

Article (refereed) - postprint

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This is a pre-copy-editing, author-produced PDF of an article accepted for publication in *Forestry* following peer review. The definitive publisher-authenticated version *Forestry* (2015), 88 (1). 13-26. [10.1093/forestry/cpu027](http://www.oxfordjournals.org/10.1093/forestry/cpu027) is available online at: <http://www.oxfordjournals.org/>

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1 **Title: The basis of resilience in forest tree species and its use in adaptive forest management in**
2 **Britain.**

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12 **Keywords:** Resilience, forests, genetic diversity, gene flow

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14 **Running head:** Resilience in adaptive forest management

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45 17 **Abstract:**
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7 18 Forest ecosystems face a range of challenges in the coming decades, of which climate change, pests
8 19 and diseases are the most serious. These challenges will be overlaid on a background of historically
9 20 modified and fragmented forests managed in a wide range of ways for different objectives. As
10 21 northern temperate forests are species-poor in a global context, their resilience to these challenges
11 22 is fundamentally dependent on the resilience of individual species. However, dealing with each new
12 23 threat as it arises is unlikely to be cost effective and in any case, probably not practically feasible. A
13 24 better strategy for establishing long term resilience would be to harness evolutionary processes, to
14 25 maximise the capability of individual tree species to respond to new threats by the reorganisation of
15 26 populations via natural selection; in other words, to be resilient. Such processes depend on the
16 27 internal variability of species, their mechanisms of dispersal and their ability to recruit new
17 28 genotypes to a population. In this paper we review the theoretical concept of resilience, examine
18 29 how it might be applied to tree populations and assess the state of knowledge of Britain's forests
19 30 from this perspective.
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32 Introduction

33 Britain's forest genetic resources are currently facing an unprecedented period of uncertainty
34 due to the effects of climate change and increased exposure to new pests and diseases from
35 global trade. Rather than tackle each new threat as it arises, it would be much more cost
36 effective to manage forests to promote their resilience, allowing them to change and adapt to
37 new pressures. In this paper, we discuss the theory that underpins the concept of resilience in
38 general and then focus on the implications for British forest ecosystems in particular. As
39 individual forest ecosystems in Britain contain relatively few tree species, we outline the
40 important role of intra-specific genetic diversity in conferring resilience via evolutionary
41 processes and discuss the major drivers of these processes. Finally, we outline the current policy
42 and practice for managing the British forest genetic resource and discuss the conflicts and
43 tensions in developing appropriate policy in the face of an uncertain future.

45 Major challenges facing British forests today

46 The forest estate is a vital provider of ecosystem services in Britain (for details of its composition
47 and management history see Text box 1). However it faces major challenges from climate
48 change and various native and exotic pests and diseases. In particular, it is the uncertainty in
49 predicting the nature and impacts of these threats that is hampering efforts to plan mitigation.

50 The threats from climate change and new pests or diseases have important parallels in the
51 policies needed to address them. Despite a huge amount of modeling aimed at predicting the
52 likely pattern, speed and intensity of climate change, there is still great uncertainty in forecasts
53 of the magnitude of change at specific locations and the ability of our forest resources to cope
54 with them. Similarly, whilst many new pests and diseases have been identified as present in
55 Britain, perhaps the greater threat lies in those that are present but have not yet been
56 identified, and those that have yet to arrive. Worldwide, it is estimated that there are at least 28
57 recognised pests and diseases that could cause substantial devastation to British trees if they
58 gained entry to Britain (Tree Health and Plant Biosecurity Expert Taskforce, 2013). There are
59 numerous examples where introduced pathogens have led to mass destruction of tree species
60 elsewhere in the world, e.g. chestnut blight and white pine blister rust in North America. In
61 addition, climate change may increase the threat from pest and diseases. This interaction could
62 operate in several ways, including:

- 63 i. increasing maladaptation. Trees which are stressed are more likely to succumb to both
64 native and introduced pests and diseases.
- 65 ii. altered balance between tree host and existing pests and diseases. For example, rising
66 temperatures may affect the synchrony between herbivore emergence and bud burst; milder
67 winters may increase the numbers of *Elatobium* on spruce crops (Broadmeadow *et al.*, 2005).
- 68 iii. novel climates cause species that were not previously damaging to develop into threats, or
69 facilitate the establishment of new species from warmer countries. For example, European
70 Spruce Bark beetle is considered a high risk for arrival and establishment in Britain under
71 warmer conditions.

73 **Multiple consequences of introduced pests and pathogens**

74 The British forest estate provides a wide range of ecological, economic, amenity and aesthetic
75 benefits. Consequently, damage from introduced pathogens could have wide ranging
76 consequences. In the case of the current high-profile threat from ash dieback, Worrell (2013)
77 identified several likely impacts, including:

- 78 • loss of ash in woodland especially as a timber tree component of native woods, a specialist
79 species in gap replacement and in riparian woods.
- 80 • reduction in biodiversity such as lichens, mosses/liverworts, fungi and invertebrates,
81 damage to designated sites, veteran trees and wood pastures.
- 82 • economic costs incurred in felling and replacement of diseased trees, felling for safety
83 reasons and short term losses to nursery trade.
- 84 • landscape and social impacts due to loss of individual trees along road sides and field
85 margins, in woods heavily used by the public and in urban situations.

86 Similar consequences are likely to arise from introduction of pests and diseases with major
87 impacts on any of the major tree species grown in Britain. In addition, longer term effects are
88 also likely due to the alteration of forest ecosystems through changes in the keystone tree
89 species and erosion of the size and diversity of standing tree populations.

91 **A need for resilience**

92 Recently, attention has begun to focus on identifying and quantifying ways to bolster the
93 resilience of ecosystems, in a move from prevention to mitigation of disturbances such as
94 climate change. Now that both climate change and globalised trade are realities, there is a need
95 to find ways to ensure the persistence of essential ecosystems in the face of new conditions, in
96 other words to maximize their potential to adapt to a changed environment. This concept of
97 resilience has been widely taken up by British policymakers as evidenced by use of the term in
98 several high level policy documents, including the UK's Tree Health Action Plan (DEFRA, 2011a)
99 and Biodiversity 2020: A strategy for England's wildlife and ecosystem services (DEFRA, 2011b) .
100 The Report of the Independent Panel on Forestry (Independent Panel on Forestry, 2012),
101 commissioned to advise government on the future direction of forestry and woodland policy in
102 England, contains no fewer than 21 mentions of resilience. However, the general enthusiasm for
103 the term masks considerable complexity; although its meaning is apparently easily grasped
104 there are a number of difficulties in reaching precise, operational definitions, including
105 quantifying when a system has resilience, to what pressures, and how success can be measured
106 in efforts to achieve it. All of these aspects are difficult to measure and, even where clear
107 negative effects are expected, results have, on occasions, been counterintuitive. For example,
108 some systems have shown unexpected resilience even in the face of pressures that had been
109 expected to cause ecosystem change (Bestelmeyer *et al.*, 2013; Ponce Campos *et al.*, 2013). The
110 policy shift towards resilience appears to be emerging from a combination of increasingly visible
111 change and the lack of progress in international efforts to address these issues. Therefore, to
112 find ways to meet policy goals and to ensure the long-term persistence of the ecosystems we

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3 113 value, it is essential to reach a working understanding of what resilience means and how it can
4 114 be optimised via appropriate management.
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7 115 **Resilience in theory**

8 116 Resilience is defined as the extent of perturbation that a system can experience before it
9 117 undergoes a shift to an alternative state (Holling, 1973; Scheffer *et al.*, 2001) or, more subtly,
10 118 “the capacity of a system to reorganize whilst undergoing change so as to retain the same
11 119 function, structure, identity and feedbacks” (Folke *et al.*, 2004). In Biodiversity 2020, DEFRA
12 120 chose to define resilience of an ecological network as its “capability to absorb, resist or recover
13 121 from disturbances and damage...while continuing to meet its overall objectives of supporting
14 122 biodiversity and providing ecosystem services“. These concepts of resilience developed
15 123 (originally from engineering theory) for the purposes of predicting how and when systems shift
16 124 from one stable state to another and are perhaps most advanced in the study of lakes, where
17 125 the essentially closed nature of the system makes them more amenable to model development.
18 126 In this context it has been possible to identify alternative possible stable states, tipping points
19 127 (and the associated warning signals (Dai *et al.*, 2012; Veraart *et al.*, 2012)) beyond which
20 128 capacity for resilience is exceeded, and consequently to develop strategies for restoring the
21 129 original state (although this is often complicated by hysteresis, where forward and reverse
22 130 tipping points occur at different levels of pressure, such that restoring the original state is not
23 131 simply a case of reversing the initial disturbance (Cote and Darling, 2010)).

