Species, genes and epigenetics: how dimensions of diversity interact for forest resilience

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Summary:
Diversity is seen as key to building the resilience of UK forests and woodlands to future environmental change. However, diversity has many dimensions encompassing species diversity, within-species genetic diversity and within-individual epigenetic effects. Current forest management strategies and policies have a strong focus on building species diversity but rarely consider how different dimensions of diversity interact and how they can be integrated to enhance resilience. In this article, we explore current knowledge on these dimensions of diversity as well as known and potential interactions. We identify key aspects of forestry for which the multiple dimensions of diversity have an impact, namely: (1) spatial scale, (2) natural colonisation and regeneration, and (3) the nursery environment. We conclude with general points to consider when using multiple dimensions of diversity to increase forest resilience.

Introduction

Diversity is seen as key to enabling UK forests and woodlands to be resilient and adapt to a changing environment (Defra, 2018; Atkinson, Morison and Nicoll, 2022). Although diversity can come from many sources, here we consider biological diversity, which covers species diversity, within-species genetic diversity and within-individual epigenetic changes and the ways they interact. We aim to highlight some of the key questions that forest managers need to consider if they wish to diversify their forests to make them more resilient to the coming environmental change.

The Tree of Knowledge project (https://www.hutton.ac.uk/project/tree-of-knowledge/), funded by UK Research and Innovation-Natural Environmental Research Council's 'Future of UK Treescapes' programme, drew on outcomes from three of the programme's research projects, DiversiTree (https://www.hutton.ac.uk/project/diversitree/), newLEAF (https://www.ceh.ac.uk/our-science/projects/newleaf) and MEMBRA (https://membra.info/about/) to examine species, genetic and epigenetic diversity. In this article, we briefly outline the different dimensions of diversity, provide examples of how these dimensions are known to or may interact and highlight options for diversifying forests.

Definitions of diversity and resilience

Diversity can be defined at different levels from the individual to whole ecosystem, and spatial scale is important. Here, we consider definitions for trees and forestry (Figure 1):

Species diversity is the number of different tree species found in a specified area e.g. stand, forest or region.

Genetic diversity is the number of different genetic individuals (DNA *genotypes*) found within one tree species and is typically measured in populations. DNA contains genes, the expression of which determine the response of an individual to its environment. Individuals that have similar genetic make-up due to local adaptation to shared environmental conditions (e.g. climate, soil type, etc.) are referred to as a *provenance*.

Epigenetic effects are chemical modifications to DNA that alter gene expression but do not change the DNA code. Epigenetic changes induced by environmental pressures may be long-lasting, hence epigenetic effects can be described as 'memory'. However, epigenetic effects may also be lost if a stress no longer exists. Some epigenetic changes may be passed among generations. The concept of epigenetic diversity is complex as it depends on an interaction between genetic diversity and the environment, so we refer to epigenetic effects rather than diversity.

Considering the definition of *resilience* laid out in Biodiversity 2020 by Defra as the ability of an ecological system to "absorb, resist or recover from disturbance and damage…while continuing to meet overall objectives of supporting biodiversity and providing ecosystem services" (Defra, 2011), we can ask what roles different levels of diversity play.

