta-omics can identify the organisms responsible for nutrient transfer<sup>71,72</sup>. The form and availability of some key nutrients, such as nitrogen, are vital for ecosystem health. Inorganic forms of nitrogen are not easily used by organisms, and it is crucial, therefore, to identify which microbial communities can fix atmospheric nitrogen and how they respond to restoration. Also, a metabolic activity map can be produced by inputting metagenomic or metatranscriptomic data to Predictive Relative Metabolomic Turnover<sup>71</sup>, a quantitative approach that characterizes microbial metabolic networks and predicts metabolomic turnover.

This concept is illustrated by the restoration of oyster reefs in coastal areas with the aim of reducing organic nitrogen concentrations in coastal water. The presence of too much organic nitrogen (for example, from agricultural fertilizer runoff) can lead to dramatic ecological impacts from eutrophication (that is, dense growth of plants or algae, which reduces the oxygenation of a given aquatic environment). Oyster reefs enhance denitrification activity by producing and releasing biosolids that provide a carbon source to natural microbial denitrifiers<sup>73,74</sup>. Monitoring the abundance, activity and response to disturbance of denitrifiers using metagenomics and metatranscriptomics can be used to monitor such restoration programmes<sup>75</sup>. However, our understanding of these ecological networks is impeded by the extensive sampling required to adequately capture their temporal flux. Nevertheless, once these networks are understood, the information can guide restoration practitioners in surveying ecosystem function more holistically (that is, at the level of both macro-organisms and microorganisms).

Our capacity to characterize the microbiobiodiversity mediated by microbial communities continues to develop. In addition, the ability to accurately detect macro-species interactions (such as those mediated by insects) is another restoration context in which genomics tools could be used to address monitoring challenges<sup>72</sup>. Mutualistic networks, such as pollination, offer insights into the potential benefits of species interactions. Pollination is a key ecosystem function that underpins



**Fig. 3 | Integrating predictive climate modelling with population genomics to guide provenance decision-making.** The spatial prediction surface of a genomics-informed aridity index across the native distribution of *Eucalyptus tricarpa* in south-eastern Australia, projected under current (1960–1990; part a) and future (2070; part b) climates. Warm (red) colours correspond to arid-adapted populations. Cool (blue) colours correspond to mesic-adapted populations. Future climate projections of the Aridity Index were modelled using the CSIRO Mk3.5 global circulation model under the extreme A1B climate scenario (Supplementary Methods). Part a adapted with permission from REF<sup>48</sup>, Wiley-VCH.

reproduction of most plants, with approximately 80% of flowering plant species (including one-third of food crops<sup>76</sup>) relying on animals to some extent<sup>77</sup>. Pollinators also depend heavily on flowering plants for habitat and resources, which creates a complex network of mutually beneficial interactions. However, producing highly resolved interaction networks represents a daunting challenge; visitors need to be differentiated from pollinators, and both common and rare plants and pollinators need to be identified<sup>78</sup>. Traditional approaches that rely on morphology-based identification alone are both time intensive

and financially costly<sup>79</sup>, which seriously limit their application<sup>80</sup>.

Despite the potential utility to restoration of unravelling complex pollination networks, meta-omics has not been widely applied in this context<sup>11</sup>. Metabarcoding or metagenomics can allow simultaneous processing of invertebrate pollinators<sup>81</sup>, and the pollen they carry<sup>82</sup> and store<sup>83</sup>, to quantify the richness of species involved<sup>84</sup>. A single organism (such as a bee) may also comprise multiple nodes of separate networks (plant–pollinator–parasite–pathogen); the increasing capacity to apply meta-omics to mixed samples (such as a

pollinator carrying a suite of different pollen grains and microbiota) promises to provide considerable insight into the complexity of multiple networks simultaneously<sup>85,86</sup>. Coupled with high-throughput sample processing, meta-omics offers the ability to capture population dynamics at previously unattainable resolutions. This knowledge can inform planning and evaluation of ecological restoration, with network characteristics used to establish milestones that reflect the reinstatement of ecosystem functions.