24 132 A key element in resilience theory is the relationship between diversity and resilience. Although
25 133 positive relationships have been shown between biodiversity and stability of ecosystem function
26 134 (Laliberte *et al.*, 2010), in theory it is the functional redundancy associated with higher diversity
27 135 that confers stability. However, measuring the extent of functional redundancy is difficult and
28 136 this becomes more complicated when applied to heterogeneous environments, where
29 137 functional roles may alter with context (Wellnitz and LeRoy Poff, 2001). Furthermore, depending
30 138 on whether ecosystem resilience (resilience of the ecosystem as a whole) or species resilience
31 139 (the resilience of individual species) is being considered, stability may depend on either species
32 140 diversity or intra-specific genetic diversity respectively, and the processes governing their
33 141 maintenance (for definitions of genetic terms see Text box 2). This distinction is critical and
34 142 encompasses a range of important questions that must be addressed if resilience as a quality is
35 143 to be successfully targeted. For example, for a particular forest, if ecosystem resilience is the
36 144 focus (preserving delivery of an ecosystem service such as watershed protection), then the
37 145 species composition of that forest might be allowed to change, as the service provision would
38 146 nevertheless be maintained. Then, if one tree species within that forest becomes the focus of a
39 147 severe threat, it might best be managed by complete removal of that species and replacement
40 148 with an alternative species or with natural recruitment. In contrast, if the forest type is
41 149 important, for example if it is a UK BAP Priority Habitat, then the resilience of particular tree
42 150 species within that woodland is essential. Exposure of that key species to severe threat risks the
43 151 delivery of the ecosystem service, and the internal diversity of the species consequently
44 152 becomes important.

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47 153 Direct evidence for the relationship between diversity and resilience is typically experimental,
48 154 but has been shown – for ecosystem resilience - in many systems (Norden *et al.*, 2009; Batt *et*

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3 155 *al.*, 2013; McGovern, 2013; Prober *et al.*, 2013). However, in the case of single species resilience,
4 156 the evidence base is much poorer, with well-cited studies of eelgrass (Reusch *et al.*, 2005) and
5 157 model organisms (yeast (Bell and Gonzalez, 2009); *Drosophila* (Bakker *et al.*, 2010), *Daphnia*
6 158 (*Latta et al.*, 2010)) providing the best demonstrations. Such studies indicate that the level of
7 159 intra-specific genetic diversity, the integrity of gene flow mechanisms and population size all
8 160 play key roles in delivering the potential for 'evolutionary rescue'. The mechanism of
9 161 evolutionary rescue involves initial population decline followed by recovery as genotypes
10 162 adapted to the new conditions prosper via natural selection. In this context, the integrity of
11 163 demographic cycling is critical, with the gradual loss of standing generations and intact
12 164 reproductive and recruitment processes allowing the establishment of new, better-adapted
13 165 generations. The latter is likely to be a major factor in extending experimental work from model
14 166 species to larger, longer-lived organisms.

19 167 **Resilience in British forest ecosystems**

20 168 In most forest ecosystems, tree species are likely to act as 'drivers' (Walker, 1992), as they have
21 169 a role which is critical to the functioning of the ecosystem. This is especially true of northern
22 170 temperate forests which are typically species-poor or dominated by one or a few species. In
23 171 some cases, successional processes will play a role in response to pressure and a 'forest'
24 172 ecosystem may be maintained whilst its character changes, e.g. where a mature tree species in
25 173 a forest is eliminated by a species-specific pathogen, the gaps may be filled by early-successional
26 174 species, maintaining the forest whilst its composition changes. In this case of apparent
27 175 ecosystem resilience, significant rearrangement of community interactions will nevertheless
28 176 take place and although a forest ecosystem is maintained, much of the associated biodiversity
29 177 and ecosystem processes may not be. Whether this is an acceptable result will depend greatly
30 178 on the management objectives of the forest concerned, and in any case represents a shift from
31 179 one state to another and should properly be considered moving beyond resilience boundaries.

32 180 Where successional change would result in an unacceptable loss of function in a forest
33 181 ecosystem, resilience necessarily depends on the persistence of tree species. Therefore
34 182 resilience of the ecosystem is unavoidably dependent on species resilience and on intra-specific
35 183 genetic diversity, gene flow and generational turnover (Figure 1).

36 184 Conservation of genetic diversity and the processes that maintain it have been considered to be
37 185 a sensible insurance against future threats for almost as long as genetic diversity has been
38 186 recognised (Ledig, 1986; Eriksson *et al.*, 1993; Koskela *et al.*, 2013; Lefevre *et al.*, 2013a; Lefevre
39 187 *et al.*, 2013b). Trees generally maintain high levels of intra-specific genetic diversity and are
40 188 usually effective at gene dispersal, especially the wind-pollinated species characteristic of
41 189 northern temperate forests. Hence, studies that examine the partitioning of neutral genetic
42 190 variation in tree species most often find the majority of variation is present within populations,
43 191 with a much smaller component due to differences between them. At the same time, adaptive
44 192 genetic variation occurs - adaptation to local environments has been demonstrated in many
45 193 tree species (Savolainen *et al.*, 2007) although the degree and geographic scale over which it is
46 194 distributed may vary depending on the heterogeneity of the landscape conditions, the character
47 195 being measured and the species under investigation. In tree species, phenotypic traits often
48 196 show high heritability, an indication that they have considerable evolutionary potential. In

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3 197 combination these factors – high intra-specific genetic variation, effective gene dispersal and
4 198 heritable adaptive traits indicate that trees should have considerable potential to evolve in
5 199 response to new selective pressures (Alberto *et al.*, 2013). Therefore, in practice, barriers to
6 200 adaptive change in tree populations are likely to be due to disruptions of generational turnover
7 201 (e.g. through overgrazing of seedlings, prevention of fires, loss of habitat), rather than to any
8 202 inherent lack of evolutionary capacity.

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11 203 In consideration of adaptive processes in forest trees, much is typically made of their long
12 204 generation times, yet in many forests generational turnover can be managed and recruitment
13 205 promoted to ensure rapid immigration of best-adapted genotypes (Savolainen *et al.*, 2007). The
14 206 increased frequency of disturbance that is commonly forecast to be an outcome of climate
15 207 change may in fact create opportunities for recruitment of new genotypes to populations and
16 208 act to promote evolutionary change. However, it is likely that in most cases, some direct
17 209 intervention to ensure that turnover is happening successfully, such as gap creation or
18 210 management of local grazing, will also be necessary.