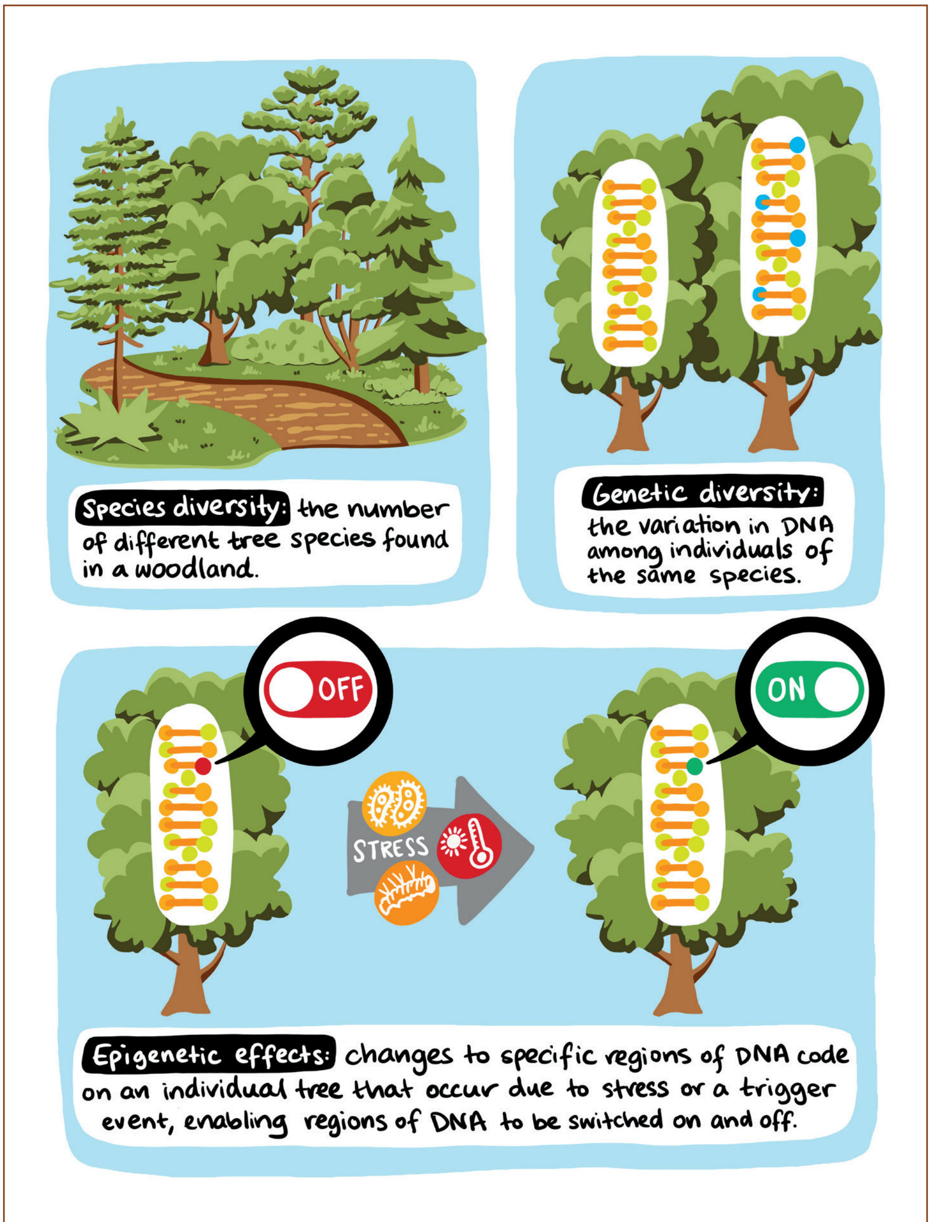

Figure 1. Infographic showing different dimensions of diversity found in UK woodlands and forests.

Genetic diversity is the raw material of evolution and supports resilience in two ways. In a forest, the *standing genetic diversity* determines the immediate range of responses in a population so underpins the resilience of the current generation. This standing diversity also provides *adaptive potential* as it determines the genetic composition of offspring through mating and therefore underpins the resilience of future generations.

As with species diversity, the genetic diversity-resilience relationship is complex. Similar to the bet-hedging mechanism, genetic diversity increases the range of possible responses of a species to its environment, including genotypes that may be less suited to the current environment but do better in a future environment. The relationship is not linear; beyond a certain level, adding genetic diversity may simply add more genotypes that are sub-optimal for both current and likely future environments.