Current methods such as metabarcoding have limitations, including PCR bias, poor taxonomic resolution of some genetic markers and poor quantification of biological abundance. However, metagenomics may overcome some of these problems by mapping resequenced whole-organelle genomes (such as mitochondria and chloroplasts) to reference data sets, thereby foregoing the need for PCR-based barcode identification<sup>87,88</sup>. The ultra-deep-sequencing capacity of modern platforms allows direct sequencing of total genomic DNA from mixed samples, with target reads then mapped and remaining reads discarded. This approach has proved effective in identifying species composition and predicting biomass in mixed samples<sup>87,88</sup> but is further benefited by capture array technologies that reduce excessive non-target sequencing<sup>89</sup>. Currently available techniques, such as Predicted Relative Metabolomic Turnover<sup>71</sup>, offer opportunities to characterize ecological networks and derive quantitative metrics to evaluate the success of restoration.

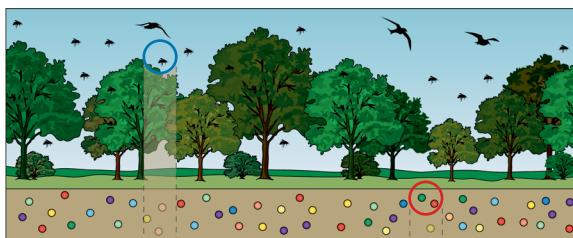
#### Genome editing for restoration

Approximately 66% of the Earth's terrestrial environments are degraded, of which nearly 40% are classified as severely or very severely degraded<sup>2,90</sup>. Indeed, approximately 2% of the Earth's soils have been classified as so severely degraded that the damage is likely irreversible<sup>3,91</sup>. Furthermore, climate change is rapidly creating climatic conditions that may exceed the physiological tolerances of naturally occurring plant genotypes. In such cases, extreme conditions might prohibit naturally occurring provenances — and even non-local species — from achieving basic restoration outcomes, such as establishment or land stabilization<sup>92,93</sup>. In some situations, therefore, new genotypes might be required for restoration to be attempted.

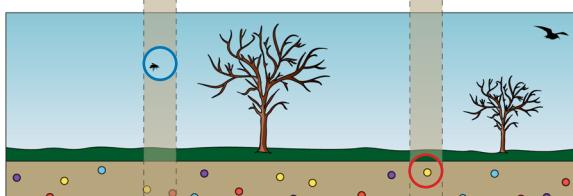
New genome-editing technologies<sup>94</sup>, and the CRISPR–Cas9 system in particular<sup>95–97</sup>, offer the potential to generate new plant genotypes quickly and cheaply. Genome

**Sampling**

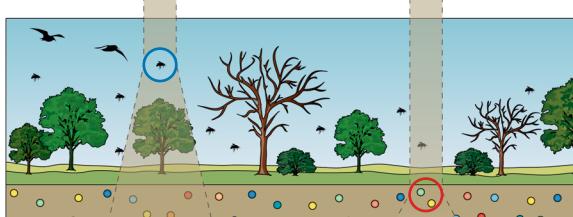
Reference ecosystem



Degraded ecosystem



Restored ecosystem

**Processing****Metabarcoding**

DNA

**Metagenomics**

DNA

**Metatranscriptomics**

RNA



Extraction

Amplification

Sequencing

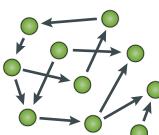
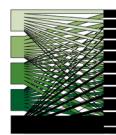
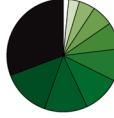
- Barcode presence
- Barcode abundance

- Gene presence
- Gene abundance

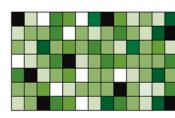
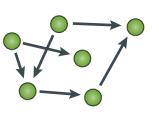
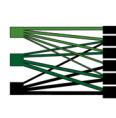
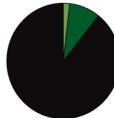
Gene expression

**Analysis**

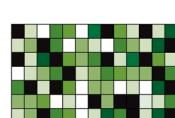
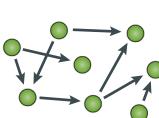
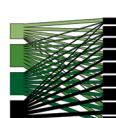
Reference