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21 211 In commercial situations, an analogy to the high diversity seen in natural forests could be
22 212 achieved by designing forested landscapes in blocks that vary in their composition, of either
23 213 species diversity or intra-specific genetic diversity, or both. Such an approach might attempt to
24 214 take advantage of distinct genotypes that have different qualities or could seek to make a
25 215 landscape less permeable to transmission of a threat by using variation in diversity as a barrier.
26 216 The latter would have to take into account information on the mode and scale of dispersal
27 217 mechanisms in the threat species. In commercial forestry, as in other agricultural markets, there
28 218 is a pressure to minimize variation in the crop to facilitate processing. Whilst increased diversity
29 219 may spread the risk and improve the probability of a crop reaching maturity without suffering
30 220 negative impacts from threats, it also acts in direct opposition to the need to deliver a product
31 221 of consistent quality. The optimal trade-off between homogeneity of product and diversity as a
32 222 hedge against loss will depend strongly on the risk factors associated with the primary threats to
33 223 a species and with the length of rotational cycle. If risk of loss is low enough over the period of
34 224 the rotation to outweigh losses incurred through product quality reduction due to variability,
35 225 then raised diversity may not be commercially attractive. However, the potential impacts on the
36 226 wider landscape of facilitation of dispersal of a threat should also be taken into account in
37 227 designing policy options to promote resilience.

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40 228 A further consideration for forest trees is how to assess when resilience has been achieved (and
41 229 if it can be). In British forests, which have established post-glacially and have since experienced
42 230 substantial change, it may be the case that a stable state as envisaged under resilience theory
43 231 has never been reached. Instead, the ‘stable’ state as experienced by tree species may be one of
44 232 constant environmental variability (considering, for example, that the comparison between the
45 233 environment experienced at germination and that at full maturity may span 500 years in species
46 234 such as oak). Therefore this stable state is underpinned by a large amount of individual plasticity
47 235 and internal population variability. In Britain, human influence over centuries has eroded the
48 236 size of national tree populations and some species probably face considerable risk of local
49 237 extinctions. A realistic goal for giving tree species the best chance of longer term resilience is
50 238 probably to seek to achieve a minimum threshold of diversity, maximize population sizes,

239 encourage the production of regular cohorts of natural regeneration, use locally-adapted seed
240 sources and expose planting stock to natural selection wherever possible. To establish a
241 knowledge base for making informed decisions, there are two clear priorities to lay a baseline
242 for assessment. Firstly, experimental work must be undertaken to test the extent to which intra-
243 specific genetic diversity might underpin stability. This should encompass testing of multiple
244 genotypes, but also multiple pressures, for example looking at pathogen tolerance under
245 different environmental regimes. Secondly, an effort to standardize and synthesize knowledge
246 on existing diversity in trees in the British landscape should be made, encompassing both
247 molecular and phenotypic variation. Numerous studies have incorporated multiple populations
248 from Britain and a few have sampled extensively within Britain, but so far the efforts have been
249 independent and remain uncollated.

250 **When can managed evolution be effective?**

251 Assuming that tree species maintain significant capacity for evolutionary responses to new
252 pressures and allowing that this may even be possible within reasonably short timescales, the
253 action taken to counter any new threat will vary depending on, amongst other things, the
254 severity of the threat and the speed with which that threat can spread. For example, a disease
255 that quickly kills a high proportion of a tree population, and has the ability to disperse rapidly
256 over considerable distances, would not be an appropriate candidate for the application of a
257 managed evolutionary approach. Clearly in this case the high proportion of dead trees and their
258 presence as a source for long distance spread of infection would be publicly unacceptable and
259 therefore physical prevention and / or species replacement is likely to be necessary. In contrast,
260 if the disease killed only a low proportion of trees leaving many affected but alive, and moved
261 only short distances, or within a particular environmental niche, then managed evolution has
262 time to be effective and should be considered. Between these extremes lie tipping points for
263 choosing different actions that depend on factors including host ecology, density & rate of
264 regeneration; characteristics of the threat organism; role of the tree species in the landscape
265 and so on (Figure 2). Furthermore, the needs of forest stakeholders also have to be taken into
266 account, for example to assess whether they might accept the temporary decline of a tree
267 population, if there was a reasonable chance of subsequent recovery via regeneration of more
268 resistant genotypes.

269 To allow a decision making framework to be developed, which lets forest policymakers identify
270 the most appropriate option for specific situations, a minimum set of parameters could be
271 defined. These would characterize the host species, its ecology, distribution and diversity; those
272 of the threat organism(s) and likely future environments. Model-based testing could then be
273 used, firstly to evaluate potential evolutionary rates in tree populations, taking into account
274 genetic diversity, adaptive potential and variations in demographic turnover and secondly, to
275 explore and prioritise different management scenarios, using both idealized populations and
276 spatially explicit simulations reflecting the known distribution of species in the British landscape.

277 **State of knowledge of genetic diversity in UK tree species**

278 A substantial amount of data already exists on intra-specific genetic variation in several
279 important British trees (Text box 3, Table 1). This is true in particular for species important in

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3 280 forestry or agriculture such as fruit trees, oak, Scots pine, ash and Sitka spruce. However in most
4 281 cases, as most British tree species have distributions that extend to mainland Europe, studies of
5 282 genetic variation have been carried out across a broad geographic scale such that resolution
6 283 within the different regions of Britain is poor. Whilst it is important to have the wider context,
7 284 the lack of fine-grained information for species in Britain is a clear knowledge gap.

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10 285 For the purposes of assessing potential evolutionary responses to emerging threats, it is also
11 286 important to be clear about the distinction between different types of data on genetic variation.
12 287 Genetic variation can either be assessed by measuring the phenotype (the set of observable
13 288 characteristics that includes morphology, phenology and physiology) or by directly
14 289 characterizing variation in DNA or closely associated molecules.

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16 290 As the phenotype is a product of both genes and the environment, the genetic component of
17 291 phenotypic variation must be extracted by accounting for environmental variation either
18 292 through experiments that control environmental variation or by statistical approaches using
19 293 data on environmental differences among sites (e.g. Phillimore *et al.* (2013)). Phenotypic data,
20 294 when obtained from controlled experiments or trials, in which plants originating from different
21 295 geographic sources are grown together, provide information on the genetic component of
22 296 variation in traits experiencing selection. Such experiments assume populations are adapted to
23 297 the local environments in which they grow. Unfortunately, the majority of these trials were
24 298 designed to examine the adaptive differences between provenances. Consequently, the identity
25 299 of seed lots from different mother trees was not maintained which prevents the heritability of
26 300 the recorded traits from being estimated. In addition, the extent to which the phenotype can be
27 301 characterised in tree trials is limited due to the expensive and time-consuming nature of taking
28 302 measurements on large numbers of individuals, and to the production-focused objectives of
29 303 most trials. Height, form and diameter are often the only traits measured and other traits of
30 304 importance in conferring resilience are not assessed. However the restricted number of well
31 305 designed trials at the appropriate scale that exist offer an important resource for the future;
32 306 more detailed assessments of phenotype and the development of high-throughput methods
33 307 (e.g. (Salmela *et al.*, 2011)) for gathering such data from these trials should be a priority.

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36 308 A critical part of making new fast-phenotyping measures effective will be to determine what the
37 309 significant selective forces are that drive local adaptation and in identifying those traits that
38 310 reflect the effects of these pressures. Furthermore, the situation is likely to be complex as suites
39 311 of different pressures and traits may be involved in local adaptation. For example, a tree species
40 312 might adapt to local climatic factors (such as temperature, rainfall, growing season length), or to
41 313 local biotic factors (such as pathogen presence, beneficial symbionts, or competition from other
42 314 tree species (Iason *et al.*, In review)) and hence may show adaptive divergence in traits such as
43 315 drought tolerance, pathogen resistance or timing of growth. For threats arising from new pests
44 316 or pathogens, resilience is likely to derive from resistance traits. However, resistance may be
45 317 inherent or may result from better adaptation to local growing conditions (lack of stress)
46 318 (Telford *et al.*, In review). Although resistance may be measured as a quantitative trait (Ennos, In
47 319 review), understanding the basis of resistance is likely to be necessary to develop meaningful
48 320 applications. Overall, the best approach is likely to involve characterization of the phenotype by
49 321 measurement of as many traits as possible.

