

Seed sourcing for woodland creation in an era of uncertainty: an analysis of the options for Great Britain

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In recent years, British seed sourcing practice has tended to focus on the principle that 'local-is-best' for native woodland creation. However, in the face of continuing and accelerating environmental change, the suitability of this approach has been called into question. In this article, we investigate the relevance and suitability of a series of seed sourcing strategies: maintaining the *status quo* by continuing to source local origin seed, sourcing seed from currently warmer locations and the addition or replacement of species. Our main findings are that there are opportunities to increase the sophistication of existing guidance and that improvements would be timely. In any case, an important consideration is the capacity for newly established populations of trees to survive immediately and amidst increasingly variable environmental conditions. The current paucity of knowledge of forest genetic resources in British populations of native tree species suggests that deviations from sourcing currently adapted planting stock are not uniformly applicable throughout the country and that any change to policy ought to be applied judiciously and only under a restricted set of circumstances.

Introduction

Initiatives are in place to restore and extend the distribution of forests around the world (Thomas *et al.*, 2014). The success of these initiatives depends, among other considerations, on the availability and selection of planting stock which is of good quality and is sufficiently adapted to conditions at the planting site in order to survive, compete and reproduce. This situation is exemplified by the case of native woodland establishment in Great Britain (GB) where high demand for planting stock is driven by ambitious policies aimed at increasing the area of forest cover (Scottish Executive, 2006; Forestry Commission, 2007; Welsh Assembly Government, 2009). If the policy objectives of increasing forest area are to be met, it is essential that there is a general understanding of the ecological and evolutionary processes underpinning appropriate seed source selection in a changing climate and how policy can encourage such practice.

Until recently, policies relating to seed sourcing in GB and elsewhere have been based on the understanding that climatic conditions are stable over the long term. Increasing recognition of rapid environmental change undermines this assumption (Rehfeldt *et al.*, 2002; Parmesan, 2006). Not only is environmental change expected to be rapid, it is also difficult to predict. While we might expect directional change in mean values of

some climatic variables, increasing variability and increases in the frequency and severity of some extreme events are probable (IPCC, 2013). The prevalence of some endemic pests and diseases is also likely to increase, as a result of climatic shifts (Battisti *et al.*, 2005; Sturrock *et al.*, 2011). Finally, increased pressure from novel, exotic pests and pathogens is anticipated, caused in part by greater long distance movement of plants by humans (Brasier, 2008; Liebhold *et al.*, 2012; Banks *et al.*, 2015; Jung *et al.*, 2015). These considerations indicate the need for a thorough re-evaluation of existing seed sourcing guidelines (Alberto *et al.*, 2013; Lefèvre *et al.*, 2014). The overall aim of seed sourcing, from an evolutionary ecology perspective, should be to ensure that planted forests have the capacity to survive initially and continually adapt to changing environmental conditions.

The aim of this article is to provide such a re-evaluation of seed sourcing guidelines for forestry in GB. We note that forestry planting stock is raised for two broad objectives in GB, native woodland planting and timber production. We acknowledge that there will be an overlap between these objectives in many situations, e.g. native woodland plantings will commonly be sustainably harvested for timber and timber plantations are capable of fulfilling benefits other than timber production. However, this review considers only seed sourcing for native woodland planting, leaving seed sourcing for timber production for

separate treatment. In native woodland planting, the imperatives are to establish a self-sustaining population of forest trees that will give rise to successive generations of individuals on the site and will support native biodiversity.

In response to the realization that rapid environmental change will continue to affect forests in the immediate future, three distinct seed sourcing strategies have been put forward aimed at creating forests that have the maximum chance of surviving under changing conditions. We have dubbed these seed sourcing strategies ‘currently adapted’, ‘predictive provenancing’ and ‘species change’. A brief description of each of these is given below.

Currently adapted

The ‘currently adapted’ strategy asserts that it is best to plant seed sources that are ‘adapted to current environmental conditions’ but have the potential for future adaptation as environmental conditions change.

Predictive provenancing

The ‘predictive provenancing’ strategy holds that seed sources should be planted that are ‘adapted to a predicted future climate’. Predictive provenancing recommends use of material from parts of the species range in which the current climate matches predicted future conditions at the planting site. A variation on this theme is ‘composite provenancing’, where a mixture of local and non-local material, the latter of which is sourced from areas matching predicted future climates, is used (Broadhurst *et al.*, 2008; Breed *et al.*, 2013). This has also been called ‘assisted gene flow’ (Aitken and Whitlock, 2013) and seed ‘portfolio’ (Crowe and Parker, 2008) and is described within the context of ‘ecosystem centred assisted migration’ (Sansilvestri *et al.*, 2015). In a GB context, this would involve sourcing seed from currently warmer climates further south.

Species change

The ‘species change’ strategy posits that the scale of future environmental change is so great that the currently planted species should no longer be used. It recommends that an ‘alternative species adapted to predicted future climate’ should be substituted.

In this review, we first analyse the ways in which forest tree populations may respond to rapid environmental change, which we consider to be manifested by rates of change in the mean and extreme values of climatic variables, caused by human activity which are likely to exceed those experienced at any other time during the Holocene (IPCC, 2013). We then consider the proposed advantages and potential disadvantages of each of the seed sourcing strategies defined above in relation to woodland creation in a situation of rapid environmental change. Our aim is not only to assess the relative merits of each strategy, but also to determine situations in which particular strategies may be more or less appropriate, highlight areas of uncertainty that hinder informed decision-making and propose research that is required to identify the best strategy to be adopted. While we focus on the situation in GB, we seek to bring out principles that are more widely applicable.