The epigenetic response of trees is an emerging area of research and as such both the theory and application of the epigenetic-resilience relationship is still developing. For UK tree species, the MEMBRA project has focused on identifying epigenetic changes in ash (*Fraxinus excelsior*) in response to ash dieback disease and in oak (*Quercus robur*) to acute oak decline, drought and CO_2 stimulation (unpublished results). These stresses were tested to a lesser extent in birch (*Betula pendula*), beech (*Fagus sylvatica*) and hazel (*Corylus avellana*).

The species diversity-resilience relationship for trees is complex and our understanding is largely theoretical, but essentially, it should operate through three principal mechanisms: (1) *bet-hedging*, where the presence of multiple species means that some species will survive even if others are lost, (2) *functional redundancy*, when two species can deliver a similar function from the same environment, and (3) *dilution* where, for pests and diseases, higher species diversity dilutes impact by reducing the number of individual trees affected. Individual tree species may differ considerably in what they add to overall resilience.

Interactions between dimensions of diversity

We collated knowledge from project leaders, project meetings, conferences and policymaker and practitioner workshops between 2023 and 2025 and identified key interactions among the different dimensions of diversity (Figure 2). These are grouped into *positive* – where outcomes increase resilience or sources of diversity complement one another in contributing to resilience, or *negative* – where outcomes decrease resilience or sources of diversity are not complementary and/or management decisions need to prioritise one source of diversity over another. This list is not exhaustive and other potential interactions exist.

Positive interaction

Species-genetic: High species diversity and high genetic diversity can reduce the impacts of some pests and pathogens via a dilution effect, in other words reducing the prevalence of a pest/disease because only a proportion of species/genotypes will be susceptible or act as hosts (Koricheva et al., 2006; Barantal et al., 2019; Jactel, Moreira and Castagneyrol, 2021; Gougherty and Davies, 2024; Keesing and Ostfeld, 2024).

Species-epigenetic: Epigenetic effects can widen a specific species' stress tolerance and this has been shown as part of emerging research from the MEMBRA project and previous work from the Epidiverse project (Epidiverse, 2022; Rodríguez et al., 2022).

Genetic-epigenetic: Genetic diversity and epigenetic effects operate at different temporal scales. Standing genetic diversity determines the immediate range of responses of a population because each individual has a different genetic makeup, whilst genetic change over generations determines the scale of adaptive response over time. Epigenetic effects operate at the single tree level and can occur within the lifespan of a tree, although the range of responses will also reflect the standing genetic diversity. Genetic diversity and epigenetic responses may allow both long- and short-term response to a stress but understanding the outcomes of this interaction requires future research.

Negative interactions

Species-genetic: In a forest area with a finite number of trees, there will be a trade-off between species diversity

Figure 2. Infographic of positive and negative interactions between species diversity, genetic diversity and epigenetic effects. Positive interactions refer to those that increase resilience or complement one another, whereas negative interactions decrease resilience or sources of diversity are not complementary and/or management decisions need to prioritise one source of diversity over another.

and genetic diversity. This can be thought of as an 'opportunity cost', where each tree of one species that is present means one tree of another is not. Focussing on species diversification with low numbers of trees for each species may lead to more short-term than long-term resilience due to the reduction in adaptive potential that comes from lower genetic diversity. The introduction of new species (or genotypes) in pursuit of species diversification risks maladaptation to current or future climate conditions and unforeseen risks, such as introducing or facilitating pests or pathogens (Ghelardini et al., 2016; Piotrowska et al., 2018).

Species-epigenetic: Emerging research suggests that the magnitude of epigenetic effects differs between tree species; therefore, resilience outcomes based on epigenetic effects may be less beneficial for some species than others.

Genetic-epigenetic: There is uncertainty over whether prioritising epigenetic effects would inhibit longer-term genetic adaptation by enabling a greater proportion of genetically poorly adapted trees to survive during the process of natural selection. This concern is currently hypothetical and requires future research.