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3 322 Molecular or other marker data provide a different sort of information. Most mutations at the
4 323 molecular level have little or no effect on the phenotype, so they are not subject to selection
5 324 (are 'selectively neutral'). As such they do not provide information about adaptive processes or
6 325 that part of genetic diversity exposed to selection. However, they are useful in guiding the
7 326 management and conservation of genetic resources as they can provide a measure of genetic
8 327 diversity, can identify differentiated groups, and inform on prioritization of populations for
9 328 protection. In addition, neutral data provide important information about historical and
10 329 contemporary population processes, about migrations and population size changes, about how
11 330 genes move in the landscape and over what spatial and temporal scales, and about how
12 331 reproduction occurs. All of these are essential to understanding the rate at which species might
13 332 be capable of responding to new pressures, and can be built into models to explore how
14 333 populations are likely to respond.

15 334 Ultimately, a key aim of evolutionary biology is to link molecular genetic data directly to
16 335 phenotypic data in order to understand the genetic basis of adaptive variation. Rapid progress
17 336 has been made in the rate at which genomic data can be gathered, to the extent that calls have
18 337 been made to increase the collection of corresponding phenotypic datasets, to prevent this
19 338 becoming a barrier to progress (Neale and Kremer, 2011). This is clearly an issue for pest or
20 339 disease resistance in trees, where appropriately designed large scale trials do not exist to
21 340 underpin and maximize the impact of advanced genomic approaches. Furthermore, even with
22 341 next-generation sequencing technology, the capability to genotype large numbers of trees
23 342 currently remains expensive and utilizing the data is heavily reliant on bioinformatic processing
24 343 where lack of expertise can lead to slow and inefficient progress. Whilst the prospects are highly
25 344 promising, for rapid progress it may be prudent to take advantage of existing resources to
26 345 deliver early results.

27 346 As an example, for the principal native species identified as suffering (or likely to suffer
28 347 imminently) from new pests or diseases on DEFRA's tree health action plan, a range of data or
29 348 trial resources exist (Table 1). However, even for this limited set of important UK tree species,
30 349 data are lacking on basic distribution of genetic diversity, genetic structure and gene flow. Lack
31 350 of trials or inappropriate design or scale of trials prevents the acquisition of information on
32 351 patterns of adaptive variation in even basic traits and more specifically, on key traits for
33 352 resistance, their heritability, and variation in expression with environment. Coordinated
34 353 collection of existing datasets should be a priority, particularly for those species as yet
35 354 unaffected but with imminent serious threats. In the latter cases, sufficient time may still be
36 355 available to adjust planting and management practice to minimize the impact of the arrival of
37 356 new problems.

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39 358 **Current policy and practice for management of British forests**

40 359 British forests exist in a variety of forms ranging from woodlands where conservation is the
41 360 major objective to single-species plantations managed almost exclusively for timber production.
42 361 A sizeable proportion of our forests lie somewhere in between these two extremes and consist
43 362 of a limited number of native species managed for a range of objectives.

44 363 i.) Woodlands of high conservation importance

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3 364 These woodlands include remnant Caledonian Scots pine forests, Atlantic hazel and oakwoods
4 365 and montane willows which are all important in terms of conservation. The management
5 366 objective here is to maintain their genetic integrity and to provide the opportunity for
6 367 continuous dynamic evolution and adaptation and therefore natural regeneration is
7 368 recommended in preference to planting wherever practicable (Anon, 2003). This provides a
8 369 regular supply of new generations of trees, a process which can be encouraged by creation of
9 370 clearings and control of herbivores.

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12 371 ii.) Existing and new native species woodlands with multiple objectives

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14 372 Both the Helsinki guidelines (MCPFE, 1993) and the UK Forestry Standard (Forestry Commission,
15 373 2011) recommend the use of local stock for planting of native species, especially in existing and
16 374 new native woodlands. These guidelines take a precautionary approach and are based on the
17 375 principle that locally sourced planting stock is likely to represent the best adapted material
18 376 available for a site under current conditions. Despite these guidelines, surveys carried out within
19 377 the last 10 years (Russell and Evans, 2003; Buckley and Blakesley, 2008) showed that of the 60
20 378 million broadleaved plants sold in Britain in 1999, up to 50% came from abroad and 80-90% of
21 379 the non-British material was sourced from non-maritime climates. The main sources of the
22 380 imported plants were the Netherlands, Hungary and Germany but 27% of the imported plants
23 381 came from Eastern Europe and were likely to be very poorly adapted to British conditions.

24 382 Due to increasing labour costs and lack of investment in mechanization in nurseries in Britain,
25 383 there has been a trend for nurseries to send British native seed to be raised on the continent
26 384 where costs are lower and growing conditions are more favourable. Such practice increases the
27 385 risk of introduction of pests and disease.

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32 386 In an attempt to guide the choice of appropriate planting stock and to provide an administrative
33 387 structure on which to base recommendations for sourcing of planting stock, the Forestry
34 388 Commission (FC) established a framework for tracking those sources of seed and planting
35 389 material that are subject to the Forest Reproductive Material Regulations. This framework
36 390 consists of four EU-recognised Regions of Provenance (RoP) which are further sub-divided into
37 391 24 voluntary Native Seed Zones (NSZ) identified on the basis of information about their climatic
38 392 and geological variation. The NSZs are further sub-divided into above and below 300 meters
39 393 (Herbert *et al.*, 1999).

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43 394 However, despite recommendations that integrated, pan-European approaches should be
44 395 adopted for the management of forest genetic resources (Koskela *et al.*, 2013), FC England and
45 396 FC Scotland have diverged in the advice on the sourcing of planting stock since concerns about
46 397 climate change have increased.

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48 398 England, which is predicted to experience the most severe effects of climate change, advises
49 399 that the option of matching a proportion of the planting stock to predicted future climate
50 400 should be considered (Anon, 2010; Ray *et al.*, 2010). Current advice from FC England for
51 401 management of ancient and native woods recommends that at least one third of the planting
52 402 stock should continue to be sourced locally but the inclusion of some planting stock from a
53 403 more southerly provenance should be considered. They suggest that sourcing such material
54 404 from 2-5 degrees of latitude further south than the site is a useful rule of thumb. Eastern

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3 405 European sources should generally be avoided as they have proved unsuited to English
4 406 conditions.

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6 407 This could result in the planting of material from as far south as Central France in England. Such
7 408 a strategy assumes that sites in England lack the adaptive capacity to cope with climate change
8 409 which is not necessarily the case when the high adaptive diversity of British populations and
9 410 long distance gene flow are taken into account. Provenances from further south might well be
11 411 adapted to the warmer conditions predicted under climate change but they are not necessarily
12 412 well adapted to other conditions at the British sites and this might only result in exchanging one
13 413 type of maladaptation risk for another. In addition, irrespective of future conditions at the
14 414 English sites, the French material will not be adapted to the current British conditions and thus
15 415 may be more at risk to succumbing to existing pests and pathogens with which they have not
16 416 co-evolved, especially if they are maladapted to current English conditions. The associated risk
17 417 of introducing novel pests and diseases should also be considering when adopting this strategy
18 418 and seeds from these sources should be raised in local English nurseries.

