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Taking a tree's perspective on forest fragmentation genetics

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Despite longstanding research, how anthropogenic disturbance affects the genetics of tree populations remains poorly understood. Although empirical evidence often conflicts with theoretical expectations, little progress has been made in refining experimental design or in reformulating theoretical hypotheses. Such progress is, however, essential to understand how forest tree species can tolerate anthropogenic disturbance. Further advances in forest fragmentation genetics research will require that processes driving reproduction and recruitment in fragmented populations are assessed from a tree's perspective instead of experimental convenience, using a multidisciplinary approach to explain the spatio-temporal dynamics of gene dispersal. In this opinion article we aim to inspire a new perspective in forest fragmentation genetics research.

Forest ecosystems in a changing world

Trees are a predominant life form on Earth and forests have a pivotal role in the carbon and hydrological cycles and the maintenance of biodiversity [1–4]. Resources and services provided by forests, such as timber or other forest products, and soil and water conservation, are essential to human society [4,5]. Despite their global importance, forest ecosystems face numerous threats imposed by anthropogenic activities both in temperate and tropical climates [6]. These threats include primary forest clearance and logging, climate change, biological invasions and plantation of improved or engineered trees in the native range of forest tree species and subsequent hybridisation [5]. Of particular concern, close to 16 million ha of forest were lost globally per year during the period 1990–2000, of which nearly six million ha was due to the loss or modification of primary tropical forest. Although these losses show some evidence of slowing down (13 million ha were lost per year during the period 2000–2010), they remain high [4,7]. Furthermore, it is estimated that, in response to altered abiotic habitat conditions following global climate change, temperate tree species might only be able to shift their distribution range by a maximum of 10–70 km over the course of a century [8]. This shift is lower than the estimated temperature isocline shift of 800 km along the European Atlantic Coast if the predicted increase of 4 °C of global temperature over 100 years occurs [9].

Such anthropogenic pressures create unprecedented habitat disturbance in forest ecosystems, with consequences ranging from the level of the global climate system to changes in biodiversity of communities and even individual genes [4,5,10,11]. Arguably, the most pressing challenge for a sustainable future remains the need to find an acceptable balance between preserving forest ecosystem integrity and function, and ongoing anthropogenic activities. Fundamentally, this implies that researchers must understand better the dynamics of processes that enable tree species to respond and adapt to habitat disturbance in the long term and therefore to anticipate change rather than to take retrospective patch-up actions in resource exploitation, habitat management or species conservation.

Movement (i.e. how the spatial location of an entity changes in time) is a universal and fundamental process that connects organisms to their habitat [12]. Therefore, understanding the causes and consequences of individual movement is essential to the management of exploited and disturbed habitats [12,13]. However, trees are sessile organisms; movement in trees occurs solely in association with reproduction, either asexually, through vegetative propagation, or sexually, by dispersal of pollen or seed, both ultimately determined by interactions with abiotic or biotic dispersal agents [14]. Direct observation of such movements in trees is challenging [14,15]. However, the use of population genetics enables researchers to quantify the clonal and sexual reproductive components of realised movement and their interannual variation [16,17] and, ultimately, to assess the impact of that movement on

Glossary

Alleles: two or more variants of a particular gene.
Demes: local random mating units in subdivided populations.
Effective dispersal: the result of dispersal of propagules that establish and breed successfully.
Gene dispersal: the dispersal of genes resulting from movement within, and flow between, demes.
Gene flow: the gene exchange among demes given by the relative proportion of newly immigrant genes in a given deme.
Genetic drift: in a population of finite size, the stochastic variation in allele frequencies between generations owing to sampling effect.
Habitat fragmentation: the breaking up of areas of larger more continuous habitat into smaller and more isolated patches, contributing to overall loss of original habitat.
Inbreeding: mating between related individuals or, in its most extreme form, through self-fertilisation.
Individual fitness: the relative reproductive success of an individual measured by the proportion of its genes that occur in all of the genes in the next generation.
Metapopulation: a model of subdivided population where a group of demes that occupy patches of similar habitat is isolated by unsuitable habitat. The persistence of the metapopulation depends on a balance between deme extinction and recolonisation through migration of individuals (in plants, seeds or plant fragments) between patches.
Specific density: the density of individuals of a particular species within a population given by the number of individuals divided by the population area.

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population genetic structure [18,19]. The population genetics approach is particularly powerful because it enables prediction of the evolutionary consequences of the contemporary ecological process of organismal movement. Indeed, a key factor in the potential adaptation of tree species to habitat disturbance is how such disturbance alters gene flow dynamics through dispersal and establishment of propagules in the changing landscape matrix [20].