Management considerations

Below we outline three key management considerations that emerged from knowledge collation, in which interactions among dimensions of diversity may have an impact (Figure 3). In each case outcomes will be context specific, depending on forest type, land manager objectives and cultural significance amongst many other factors. Managers will need to develop a clear, operational understanding of resilience for their context: consider what needs to be resilient (e.g., a particular species, or an ecosystem service such as timber production), and to what pressure (e.g., a particular disease, or increased drought).

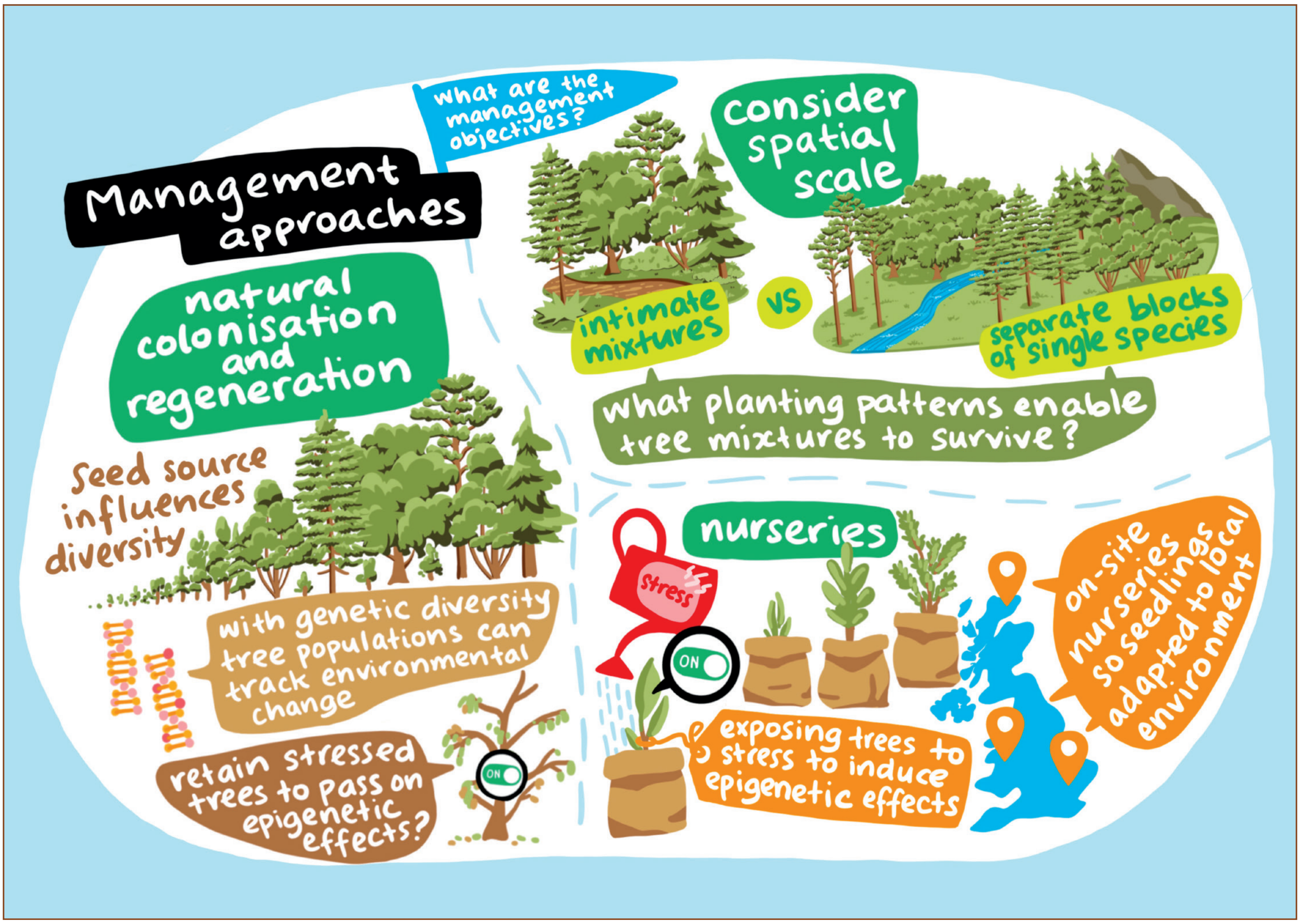

Figure 3. Infographic overview of three key management considerations for integrating species diversity, genetic diversity and epigenetic effects.