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21 419 In contrast, FC Scotland, continues to recommend the use of locally sourced planting stock
22 420 (Anon, 2006), on the assumption that populations contain sufficient adaptive capacity for them
23 421 to evolve to cope with the effects of climate change in Scotland where the effects of climate
24 422 change are predicted to be less severe than in England. However, in practice there have been
25 423 problems associated with this approach in the form of low availability of locally sourced seed
26 424 and planting stock. The reasons for this are attributable to poor availability of Scottish seed
27 425 sources, lack of knowledge of where the seed sources occur, erratic seed cropping due to
28 426 seasonality or low seed production in certain species, and seed predation by squirrels and birds.
29 427 FC Scotland has appointed Seed Liaison Officers whose remit is to identify good seed sources,
30 428 communicate with suppliers and planters, monitor populations for good mast years and advise
31 429 on management for good seed production. Difficulties in obtaining locally sourced materials can
32 430 delay planting schemes.

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36 431 The FC Woodland Grant Scheme is managed by FC Woodland Officers who practice discretion in
37 432 their adherence to recommendations for local sourcing of planting material – an overly strict
38 433 approach can lead to delays in planting whereas an overly relaxed attitude can lead to the use of
39 434 maladapted material. Forest owners who elect not to source grant support for their planting are
40 435 free to make their own decisions regarding source of planting material.

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44 436 In Britain, forest nurseries are often small scale family run businesses and few of these, at the
45 437 time of the (Russell and Evans, 2003) survey, operated at a national scale or were able to offer a
46 438 wide range of origins for any particular tree or shrub species. However, the situation may have
47 439 improved somewhat since then. FC Scotland is also improving its long term planning to provide
48 440 nurseries with a better idea of future requirements. Strenuous efforts should be made to ensure
49 441 that seed are raised in British nurseries and not sent to the more highly mechanized nurseries
50 442 abroad (e.g. the Netherlands) to be raised as this increases the threat of pest and disease
51 443 introduction. The Scottish Tree Health Advisory Group is currently in discussions with
52 444 stakeholders and nurseries to identify sources of problems in the seed and plant supply chain.

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56 445 Good seed collection practice is important in ensuring that as much as possible of the genetic
57 446 diversity available in a stand is captured in the seed collection. However, this is not always the

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3 447 case in practice, e.g. (Kettle, 2001) found that locally sourced planting material used in a
4 448 restoration site in the Scottish Borders had low genetic diversity and he attributed this to poor
5 449 collection practices. Current FC advice for seed collection (Herbert *et al.*, 1999) is as follows:

- 7 450 • Collect from defined populations of interbreeding individuals of the required
8 451 species
- 10 452 • Do not select trees with particular characteristics, and sample to reflect the range of
11 453 growth and morphological diversity present in the population
- 13 454 • If possible, collect from trees that are isolated from non-native sources of the same
14 455 species
- 16 456 • Collect from at least 20-30 individuals, harvesting a similar quantity of seed from
17 457 each tree
- 18 458 • Collect from trees that are at least 50 meters apart.
- 20 459 • Following extraction ensure that the seedlot is thoroughly mixed, especially when
21 460 the seedlot is divided and sent to several different growers.

23 461 In order to assess the appropriateness of these different strategies a better understanding of
24 462 the scale of adaptive capacity in British provenances is required. This demands the
25 463 establishment of native species provenance trials based both at British sites and in sites which
26 464 currently experience the climate that Britain is predicted to experience in the future. This would
27 465 clarify whether British provenances have the adaptive capacity to cope with warmer conditions.

29 466 iii.) Commercial plantations for timber production.

31 467 As with natural woodlands, species diversity and within-species adaptive variation are
32 468 important in conferring resilience on our plantation forests. However, this has to be balanced
33 469 against the requirement for high yield and a uniform timber product for the saw mills. A
34 470 common theme amongst processors is the need for uniformity and it is well known that clonal
35 471 forestry can provide a dramatic increase in both forest productivity and product uniformity
36 472 (Park (2002) and Table 2)). In Britain, our main timber species is Sitka spruce, an introduced
37 473 species from the Pacific Northwest. It is usually grown in large, single age monoculture stands
38 474 where the production of timber of construction strength is the primary objective. The breeding
39 475 programme started in the early 1960s with the genetic testing of 1800 plus trees followed by
40 476 the establishment of seed orchards consisting of 40 superior genotypes in intimate mixtures.
41 477 The seed harvested from these seed orchards are raised entirely within Britain to provide bare
42 478 rooted seedlings for planting. However, since the early 1990s there has been a move to provide
43 479 nurseries with seed produced via controlled pollination between highly selected parents. Until
44 480 recently, most of the seed produced by this means was made available as a mix of seed
45 481 collected from about 20 maternal trees which had been pollinated by a mixture of pollen from
46 482 15-20 unrelated, but highly selected fathers (diverse family mixtures). Seed produced in this way
47 483 was likely to have similar levels of diversity to that derived from the seed orchards which in turn,
48 484 are likely to be at least as diverse as the unimproved material collected in Canada or USA. This
49 485 is because breeders ensure that the parents in a seed orchard or a family mixture are unrelated
50 486 whereas the number of seed trees involved in a collection abroad is often unknown and there is
51 487 a risk that it might be rather narrow. The seed derived from controlled pollination was

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3 488 expensive to produce and was therefore grown into 'donor' stock plants from which large
4 489 numbers of cuttings were raised. More recently, the 'diverse family mixture' seed have been
5 490 replaced by 'full-sibling families' which have a single known male and female tested parent. The
6 491 advantages over the more genetically diverse family mixtures are the more uniform crop and
7 492 superior timber yield. However, these advantages have to be considered against the increased
8 493 risk associated with the reduction in diversity which is a consequence of this approach.
9 494 Improvements in somatic embryogenesis and cryopreservation will soon offer the opportunity
10 495 to produce vast numbers of individuals from a single seed and therefore, as we are at the
11 496 threshold of clonal forestry becoming a realistic and practical option, more consideration needs
12 497 to be given to the risks of adopting these strategies into commercial forestry. Currently, there
13 498 are no rules regarding the size of plantation that can be established from this material of narrow
14 499 genetic base.

15 500 Much less breeding and selection has occurred in our native broadleaf species that are used to
16 501 create commercial plantations and this is largely due to the poor economic returns on
17 502 hardwood timber. Future Trees Trust (FTT) is the main organization responsible for British and
18 503 Irish hardwood breeding and they are alert to the risks of basing their selections on an overly
19 504 narrow range of genotypes. The FTT currently work on the following seven species: ash, birch,
20 505 cherry, sweet chestnut, sycamore and walnut. The production of forest reproductive material is
21 506 regulated by the European Directive which has four seed categories based on different levels of
22 507 genetic quality. The FTT is about to make available 'tested' ash seed, with small quantities of
23 508 'qualified' birch and cherry to follow soon (Anon, 2012). Tested seed originates from individual
24 509 trees or stands which have been evaluated for genetic quality or, in comparison to accepted
25 510 standards, have been shown to be superior. Qualified seed originates from individual trees that
26 511 are in the process of undergoing testing.

32 512 **Conclusions**

33 513 Forests in Britain exist in many forms which include native woodlands with very low levels of
34 514 intervention, low impact silviculture plantations and woodlands of native and exotic species in a
35 515 mixture of man-made plantations composed of fast-growing exotic conifer species.