Resolving the paradox of forest fragmentation genetics

One major prediction is that habitat fragmentation (see Glossary) will reduce gene exchange among populations and that small, chronically fragmented patches of a once-large continuous forest tree population will display reduced genetic diversity, increased inbreeding and increased genetic structure (Box 1 [10,21]). However, despite considerable research activity over recent decades, the effects of anthropogenic disturbance on the genetics of tree populations remain controversial [20,22]. Empirical evidence frequently does not fit with theoretical expectations, a disparity that has recently been dubbed the ‘paradox of forest fragmentation genetics’ [22].

Box 1. The paradigm of small population genetics

When population size declines, only a sample of the original individuals and their genes will survive. The severity of genetic loss associated with a sudden population size reduction, termed a ‘genetic bottleneck’ [66], will depend on how severely the population size is reduced. Following fragmentation, populations that remain small and isolated for many generations suffer an increase in genetic drift and consequent loss of allelic diversity and increase in differentiation between populations [23,66]. Although rare alleles will be lost first, continued drift acting over many generations can result in the loss of more common alleles, and can result in severe depletion of genetic diversity [67]. Loss of genetic diversity can affect population viability within a relatively short period, because genetic drift acts equally on neutral and selected genes, and deleterious alleles can become fixed by chance [68].

A reduction in population size can also alter the structure of genetic variation both within and among populations by altering levels of gene flow between individuals [23]. In particular, inbreeding can increase owing to changes in mating patterns within populations that lead to increased mating between relatives or increased self-fertilisation. If spatial separation increases between individuals, the exchange of genes between more distant individuals is reduced and mating between nearer neighbours becomes more likely. As neighbours are often also likely to be relatives (which share common alleles at many loci), such mating patterns result in elevated levels of biparental inbreeding [66].

Increased inbreeding leads to an increase in individual homozygosity (reduced variation within individuals). Theory predicts that a reduction of individual fitness or ‘inbreeding depression’ should result [69–74]. Inbreeding depression will affect individual fecundity, establishment and survival and can ultimately affect population viability [69,72], although the relative importance of genetic and demographic factors in the decline of tree populations remains to be understood [22,75]. The severity of inbreeding depression is expected to be higher in historically outcrossing populations, because the effects of deleterious recessive alleles can be masked by their typically high individual heterozygosity; if small remnant populations are able to persist, inbreeding depression can decrease over time as deleterious mutations are purged by selection. For typically outcrossing species, such as most trees [14,76], a shift to mating patterns that increases inbreeding following habitat disturbance is therefore expected to have a negative impact on fitness [73,77].

These predicted genetic impacts of forest fragmentation are based on the sole assumption that habitat fragmentation, by increasing the spatial distance between remaining forest patches, results in genetic isolation of small extant population fragments [22], which subsequently experience the detrimental genetic effects of a small population size (Box 1 [23]). Although this effect has been verified for some organisms (e.g. common beech *Fagus sylvatica* [24]; and the conifer *Araucaria nemorosa* [25]), this is not always the case (reviewed in [21,22]). Noticeably, empirical measurement of contemporary gene flow in modified landscapes reveals that the spatial scale and quantity of gene exchange among population fragments can also increase, when mediated either by pollen [26–29] or seed [30] in tropical and temperate forest systems.

The apparent paradox of forest fragmentation genetics has been well articulated [21,22,31], yet empirical research in this field has not yet risen to the challenge of resolving this paradox, but continues to draw conclusions on the basis of classic theoretical models that have been found to be inadequate [22]. Our aim here is to inspire a new perspective in forest fragmentation genetics research. We argue that experience gained from empirical research to date should be combined with methodological and theoretical advances made in several related disciplines, which we highlight. Essentially, researchers must move away from the paradigm of small population genetics (Box 1) and redefine fragmented population genetics theory with the mechanism of gene dispersal at its heart. The multidisciplinary approach that we advocate can drive a major advance in the field of forest fragmentation genetics research and help address the problems faced by tree species in a highly anthropogenically altered environment.

Shifting expectations in empirical study design

Tree species maintain high genetic diversity and low genetic structure owing to typically high outcrossing rates and extensive inter- and intra-specific gene flow [3,31]. Trees have a wide range of specific density and are unique in the plant kingdom for reasons that include: (i) they are large in size, which is associated with abundant pollen and seed production and long-distance dispersal in interaction with a large range of pollinators and seed dispersal agents [3,22,31]; and (ii) they are long lived, which is associated with delayed maturity, high recruit mortality and long generation times [3,31]. These distinctive characteristics mean that it is often of limited validity to extrapolate findings from population fragmentation research carried out in model plant species [32–34] and apply them to trees.