Spatial scale

Species and genetic diversity can be considered at different spatial scales. For example, a single species stand is much less diverse than a stand containing multiple species (Figure 3). Yet if a landscape is filled with identical stands of the latter, it may be no more diverse than a landscape filled with single species stands, if each stand contains a different species. There are many ways to achieve stand-level diversity, for example Forest Research have produced guidance on Forest Development Types which includes options for decision-making at multiple scales (Haufe et al., 2024).

At the stand scale there are broadly speaking two contrasting approaches to increase species or genetic diversity:

- *A mixture design of two or more species* in close proximity achieves higher species diversity at a local scale. Mixed forests are more resilient on average than monocultures to mammal and insect herbivores, and soil-borne fungal diseases, but effects are contingent on species composition (Jactel et al., 2017; Jactel, Moreira and Castagneyrol, 2021). Admixing broadleaves to conifer stands can increase fire and wind resistance compared to conifer monocultures (Jactel et al., 2017). However, the benefits of mixed stands for threats such as drought are less clear and depend on species. In the UK, intimate mixes of Sitka spruce and Scots pine did not result in greater resilience to spring drought compared to monocultures after 24 years (Ovenden et al., 2022). A diversity experiment using intimate mixtures in Germany showed higher mortality following drought, concluding the need to select drought tolerant tree species as opposed to higher diversity per se (Shovon et al., 2024). Managing mixtures can be logistically challenging and costly, especially if one species needs to be selectively removed. Also, commercial harvesting and processing systems are better able to manage uniform products as opposed to diverse products (although rotations are long enough to allow the processing sector time to adapt).
- *Separate blocks of different single species* also result in diversification at a larger spatial scale. Many tree species are not compatible in some mixture designs and planting separate blocks of different single species may provide a suitable alternative (Kerr et al., 2020). This has been recommended for diversification of Sitka spruce by DiversiTree (Mitchell et al., 2025). Planting in blocks can introduce a second species unaffected by the primary threats to Sitka, providing resilience at the spatial scale of the blocks. Logistically, planting in blocks aligns with current conifer harvesting practices and aids selective removal of a species. However, single species blocks come with some of the issues associated with monocultures and clear-felling.

For genetic diversity, questions of scale concern the balance between local adaptation and gene flow, the natural dispersal of genes via seed and pollen. The former tends to narrow diversity as natural selection favours locally optimised genotypes, whilst the latter tends to widen diversity, bringing non-local diversity into a population (Figures 3 and 4). The balance between these two depends on the strength of local selection and the spatial extent at which gene dispersal happens for a species. In the UK, although local adaptation is present, it is typically weak and, as most species are effectively dispersed by wind or birds, gene flow is extensive.

Concerns about diversity arise mainly where populations are small and fragmented, or where the spatial extent of gene flow is not thought to be sufficient to bring new diversity into the population fast enough to match the rate of environmental change. In the latter case, strategies to augment genetic diversity have been proposed, such as *assisted gene flow* (Alberto et al., 2013) also termed *assisted migration* (Richardson et al., 2009). This aims to introduce future-adapted genotypes by importing provenances from sites in which current conditions match those predicted in future at the planting site (Whittet et al., 2019). There are many concerns around assisted gene flow/migration including the risk of maladaptation and potential failure of introduced non-local provenances (Fady et al., 2016), homogenising genetics at larger spatial scales (NatureScot, 2019), and the uncertainty of forecasts of future conditions. Forest managers should avoid drastically reducing diversity of small, fragmented populations, build population sizes and avoid homogenisation, but otherwise actively encourage the processes that enable natural gene exchange.