36 516 All are subject to biotic and abiotic change in the form of pests, diseases, climate change and
37 517 increasing frequency of weather extremes. Their ability to adapt to these challenges is
38 518 dependent on a number of factors including inter- and intra-specific diversity. The main factor
39 519 influencing adaptedness is the balance between natural selection and geneflow and therefore
40 520 consideration needs to be given to the best means of conserving the evolutionary process
41 521 rather than the genetic structure present at a given point in time. The importance of integrating
42 522 evolutionary considerations into adaptive forestry is being stressed in Southern Europe where
43 523 compared to Britain, more extreme climate change is predicted (Lefevre *et al.*, 2013a).

44 524 Forest managers need to be aware of the risks associated with the influences they can have on
45 525 this evolutionary, adaptive process including the balance between maximizing gain whilst
46 526 reducing genetic diversity, assisted migration of planting stock from further south, and
47 527 importation of seed and plants of local provenance or otherwise from non-UK nurseries. At
48 528 the same time, there should be awareness of the clear, practical actions that could be taken to
49 529 bring evolutionary processes into management: in practice, barriers to adaptive change in tree

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3 530 populations are likely to be due to disruptions of generational turnover (e.g. through
4 531 overgrazing of seedlings, prevention of fires, loss of habitat), rather than to any inherent lack of
5 532 evolutionary capacity. Strategies to minimise these impacts would make best use of the
6 533 inherent adaptive potential in tree populations.

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9 534 In the contemporary British landscape, trees exist in many forms and under a range of
10 535 ownership. As neither gene flow in trees nor dispersal of pests and diseases respect land
11 536 ownership or national boundaries there is a need for more integrated management of British
12 537 forest genetic resources to reduce the risk from an uncertain future.

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15 539 Recommendations for future research

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- 18 541 • Experimental work is needed to test the extent to which intra-specific genetic diversity
19 542 underpins stability. This should encompass testing of multiple genotypes, but also multiple
20 543 pressures.
 - 21 543 • A decision making framework should be developed, to let forest policymakers identify the
22 544 most appropriate action in specific pest / pathogen threat situations. This should define a
23 545 minimum set of parameters for a host tree species, such as its ecology, distribution and
24 546 diversity; those of the threat organism(s) and likely future environments. Model-based
25 547 testing could then be used firstly to evaluate potential evolutionary rates in tree
26 548 populations, taking into account genetic diversity, adaptive potential and variations in
27 549 demographic turnover and secondly, to explore and prioritise different management
30 550 scenarios using both idealized populations and spatially explicit simulations reflecting the
31 551 known distribution of species in the British landscape.
 - 33 552 • New information on genetic and adaptive variation for British tree species should be
34 553 collected at a fine spatial scale.
 - 36 554 • Detailed assessments of phenotypic variation in existing trials should be made, including
37 555 development of high-throughput methods for gathering such data.
 - 38 556 • New, large scale trials should be established to test resistance-related trait variation and to
39 557 maximize the impact of advanced genomic approaches.
 - 41 558 • The coordination and collation of existing datasets on intraspecific variability diversity in
42 559 trees in the British landscape should be carried out as a priority, particularly for those
44 560 species as yet unaffected but with imminent serious threats, and encompassing both
45 561 molecular and phenotypic variation.

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3 563 **Funding**

4 564 This work was supported by DEFRA grant TH0126 awarded under the Tree Health and Plant
5 565 Biosecurity Initiative (Phase 1).
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9 567 **Acknowledgements**

10 568 We thank Steve Lee for input on the manuscript, our other collaborators on the project and all of the
11 569 workshop participants for their comments and feedback on the review.
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Text box 1: The British forest estate

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The present day land-cover of woodlands and forests in Great Britain (13%) is low compared to some of our European partners (France 29%, Germany 32%, Finland 73%). However, it is considerably greater than at the end of the First World War in 1918, when it was only 5%. At that time it was recognized that there was a need to increase the forested area in Britain, resulting in the establishment of the Forestry Commission in 1919. Its remit was to increase the forested land area in both public ownership and, via grant schemes, in the private sector. The existing forests were a combination of native woodlands and commercial forests of predominantly native species. The new forests were created through afforestation of land previously used for sheep or deer grazing. These new forests were mostly intensively managed, even-aged, monoculture plantations, often involving an introduced exotic species. General practice involved clearfelling after an economic rotation of between 40 to 70 years, and then replanting with a similar exotic species. The seed for new planting stock was sourced from either a seemingly well adapted, vigorous, good quality stand of the exotic species, or early products from a domestic breeding programme. Over the last 20 years woodland and forestry management in Britain has diversified such that the current national complement consists of native woodlands; woodlands managed under a less intensive silvicultural system of mixed ages and species, and highly intensive, monoculture plantations of even-aged, exotic crops with various levels of improved and selected stock.

The British forest estate consists of 49% conifer, 32% broadleaf, 8% conifer/broadleaf mixtures. There are 66 native British trees and shrubs, only a small proportion of which are grown commercially for timber. Many of the native shrub species have scattered distributions and are rather rare.

The principal conifers grown in Britain are Scots pine (native), Sitka spruce (ex USA/Canada), Lodgepole pine (USA/Canada), Larch (Central Europe or Japan), Norway spruce (North-Central Europe) Corsican pine (Southern Europe) and Douglas fir (USA/Canada). The main commercial conifer species is Sitka spruce which represents 50% of the area covered by conifers (Anon (a) In press). Our only native conifer timber species, Scots pine (ancient semi-natural remnants and plantations) represents 18% of the area occupied by conifers. The principal broadleaf species are oak, beech, sycamore, ash and birch. In terms of standing volume oak and ash represent 30% and 14% respectively of the total broadleaf species in Britain (Anon, 2013).

The Forestry Commission owns or leases 35% of all woodland over 2 ha and the remaining 65% is in other ownership.

The process of breeding and selection is more advanced for the exotic conifer species. The country is largely self-sufficient in Sitka spruce and Scots pine planting stock, but native species are neglected in terms of domestic planting stock, leading to mass importation of trees from continental nurseries.

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Text box 2: key terms

612 **Molecular markers** – specific fragments of DNA that can be used as tools to measure genetic
613 diversity, gene flow and migration history.

614 **Genetic diversity** – the full complement of genotypes present; referred to as *intra-specific* genetic
615 diversity for discussing within-species variation. Determined by:

616 **Natural selection** – process through which the individuals that are best adapted to current
617 local conditions survive, reach maturity and produce offspring. Generally most intense when trees
618 are at the seedling/sapling stage, when mortality is highest. It causes traits that contribute to
619 adaptedness to increase in frequency in a population and, over time, may cause populations to
620 differentiate from each other.

621 **Gene flow** - the dispersal of genes via seed, pollen or vegetative propagules. Tends to
622 counteract the effects of natural selection and acts to homogenise intra-specific genetic diversity
623 within and between populations. Pollen and seed migrating into a forest will be adapted to their site
624 of origin rather than the site to which they have migrated. However, under changing conditions, this
625 may introduce diversity that will help the local population to adapt. Gene flow is often extensive in
626 tree populations and studies on a range of species have shown that around half of the paternal
627 contribution to the seed originates from outside the stand and in wind pollinated trees can come
628 from as far away as 100 km (Robledo-Arnuncio and Gil, 2005; Bacles and Ennos, 2008).

629 **Genetic drift** – the loss of genetic diversity that occurs during random mating; occurs most
630 strongly when populations are small and genetically isolated.

631 **Mutation** – DNA copying errors that generate new intra-specific genetic diversity. A
632 mutation may confer selective advantage, disadvantage or make no difference. It is a slow process
633 and, as most of our tree species only reached Britain in the last 10,000 years, its impact since
634 colonization is likely to be small.

635

636 **Adaptive variation** - the raw material on which selection (natural or human-mediated) acts. It is the
637 basis for the evolutionary potential of a species or a population, allowing a response to
638 environmental changes and provides the raw material for tree breeders to select for improved
639 resistance to disease.