Degraded



Restored



Ecological interactions

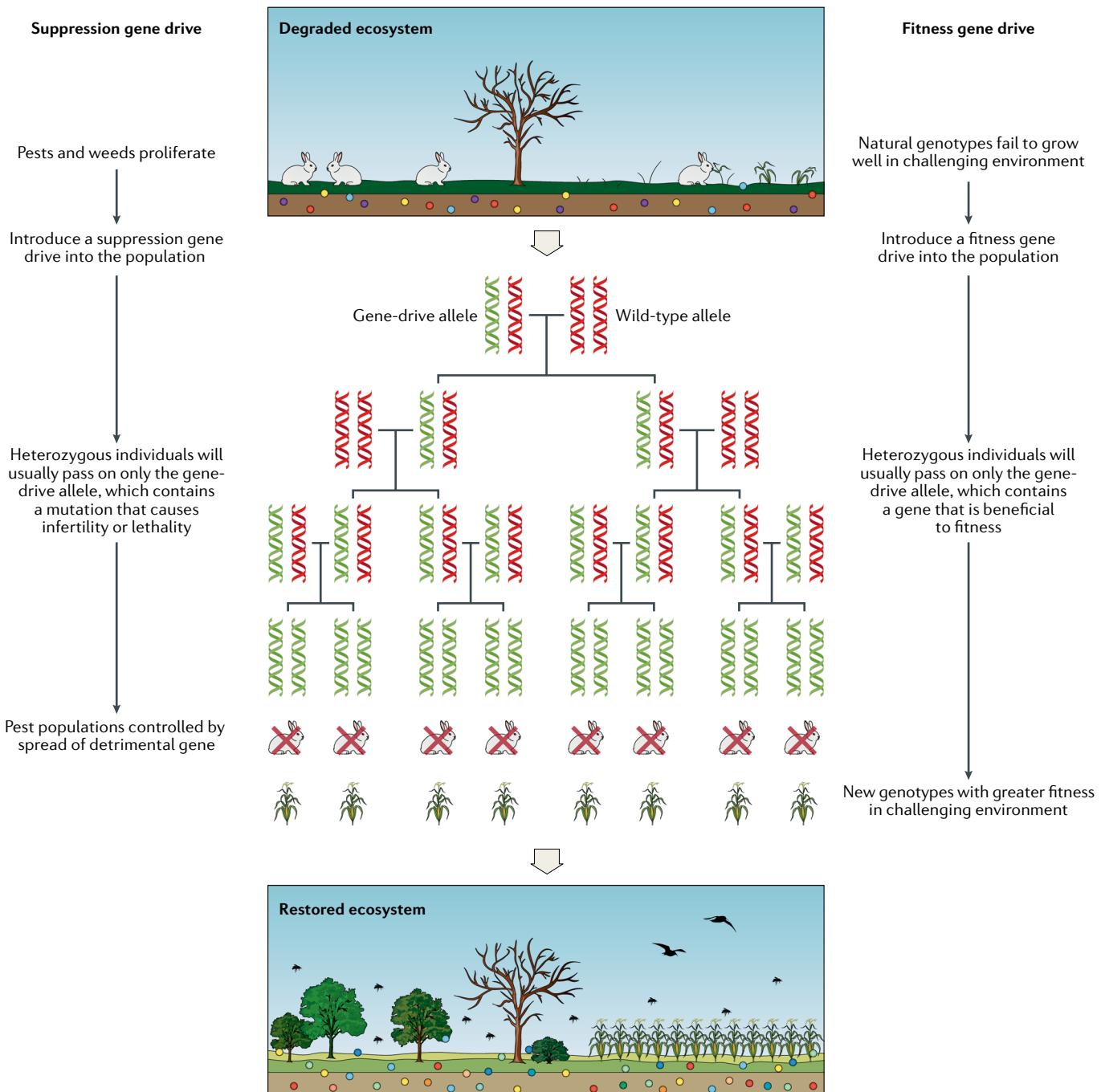
Ecosystem components

**Fig. 4 | Schematic overview of how meta-omics can be used to improve restoration assessment and monitoring.** The sampling, molecular processing and analysis steps typically involved in meta-omics approaches are shown. Top panel: sampling — a variety of bulk or mixed samples are shown, including collections of soil microbiota and flying insects with pollen from reference, degraded and restored environments. Middle panel: molecular processing — three commonly used meta-omics approaches are shown: metabarcoding, metagenomics and metatranscriptomics. The corresponding data outputs from these approaches are also shown. Bottom panel: analysis — the main outputs are shown, including diversity profiling, species interactions, functional interactions and functional activity, each linked to its application in assessing ecosystem components and ecological interactions.