However, obtaining evidence of the genetic consequences of habitat fragmentation in natural or experimental tree populations is challenging from the perspective of the experimenter. Forest fragmentation primarily occurs as a consequence of resource exploitation rather than for scientific study. The consequent lack of experimental design can result in the implementation of suboptimal, largely descriptive and idiosyncratic sampling designs, often without the possibility for replication of measurements and comparison with undisturbed conditions. However, examples of better sampling design do exist [24,35,36]. Further difficulties in sampling design occur because,

Table 1. Comparison of experimenter-centred and tree-centred hypothesis testing in forest fragmentation genetics

	Experimenter-centred hypothesis	Tree-centred hypothesis
Population fragmentation	Anthropogenic alteration of the landscape always results in fragmentation of forest tree populations	Depending on the time and spatial scale of habitat disturbance, the historical distribution and life history of the species, populations can be as genetically connected as pre-fragmentation (fragmentation threshold)
Sampling area	Trees separated by a few hundreds of metres or less are adequate to sample reproductively isolated populations	Gene flow in tree species can occur over distances of several tens or hundreds of kilometres
Specific density	Specific density is assumed to be lower in fragmented than in continuous landscapes	Tree species can maintain a scattered habit in continuous landscapes and their specific density might be unchanged by habitat disturbance
Gene flow	Population fragments are genetically isolated from one another	Gene flow among population fragments might be unaffected, decrease or increase depending on the dispersal mode of a species and the characteristics of the intervening landscape
Genetic diversity	Genetic diversity is reduced in a fragmented population compared with that of a continuous population	The quantity and quality of immigrant gene flow relative to local gene movement will ultimately affect the genetic composition of population fragments
Individual fitness	In typically outcrossing species, inbreeding depression will be more pronounced in fragmented populations	Impacts on individual fitness will be determined by the quantity and quality of immigrant gene flow relative to local gene movement in population fragments

when habitat disturbance results in limited gene dispersal, it can take several hundred years for the impact of disturbance to be detected in the genetic structure of forest remnants. Additionally, if gene dispersal remains unchanged or increases as the landscape becomes more open with disturbance [29], or if a change of pollinators occurs [27], then the total reproductive population that should be sampled to estimate accurately population genetics and dispersal parameters will encompass several hundreds to thousands of individuals over an area of several tens to hundreds of kilometres [37].

The ecological characteristics of the tree growth form, which affect the spatiotemporal scale of the impact of habitat fragmentation, have generally been overlooked in sampling designs or in the interpretation of population genetics parameters, thereby fuelling the paradox of forest fragmentation genetics [21]. To address this paradox, refocusing forest fragmentation genetics research on the direct measurement of instant gene dispersal will remove ambiguity from conclusions drawn from empirical studies because the fundamental hypothesis of genetic isolation among forest fragments can be directly tested rather than assumed to be verified (Table 1). Direct measurement of gene dispersal and its interannual variability is informative of both the distance travelled by gene dispersing propagules [38–43] and the composition of dispersed genomes [14,16,44] and can enable forward predictions of evolutionarily stable dispersal and colonisation probability in unoccupied habitats and heterogeneous landscapes [45,46]. It is important that such measurement of gene dispersal is based on the spatiotemporal scale relevant to tree biology, rather than on a scale used for experimental convenience (Table 1 [19,37]).

In addition, the emphasis of empirical studies in forest fragmentation genetic research must be on evaluating the change in gene movement induced by habitat disturbance. To evaluate the appropriate context for change, an explicit assessment of how and which landscape characteristics specifically affect inter-population connectivity [47–49] and how these have changed over time must be made [20]. Such an assessment requires that, at the regional scale, both historical and current species distributions are known, and that at the local scale, specific density and landscape openness are measured comparatively in undisturbed and disturbed landscapes (Figure 1).

The spatial distribution of both conspecific individuals and of individuals of other tree species directly influences the scale and patterns of propagule dispersal and establishment [50–53]. The ecology of individual tree species is a strong determinant of local specific density and regional species distribution. For example, animal-dispersed trees might be less susceptible to impacts of habitat fragmentation, as seeds can be preferentially dispersed to favourable patches [51]. High tree species richness in tropical forests results in a lower specific density and, therefore, low absolute numbers of an individual species that occur in forest fragments [22]. The effective long-distance dispersal and pollination mechanisms that such low-density tree species have evolved renders them more resilient to the genetic impact of habitat disturbance than would be expected based on the change in the spatial distribution of individuals [22,28]. Even in relatively low diversity temperate systems, some tree species, such as the conifer *Taxus baccata* [54], bur oak *Quercus macrocarpa* [55] and *Sorbus* spp. [56–58] naturally occur as small, scattered populations and their specific density, and thus interactions with dispersal vectors,might not be adversely affected by forest fragmentation. Similarly, in established forests, early successional species typically occur for a short duration in forest gaps after disturbance events. Such species, which occur naturally as small and isolated populations or as transient components of a metapopulation [59], might be less susceptible to change owing to disturbance than are their late successional counterparts. The most dramatic change in effective gene dispersal is likely to be detected for species living at high density in continuous landscapes for which habitat disturbance increases the distance between mates [24,29], but the directionality of the change in effective dispersal distance will depend on how disturbance modifies landscape openness and establishment probability [48,60].