640 **Effective population size** – the number of individuals in a population reproducing and contributing
641 genetic material to the next generation

642 **Local adaptation** – the result of natural selection acting on intra-specific genetic diversity. Influenced
643 mainly by the balance between natural selection and gene flow. Under changing conditions, the
644 composition of genotypes in a population may gradually alter, e.g. those that are more tolerant of
645 drought may be favoured as conditions become drier. Local is not fixed but dynamic, resulting from
646 a combination of chance events (mutation, genetic drift, gene flow) and natural selection, acting
647 under a changing biotic and abiotic environment.

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Text box 3: Genetic characteristics of trees

652 Trees differ from other plant species in that they are long lived, reach sexual maturity at a relatively
653 late age and exist in populations in which the generations overlap. In contrast to many herbaceous
654 species, they are usually outcrossing, a characteristic which promotes high genetic diversity.
655 Compared to herbaceous plants, tree populations usually exhibit low differentiation at neutral
656 markers due to extensive gene flow yet may be highly differentiated for adaptive traits. This is likely
657 to be due to the combined effects of the enormous fecundity of trees and the strong selection
658 pressures to which young tree seedlings are subjected (Petit and Hampe, 2006). Translocations of
659 tree species have demonstrated that forest genetic resources have the capacity to adapt to
660 conditions very different from those experienced in their native range. For example, the worldwide
661 transfer of *Pinus radiata* (Yan *et al.*, 2006) and the south to north translocation of *Picea abies*
662 (Skroppa *et al.*, 2010).

663

664 Large scale differences in adaptive variation of native tree species

665 In terms of adaptive diversity, our native tree populations tend to show a degree of adaptation to
666 environmental conditions in Britain such that native provenances outperform those from mainland
667 Europe when grown in trials based in Britain (Gerber *et al.*, In Press). For example, on the basis of
668 provenance trials of Scots pine, silver birch, sessile oak and alder, British provenances showed
669 superior growth and survival in 90% of cases compared with those from continental Europe (Fletcher
670 and Samuel, 1997 ; Gerber *et al.*, In Press). Even those continental provenances that came from
671 similar latitudes to Britain e.g. Denmark, Germany, Latvia performed more poorly than British
672 material and their survival on upland sites was poor (Ennos *et al.*, 1998). British and continental
673 Scots pines also differ in various phenological traits. For example, (Perks and McKay, 1997) showed
674 that Scandinavian seedlings had greater frost resistance, earlier frost hardening and a longer period
675 of frost hardiness than their British counterparts. These results demonstrate that British
676 provenances are adapted to the current conditions in Britain and material introduced from
677 continental Europe tends to suffer from the effects of late spring frosts which are typical of the
678 British climate.

679

680 Differences in adaptive variation within Britain

681 Less data are available at the British scale. However, Pelham *et al.* (1988) found differences in leaf
682 length along a north-west to south-east transect in Scottish populations of *Betula pubescens*. Recent
683 work demonstrated differences between Scottish provenances of Scots pine in phenology and levels
684 of tolerance to drought and cold stress (Salmela *et al.*, 2010; Salmela *et al.*, 2011; Salmela *et al.*,
685 2013). In the case of cold stress, populations from lower altitudes performed more poorly when
686 exposed to cold than those from higher altitude, drier sites. These findings provide evidence that
687 despite the homogenizing effects of large scale gene flow in wind pollinated and wind dispersed
688 Scots pine it is nevertheless possible to detect evidence of local adaptation on short geographic
689 scales. However, due to the lack of suitable trials which include good representation of British
690 provenances and species we do not yet have detailed data on which to base an understanding of the

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3 691 pattern, scale and environmental drivers of local adaptation in Britain. Very little is known about
4 692 whether provenances differ in terms of their susceptibility to existing/novel pests and diseases.
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6 693 However, when examined it was discovered that Scots pine from provenances from the east and
7 694 west coast of Scotland differed in their susceptibility to *Peridermium pini* (Lines and Mitchell, 1965).
8 695 Studies are currently underway to explore the susceptibility of Scottish provenances of Scots pine to
9 696 *Dothistroma pini*. Such information is urgently needed to allow the development of informed policy
10 697 on planting sources.
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699 Genetic diversity within populations

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15 700 Despite having found evidence for local adaptation it is also well recognized that genetic diversity in
16 701 tree populations is high. Tree species tend to be outcrossing, often wind pollinated with large
17 702 effective population sizes and these characters tend to maintain high levels of adaptive diversity.
18 703 Prior to the advent of molecular markers, it was thought that tree populations in northern Europe
19 704 might contain lower diversity than those further south due to their long distance from glacial refugia
20 705 but this has not been found to be the case (e.g. (Wachowiak *et al.*, 2011; Wachowiak *et al.*, 2013)).
21 706 This high diversity provides the basis for adaptation to novel challenges. Changing climate and new
22 707 pests and diseases will present new challenges and through the process of natural selection,
23 708 individuals with certain variants of genes or gene combinations will be favoured if they confer
24 709 resistance. Consequently these will be the individuals which survive the challenge and produce the
25 710 next generation.
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713 Figure 1: Processes conferring species resilience for forest trees. The capability to adapt to new
714 pressures depends on genetic diversity, gene flow, and rate at which new genotypes can be
715 recruited to the population.

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717 Figure 2: Tradeoffs in the decision making process for action against new pests / diseases.
718 Tipping points may exist between extremes, beyond which resilience has been lost to such an
719 extent that managed evolutionary processes cannot act fast enough to achieve recovery.

720

721 Table 1: Knowledge of genetic diversity in UK native tree species with listed threats on DEFRA THAP (excludes longhorn beetles, which have wide host
 722 range). Publications cited where populations or provenances of UK origin have been included. Where known experimental resources are available but not
 723 necessarily published data, this is indicated with a ✓

Genus	Species	Disease threat	Neutral data					Adaptive data			
			Fine scale structure	Gene flow	Mating system	Wide scale population structure	Phylogeography	Rangewide provenance trial	UK provenance trial	Provenance - Progeny trial	Reciprocal transplant expt.
<i>Alnus</i>	<i>glutinosa</i>	Phytophthora, Rust, (Melampsoridium)					14		11,35		
<i>Fraxinus</i>	<i>excelsior</i>	Chalara dieback	13	1, 2, 3		13, 30	12		5, 27	47, ✓	✓
<i>Betula</i>	<i>pendula / pubescens</i>	Birch borer			21		19, 21		4, 18, 23, 31, 35, 36	✓	✓
<i>Juniperus</i>	<i>communis</i>	Phytophthora		26, 32		26, 32					
<i>Quercus</i>	<i>robur / petraea</i>	Acute Oak decline, SOD, Proc. Moth	7	47		6, 20, 39	6, 10, 16, 17, 24, 25	8, 11, 15, 38, 39, 40	35, 40	✓	
<i>Pinus</i>	<i>sylvestris</i>	DNB, Lappet moth, pine weevil, PPM				33, 34, 37	28, 29	38	9, 41-46	✓	✓