Where timber production is the primary objective, breeding can improve key traits for production, such as vigour and timber quality, but tends to reduce genetic diversity (Trivedi et al., 2019; Finžgar et al., 2023). Deliberately increasing genetic diversity could introduce more sub-optimal genotypes, so reducing overall productivity in the current environment. However, resilience could be achieved if the environment changes to become less suitable for current optimal genotypes and more suitable for some of the sub-optimal genotypes (Figure 4).

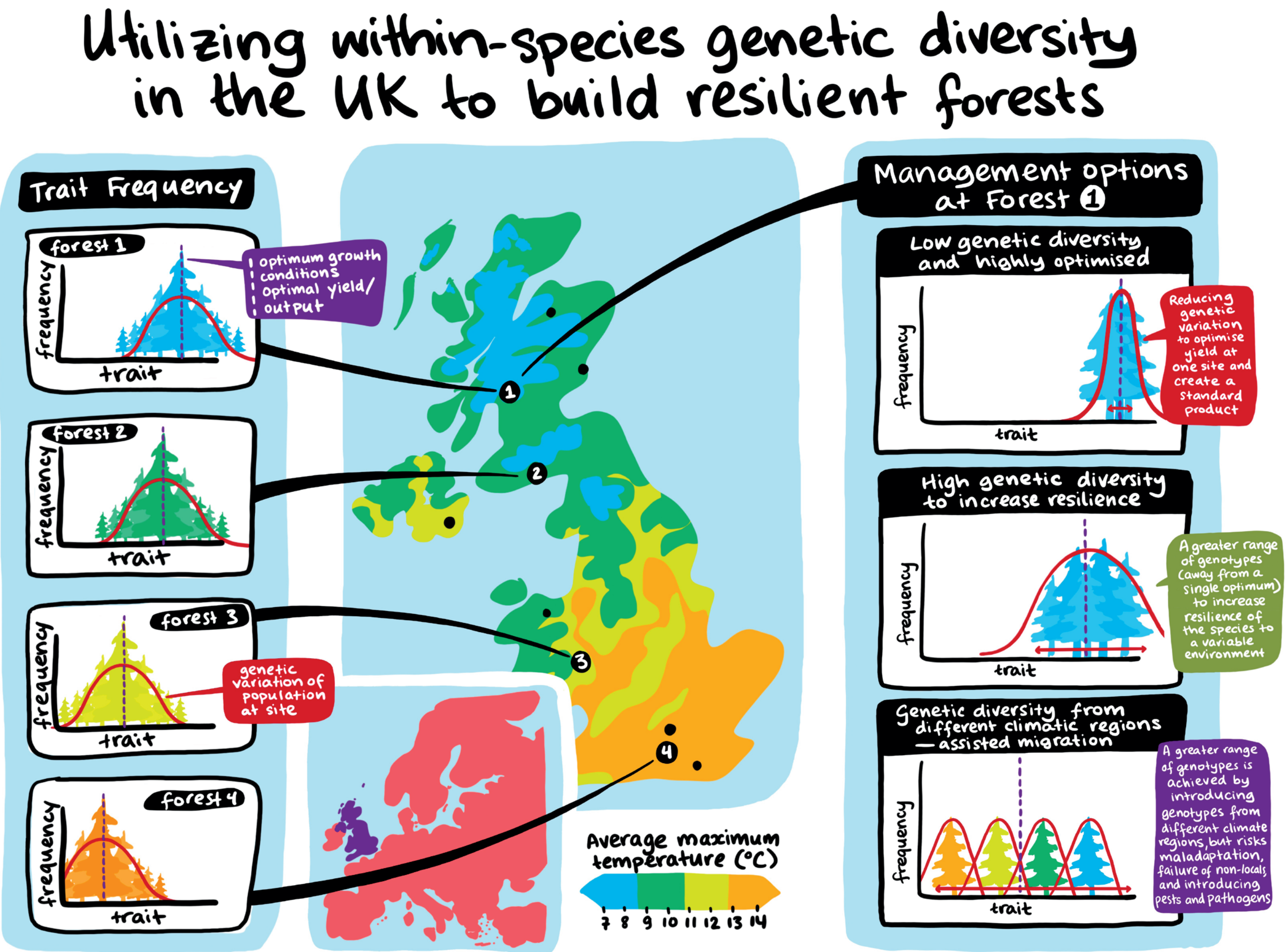

Figure 4. Infographic displaying breadth of trait variation in relation to genetic variation across the UK climate and how different forest management options shape genetic diversity.

Natural processes

Natural colonisation is where trees self-seed onto open ground (unwooded for >20 years), whilst natural regeneration occurs in existing woodland (FitzGerald et al., 2023). Both processes allow natural selection to operate but require nearby seed sources and could be vulnerable if climate change inhibits reproduction. Nevertheless, these processes can effectively support multiple dimensions of diversity (Figure 3):

- *Species diversity*: Natural processes allow recruitment of any species with seed sources nearby, resulting in species composition which is suited to the current environmental conditions (Harmer, Tucker and Nickerson, 2004). However, natural colonisation and regeneration can result in low species diversity if the diversity of seed sources is low, competition is intense between species, or through herbivory.
- *Genetic diversity*: Natural colonisation and regeneration enables selection to optimise genotypic composition to current environmental conditions (Cottrell, 2020) providing population-level resilience. As selection is strongest in early life stages, if opportunities for natural regeneration are spatiotemporally diverse, seedling populations can track rapidly changing environments, but this is limited by the rate of recruitment (Whittet et al., 2019).
- *Epigenetic effects*: Retaining stressed trees to set seed may take advantage of epigenetic effects that, if inherited, could be passed on to the next generation. This appears to be occurring in the ash dieback and acute oak decline epidemics (MEMBRA preliminary results). A balance between removal of severely infected