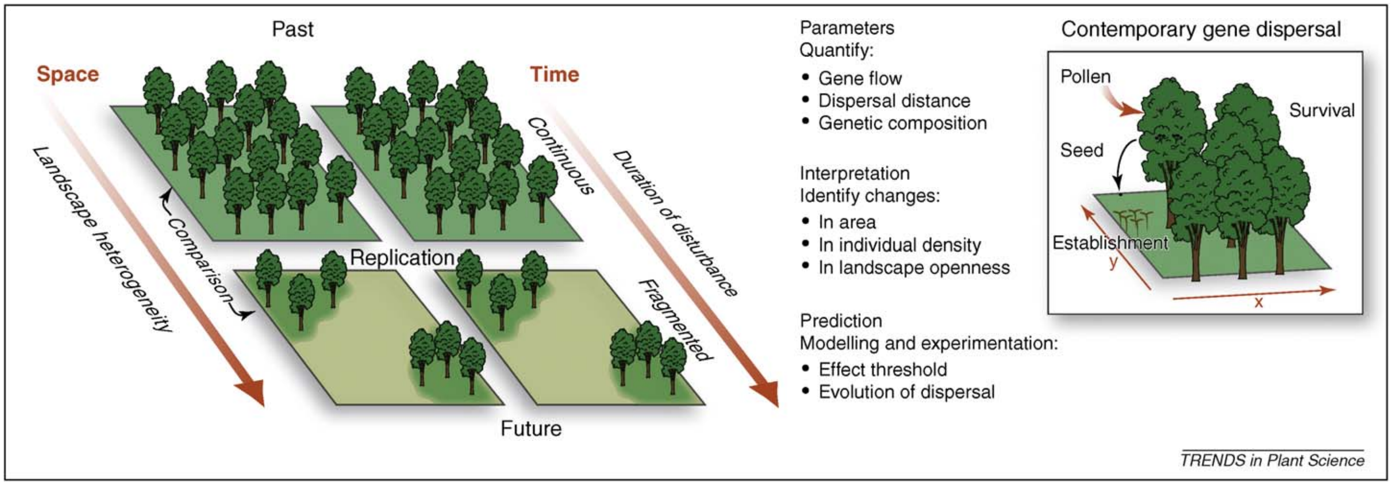


Figure 1. Standardised and comparative empirical study design for research in forest fragmentation genetics. Research should focus on determining how gene dispersal has been altered at the level of the individual by working at the spatial scale relevant to individual species based on their ecology. Such knowledge must involve the characterisation of spatial and temporal changes in tree distribution at the landscape scale through controlled and replicated sampling. Modelling and experimental work integrating distributional changes and dispersal ecology can be applied to identify potential habitat fragmentation thresholds and how changing distributions can alter individual dispersal capabilities through time.

A spatially explicit consideration of specific density and species distribution therefore enables a better characterisation of the nature of habitat disturbance. Community ecology recognises a diversity of processes that are reported under the umbrella of habitat fragmentation, including reduction in habitat area, habitat subdivision, increased habitat isolation and edge:area ratio [61–63], and the occurrence of threshold effects, where diversity initially remains little impacted as habitat fragmentation progresses, but declines suddenly once a certain threshold of fragmentation severity has been reached [63,64]. The importance of the distinction between these processes is generally overlooked in forest fragmentation genetics studies, despite the potential to explain the diversity of responses found to habitat disturbance in these systems. Fragmentation thresholds occur in forest trees partly as a consequence of how decreased population size and increased isolation interacts with pollinator and disperser behaviour [28]. Reduced population size can lead to an increase in the proportion of long-distance pollination events, thereby counteracting impacts of fragmentation. However, if maximum pollinator dispersal distances are exceeded, then long-distance pollination might decline rapidly, leading to a sudden decline in outcrossing and genetic diversity within an isolated population [28].