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 725 1 - Bacles *et al.* (2005), 2 - Bacles and Ennos (2008), 3 - Bacles *et al.* (2006), 4 - Billington and Pelham (1991), 5 - Boshier and Stewart (2005), 6 - Cottrell *et al.* (2002), 7 - Cottrell *et al.* (2003) 8 - Deans and Harvey
 726 (1996), 9 - Ennos and McConnell (2003), 10 - Ferris *et al.* (1998), 11 - Gosling *et al.* (2009), 12 - Heuertz *et al.* (2004), 13 - Anon (2013), 14 - King and Ferris (1998), 15 - Kremer *et al.* (2002b), 16 - Lowe *et al.* (2004) 17 -
 727 Lowe *et al.* (2005), 18 - Malcolm and Worrell (2001), 19 - Maliouchenko *et al.* (2007), 20 - Mariette *et al.* (2002), 21 - Anon (2012), 22 - Palme *et al.* (2003), 23 - Pelham *et al.* (1988), 24 - Petit *et al.* (2002a), 25 - Petit
 728 *et al.* (2002b), 26 - Provan *et al.* (2008), 27 - Savill *et al.* (1999), 28 - Sinclair *et al.* (1998), 29 - Sinclair *et al.* (1999), 30 - Sutherland *et al.* (2010), 31 - Thomas *et al.* (2007), 32 - Park (2002), 33 - Wachowiak *et al.*
 729 (2013), 34 - Wachowiak *et al.* (2011), 35 - Gerber *et al.* (In Press), 36 - Worrell *et al.* (2000), 37 - Ennos *et al.* (1997), 38 - Jensen and Hansen (2008), 39 - Kremer *et al.* (2002a), 40 - Pilcher and Gray (1982), 41 - Iason
 730 *et al.* (2011), 42 - O'Reilly-Wapstra *et al.* (2007), 43 - Pakeman *et al.* (2006), 44 - Perks and Ennos (1999), 45 - Salmela *et al.* (2011), 46 - Salmela *et al.* (2010), 47 - Rendell and Alstom (2004)

731 Table 2: The extra gain available to the forest manager as genetic diversity narrows. Figures are
 732 percentage gains over the unimproved and genetically diverse control for three traits, when
 733 different numbers of improved clones are deployed (S.J. Lee pers. comm.): 100 clones represents the
 734 highest diversity, 1 clone represents pure clonal forestry. These improvements are associated with
 735 major economic benefits at the sawmill and to the value of the timber in the forest. Forest managers
 736 must weigh up these gains against the risk of losing the crop to pest or disease and any constraints
 737 through compliance with sustainability guidelines.

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Number of clones	DIAMETER	STRAIGHTNESS	WOOD DENSITY
100	24	25	13
50	26	30	17
40	27	31	18
20	29	34	20
10	31	37	23
1	37	45	27

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Figure 1: Processes conferring species resilience for forest trees. The capability to adapt to new pressures depends on genetic diversity, gene flow, and rate at which new genotypes can be recruited to the population.

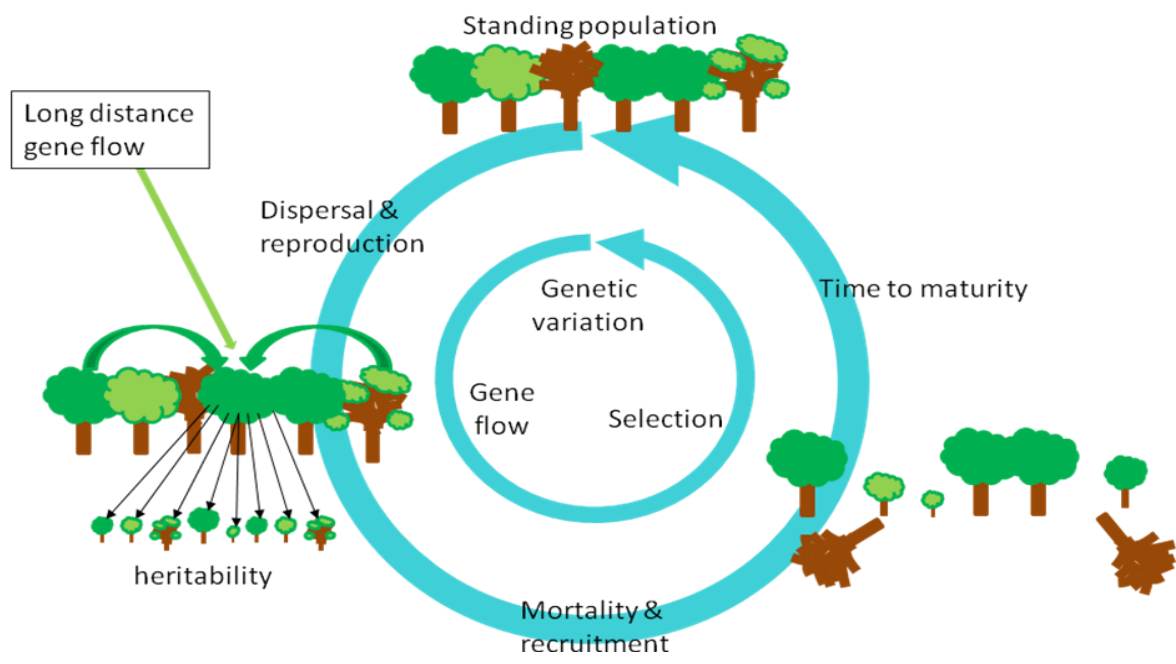
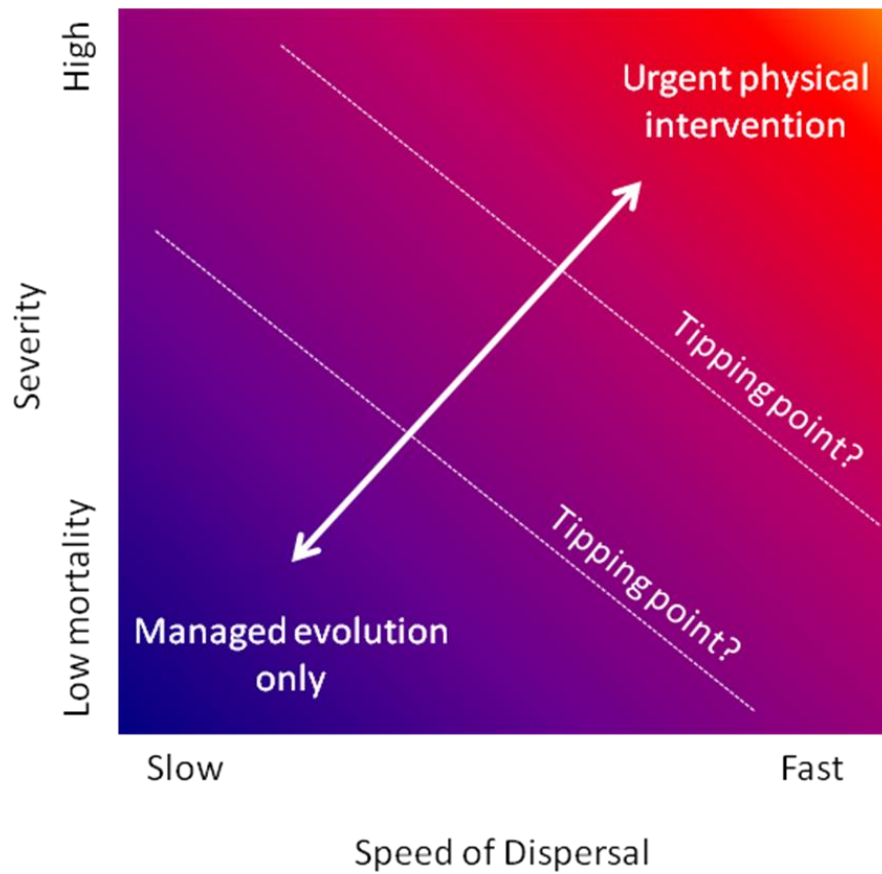


Figure 2: Tradeoffs in the decision making process for action against new pests / diseases. Tipping points may exist between extremes, beyond which resilience has been lost to such an extent that managed evolutionary processes cannot act fast enough to achieve recovery.



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