editing allows the insertion, deletion or replacement of DNA within an organism's genome and provides the opportunity to modify regions of the genome that affect specific functions<sup>98,99</sup>. The CRISPR–Cas9 system has been shown to be an efficient method for genome editing in model systems<sup>100,101</sup> and has the potential to be applied in restoration<sup>102</sup>, either to modify or upregulate key functional genes or to engineer synthetic gene drives for spreading positive or negative genetic elements throughout populations<sup>103</sup> (FIG. 5).

Although genome editing is already technically feasible, we emphasize that there is much work to be done before the technology can be safely implemented in the context of ecological restoration. Substantial investment is required to determine whether genome editing could aid restoration efforts in the future, to understand the risks of releasing genetically modified plants or animals in the wild and to develop the scientific, regulatory, ethical and social licences required for such technology to be deployed in natural ecosystems. Thus, our intention here is to initiate a discussion on the potential of these 'over-the-horizon' technologies for restoration purposes.

**Developing novel plant genotypes for challenging conditions.** The CRISPR–Cas9 system could be applied in a restoration context to rapidly develop new plant genotypes with desirable traits. In crop research, genome editing is already being used to create new varieties<sup>104</sup>. Although this approach may be challenging for traits controlled by multiple genes<sup>105</sup>, the production of simple (that is, single gene) variants should be quicker and cheaper using CRISPR–Cas9 methods than through selective breeding techniques<sup>106</sup>.



**Fig. 5 | Gene drives for modifying the genomes of wild populations.** CRISPR–Cas9-based gene drives, with biased inheritance, could rapidly spread genetic elements through populations. Suppression gene-drive technology could be used to control unwanted pest and weed species by distorting sex ratios or disrupting the expression of developmental or fertility genes (left). Fitness gene drives could also spread beneficial genes through populations of key restoration species (right). Coloured circles represent environmental microbiota.

For example, loss-of-function mutations occur naturally and can be imitated by mutations produced with targeted genome editing. Gene ‘knockouts’ produced in this way have been used to modify the starch content of maize grains, producing new varieties that are essentially indistinguishable from those that could be obtained through conventional breeding<sup>107</sup>. Similarly, novel functional gene variants can be generated

using CRISPR and have been used to improve maize yield in drought conditions<sup>108</sup>.

In a restoration context, genome editing has the potential to generate new genotypes suited to challenging environments, while retaining existing desirable traits and a local genetic background<sup>102,104</sup>. However, this application would require detailed knowledge of desirable genes and traits in a specific restoration context. Realizing the

potential of CRISPR-based technology for developing new plant strains that are tailored for restoration purposes also would require the genetic basis of plant functional traits to be understood in detail, for which a well-annotated reference genome and functional genomic studies are needed. Hence, although genome-editing technologies are facilitating the generation of new genotypes, substantial empirical research

will be required to link different genetic variants to restoration outcomes in specific environments. However, engineering disease resistance in key restoration species is potentially achievable now, by augmenting plant genomes with CRISPR constructs that interfere with viral or bacterial pathogens<sup>109</sup>.

**Gene drives to spread beneficial genes or control pest populations.** Synthetic gene drives could aid restoration in challenging ecological situations in which more established approaches are unsuccessful<sup>110,111</sup>. A gene drive is a genetic element that is more likely than usual to be passed on from parents to offspring (that is, an element that achieves super-Mendelian inheritance; FIG. 5). Such drives are found in nature<sup>12</sup> and can be achieved by various mechanisms. A synthetic CRISPR-based gene drive consists of a DNA cassette encoding Cas9, a guide RNA (gRNA), and a cargo gene if required. This gene drive sequence is inserted into one chromosome, along with a carefully selected promoter to ensure the cassette is expressed only in the germline<sup>113</sup>. During meiosis, the gene drive is expressed and the gRNA guides Cas9 to cleave the partner chromosome at the target site. When the double-stranded DNA break is repaired by homologous recombination, the gene drive is replicated, resulting in germline homozygosity. In theory, this ‘homing’ process should allow the target gene to be passed on to almost 100% of offspring. Homing-based gene drives could spread beneficial genes and associated traits (such as tolerance of high salinity or drought) through declining populations or populations of key restoration species. This application would require the identification of beneficial genes and the successful in situ reproduction and development of gene-drive carrying individuals in spite of possible fitness costs associated with the integration of Cas9 within eukaryotic genomes.