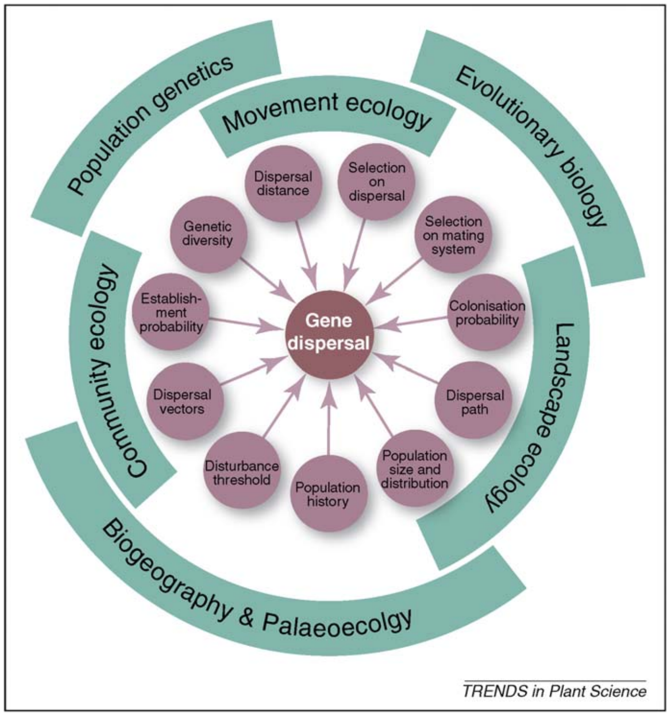
Indeed, a key element to consider is whether the present-day species distribution represents a response to human-induced disturbance or is representative of a long-term historical distribution. Consequently, it is important to determine the magnitude of the change that has occurred at the level of individual species, rather than for the forest as a whole. Integrating population genetics with palaeoecology to determine the extent of historical forest cover and loss can be a first step in hypothesis formation. Furthermore, these fields are advancing toward enabling researchers to determine the genetic composition of tree populations through time [65], which would represent a major breakthrough for those systems where present-day comparisons with undisturbed conditions are not possible. Establishing the picture of how past change in landscape features has affected gene dispersal processes through time not only puts current human-induced disturbance into its historical context, but could also be used to model predictions of future impacts and therefore facilitate decision-making in forest exploitation and conservation [9].

Conclusion and perspectives

As tree species vary widely in their life history [3], responses to habitat fragmentation are understood to be highly species and habitat specific, necessitating a thorough understanding of the ecology and history of a species, before its response can be understood or predicted [51,63]. This highlights that any attempt at drawing general trends from evidence gathered in anecdotal and descriptive empirical field studies is difficult. The current challenge is therefore to standardise the design of empirical studies and to quantify habitat and species variables that can be compared between undisturbed and disturbed landscapes, and between systems, including the explicit quantification of the spatial scale and timing of disturbance (Figure 1).

The argument that a focus on mechanisms that generate patterns is necessary to move away from idiosyncrasy has been made elsewhere, in habitat fragmentation ecology [61] and in organismal movement ecology [12]. Although these are both relevant to forest fragmentation genetics, neither addresses gene movement and its consequences for the preservation of genetic diversity. Authors in these parallel disciplines have argued that lack of communication between disciplines has impeded scientific progress [12,61]. Likewise, we think that forest fragmentation genetics has not benefited from developments in several fields that have individually addressed questions of habitat fragmentation, landscape heterogeneity, tree population genetics and dispersal ecology in isolation (Figure 2).

There is an urgent need to recognise that, if one is to understand how forest resources can be sustainably used, conserved and restored in a changing environment, a multidisciplinary approach must be adopted in large-scale comparative studies to draw up general principles and



TRENDS in Plant Science

Figure 2. A multidisciplinary framework for forest fragmentation genetics research. The refocusing of forest fragmentation research would investigate changes in gene dispersal rather than assuming such impacts based on changes in forest distribution. A multidisciplinary approach integrating components of gene dispersal (circles) derived from a range of related fields (arcs) can be exploited to determine how gene dispersal is likely to be impacted by changes in tree distribution as a consequence of forest fragmentation.

redefine forest fragmentation genetics around the actual dynamic processes that are affected by disturbance.

Acknowledgments

This work was partly funded under ERA-net BiodivERsA project: Beech Forests for the Future, via Natural Environment Research Council (NERC) grant NE/G002118/1 to A.S.J. and NERC grant NE/H012435/1: Restoration genetics of degraded forest landscapes: Land management and evolution of reproductive strategies in keystone tree species to C.F.E.B. We thank Bill Jamieson for preparing Figures 1 and 2.

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