trees and retention of those healthy enough to reproduce should be considered when diseases become endemic. Retention may help when woodland recovery is the goal, as opposed to timber production. However, Statutory Plant Health Notices must be followed for high-risk pathogens and pests as the aim is to eliminate or significantly slow the spread of the disease.

The nursery environment

The nursery environment can have large and lasting impacts on growth and survival even after the trees are planted out (Figure 3). NewLEAF research showed that differences among plants from contrasting nursery environments were detectable more than a decade after planting (Perry et al., 2024). Epigenetic changes could be induced in a nursery by exposing seedlings to stress or chemical treatments, a process known as *priming* that increases seedling resilience to these stresses when planted out (Amaral et al., 2020). Results have shown that oak seedlings can be primed for defence against powdery mildew (Sanchez-Lucas et al., 2025), whilst elder (*Sambucus nigra*) cuttings can be primed for resistance to drought (Tidy, 2024).

Conclusions

Diversity has multiple dimensions and general points to consider for a forest context are: (1) diversification will not always equal greater resilience; (2) whatever approach is taken, we need to maintain within-species genetic diversity, to allow a range of responses to environmental change; (3) there is no 'one right answer' to the question of how to diversify and management objectives are key. Given the range and uncertainty of unknown future threats, a range of diversification approaches across sites may provide maximum resilience at the landscape scale; (4) diversification may involve challenging decisions, and failure may be part of the process. For example, we expect higher mortality of ill-adapted species or genotypes, and there may be a trade-off between ecological resilience and performance/productivity. However, the cost of not diversifying may be greater.

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Other resources

- Tree of knowledge video: https://www.youtube.com/watch?v=z30ueryKo-k
- Zenodo link to the full research note: https://zenodo.org/records/15976097 and DOI 10.5281/zenodo.15976096.

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