Restricting the gene-drive homing event to the germline also provides a means of propagating detrimental DNA constructs that cause infertility or lethality<sup>111</sup>, which can be used for population control<sup>110</sup>. To date, such suppression drives have been studied as a means to control the mosquito vectors of malaria<sup>114–116</sup>. For example, recent work has engineered a CRISPR-based gene drive that caused loss-of-function of the female version of the *doublesex* gene in the mosquito *Anopheles gambiae*<sup>117</sup>. The drive spread rapidly after being introduced into experimental mosquito populations, in which it caused sterility

in homozygous females and led to total eradication of the population. In a similar way, gene drives that disrupt maturation, seed generation or germination pathways could be used to control exotic weeds<sup>118</sup>. Furthermore, mammalian gene drives could be developed to suppress the abundance of damaging herbivores<sup>19,21</sup>, such as invasive rabbits and mice. Efficient and cost-effective weed or herbivore suppression has the potential to improve restoration outcomes<sup>119</sup>.

Although gene drives could facilitate rapid delivery of genes throughout a population, several limitations may inhibit their spread. For example, wild populations of *Tribolium castaneum* (red flour beetle) were used to demonstrate that natural populations may harbour individuals with ‘resistant’ alleles that cannot acquire a gene drive<sup>120</sup>. These simulation studies indicated that natural selection favouring these resistant alleles could purge a drive within <10 generations. However, in silico studies showed that existing polymorphic resistance within target populations could be overcome, at least theoretically, by designing gene drives with multiplexed gRNAs that target multiple DNA recognition sites for cleavage<sup>19</sup>. Another potential hurdle to the dissemination of drives is metapopulation structure<sup>19</sup>, which could prevent the drive reaching some relatively isolated populations; the release of many drive-carrying individuals would be required in these populations<sup>121</sup>. Finally, the spread of gene drives would be slow in clonal plant species or plant species with long generation times. On the other hand, the uncontrolled spread of self-sustaining gene drives beyond a population targeted for management is also a serious consideration<sup>122</sup>. To limit the non-targeted delivery of the gene drive or to reverse its effects, self-limiting and reversal drive systems are being tested with simulation modelling but to date have not been demonstrated empirically<sup>19,123,124</sup>.

**Risk analysis frameworks for genetic modification in restoration.** The use of genome-editing technologies in environmental systems needs to be undertaken within a risk-assessment framework<sup>20,124</sup> to evaluate the risks for the unintended spread of engineered genotypes beyond their intended use, either geographically and/or biologically (for example, as a result of unexpected intra-species and inter-species hybridization). The risk assessment must address the potential for inadvertent negative genetic, ecological or health effects using the precautionary principle,

acknowledge the trade-offs between positive, negative and neutral impacts, and incorporate sources of uncertainty associated with those effects<sup>125</sup>. Risk assessment of genome-editing technologies in a restoration context must include ecological, biological and genetic information, as well as economic and cultural considerations, and extensive public discussion and engagement<sup>125–128</sup>. The decision framework should evaluate the potential degree and probability of harm and how to manage that harm. Here, we briefly highlight the data required for risk assessments; possible ways to address data limitations; the uncertainty regarding the data and a few options regarding ways to handle uncertainty; and the importance of linking risk assessments to human well-being.

Risk assessments require data, and “little information exists on the impacts of releasing [genetically modified organisms] into minimally managed or unmanaged systems”<sup>125</sup>. The requisite information might take years — even decades<sup>106</sup> — to compile and, in the meantime, decisions must be made. Hence, data from genome-editing field trials could be combined with data from other types of plant releases to parameterize simulation models to inform impact assessments. Scenario modelling can integrate ecological, economic and cultural considerations, including the risks and/or benefits of proposed actions and the risks and/or consequences of not carrying them out<sup>129</sup>. The invasive potential of a species could additionally be used to inform an impact assessment<sup>130</sup>. Risk assessments developed for other domains, including, for example, agricultural biotech crops<sup>131</sup>, transgenic fish<sup>132</sup> and nanoparticles<sup>133</sup>, might also provide useful models for developing a framework for use in ecological restoration, while being aware that more highly managed systems, such as agriculture, differ substantially from the systems involved in ecological restoration.

Modelling uncertainty in risk assessment is critical<sup>134,135</sup> and various ways to manage uncertainty have been proposed, including different classifications of uncertainty (uncertainty about outcomes versus uncertainty about probabilities<sup>126</sup>) or creating tiers for different levels of uncertainty, with risk-assessment frameworks then tailored to the level of risk and/or uncertainty<sup>136</sup>. Finally, it has recently been strongly advocated that risk-assessment frameworks balance the risk of loss of ecosystem services against the potential to recover ecosystem services<sup>125</sup>; both with and without the biotech intervention<sup>137</sup>.

The use of ecosystem services is recommended as a key outcome variable in risk assessments because it makes clear the connection between the ecological restoration and human well-being for the various stakeholders and policy-makers<sup>138</sup>.

### Conclusions and perspectives

Genomics has been termed transformational in health care, agriculture and even the global economy<sup>139</sup>. However, restoration scientists and practitioners are yet to harness its potential. Recent reviews have called for innovation to bridge the gap between knowledge and restoration action<sup>140</sup> and have framed future innovation as imperative for restoration<sup>141</sup>, but neither article considered genomics. We have outlined only a few examples of how genomics offers the potential to improve ecological restoration through informed seed sourcing, monitoring of restoration processes, generation of new genotypes and genetic biocontrol of pest and weed populations.

Empirical studies of innovation across disciplines show that early in their development, new technologies tend to have several limitations that inhibit their use<sup>142</sup>. However, with time and additional development, new technologies may well outperform incumbent approaches<sup>143</sup>. Genomics offers one such innovation to assist with some of the pressing issues facing ecological restoration. However, successful and cost-efficient restoration practices will rely on more than just applying genomics, and many restoration challenges, such as land ownership and site accessibility, fall outside the scope of genomics. Furthermore, technical, analytical and ethical issues need to be addressed before genomics can be applied in a restoration context. More general barriers, such as access to molecular laboratories, sequencing facilities and bioinformatics capabilities, also need to be overcome and restoration ecologists need to be trained in the use of genomic technologies. Strategic collaboration between the restoration sector and other disciplines is one of numerous routes that could be explored to gain access to genomics capabilities.

Moreover, as for any innovation, proof of concept is needed in order to provide evidence for the viability of the proposed techniques<sup>144</sup>. Validation of the proposed uses is therefore essential. In addition, developing the risk frameworks and engaging relevant stakeholders (such as legislative, scientific and community groups) to evaluate possible drawbacks against the potential benefits of applying genomic

tools are necessary. Proactive consideration of risks helps identify possible ways to mitigate unintended consequences of new technologies<sup>20,57,98,125,126</sup>, such as genome editing. Moreover, many new technologies require the development of related technologies in order to unleash their full potential, and genomics is no exception<sup>144</sup>. For example, the application and uptake of restoration genomics will require development of dedicated bioinformatic tools, which is a recognized barrier in conservation genomics<sup>13</sup>. Finally, as with all new technologies, communication<sup>145</sup> of the possible value that genomics brings to the science and practice of restoration is necessary in order to achieve its full potential in this arena.

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M.F.B., P.A.H., R.H. and D.A.S. researched data for the article. M.F.B., P.A.H., C.B., M.B., V.G., S.V.C.G., R.H., J.G.M., T.A.A.P., D.A.S. and J.J.M. made substantial contributions to discussions of the content of the manuscript. M.F.B., P.A.H., C.B., V.G., N.J.C.G., S.V.C.G., J.G.M., T.A.A.P., D.A.S. and J.J.M. wrote the article. All authors reviewed and/or edited the manuscript before submission.

**Competing interests**

The authors declare no competing interests.

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