Response of forest tree populations to rapid environmental change

The immediate response of forest trees to rapid environmental change will be a plastic one involving a change in their physiology or morphology but no change in their genetic composition (Nicotra *et al.*, 2010; Reich *et al.*, 2016). Where this change improves the chances of individual tree survival and reproduction during the period of extreme environmental conditions, the change is known as acclimation. As long lived organisms that survive naturally through environmental conditions that can be highly variable in time and space, acclimation or plastic responses to environmental change can be highly developed in trees (Rehfeldt *et al.*, 2001; Aitken *et al.*, 2008; Chevin *et al.*, 2013). Acclimation responses are often associated with ontogenetic costs, or trade-offs among traits (DeWitt *et al.*, 1998; Valladares *et al.*, 2007; Richter *et al.*, 2012). Furthermore, there are limits to acclimation responses and trees may die either directly or as a consequence of stress which compromises their herbivore and pathogen defences (Telford *et al.*, 2015).

Within a tree population, there are very high levels of genetic variation among individuals for adaptive characters such as timing of growth, cold, drought and flooding tolerance and resistance to herbivores and pathogens (Petit and Hampe, 2006). Even where population sizes of trees are very small, there can still be substantial genetic and phenotypic variation among standing trees and offspring, in situations where genetic variation is delivered by long distance gene flow (Bacles *et al.*, 2004; Hampe *et al.*, 2013). Over a long period of relatively constant environment at any one site, a range of genotypes will have been selected that are adapted to the combination of abiotic and biotic conditions at that site, known as local adaptation (Ennos *et al.*, 1998; Savolainen *et al.*, 2007). Local adaptation does not necessarily mean that the local genotypes in a site will show greater growth over any particular duration than genotypes from other sites. This is because populations will possess a conservative legacy of adaptation to extreme events which may not be recognizable as intrinsically advantageous within a single generation if extreme events do not occur. However, it does mean that the local population is likely to be the most successful if one of these extreme climatic events does occur during a generation.

If a novel environment is imposed on a genetically variable, locally adapted population, individual trees will respond differently and the most successful will make the greatest contribution of offspring to the next generation. If the offspring of these fitter individuals are able to establish, the population will evolve genetically, producing a subsequent generation that is better adapted to the novel environmental conditions, i.e. natural selection occurs. The rapidity of this evolution will be proportional to the amount of adaptive variation present in the original population (Davis and Shaw, 2001; Alberto *et al.*, 2013). However, adaptive evolution comes at a cost. Trees that respond poorly to the change in environment may either die or grow very slowly, leading to a reduction in size of the reproducing population. The magnitude of this cost of adaptation will increase with the rapidity of the environmental change imposed. If the environmental change is too rapid, populations may go extinct before they adapt (St Clair and Howe, 2007). In any

event, there will always be some degree of lag in adaptation to the new environmental conditions (Aitken *et al.*, 2008; Kuparinen *et al.*, 2010).

The potential for acclimation and patterns and quantities of adaptive genetic variation within a forest tree species can be measured from appropriate provenance/progeny trials in multiple sites (Rehfeldt *et al.*, 2002; St Clair *et al.*, 2005). These will be especially useful where provenances are planted in sites that possess one or more features of the novel environments that they are predicted to encounter under rapid environmental change.

A proxy for the limits of adaptation of the species can be found by analysing the limits of the environmental envelope naturally occupied by the species, with the caveat that recognized natural distributions may not reflect the total fundamental niche of that species. If the predicted environmental conditions lie far outside that envelope, it will be unrealistic to expect future adaptation to those conditions.

Bearing these points in mind, we now consider the merits of the three proposed strategies for seed sourcing for native woodland creation and expansion under rapid environmental change.

Seed sourcing for woodland creation under rapid environmental change

Currently adapted

The obvious advantage of planting currently adapted seed sources is that during the initial phase of establishment, the trees will be well suited to the conditions that they encounter. This will be the consequence of local adaptation not only to the current climate, but also many other factors by which populations differ in their home environments, e.g. soil conditions, herbivore and pathogen pressure. It is often considered that for trees, the initial establishment phase is the most critical and a point at which selection against poorly adapted genotypes is most intense, both for naturally regenerated seedlings and for nursery raised stock (Persson and Ståhl, 1990; Petit and Hampe, 2006). Significant death of transplants at this stage will mean failure to establish woodland cover. Using currently adapted material will minimize the probability of this occurring. A caveat to this is that it may not be easy to determine whether local seed sources are indeed adapted to similar conditions—as environmental similarities are not necessarily dictated by proximity of seed source to planting site (Bischoff *et al.*, 2006; Salmela *et al.*, 2010). In this case, seed sources from sites whose environments match most closely those of the planting site may be more appropriately adapted than a local (geographically proximal) seed source, especially where topography is complex at narrow spatial scales.

The major concern over the ‘currently adapted’ strategy is that over the first generation of the new woodland, the planted trees will become maladapted to those features of the environment that are rapidly changing (St Clair and Howe, 2007). To some extent, this will be buffered by acclimation in the tree population (Alberto *et al.*, 2013; Chevin *et al.*, 2013). However, genotypes will respond differently to the novel environment with some individuals doing worse than others throughout their life spans or with different responses in different years (Jump *et al.*, 2008). Overall, the actual growth observed in a population

may be lower at the end of the first tree generation than for a population which was closely adapted to the changed environmental conditions prevailing at that particular time. The extent to which this is a serious problem will very much depend on context, varying by species and by management objectives.

In the case of forestry in GB, major climate warming and different seasonal patterns of precipitation are anticipated to be a problem in southeast England where increasing summer drought may mean that within the course of a single generation certain individuals are taken beyond the limits to which they can acclimate, leading to tree death or intense physiological stress. Beech, *Fagus sylvatica* L., is one such drought-sensitive species (Jump *et al.*, 2006; Packham *et al.*, 2012; Cavin *et al.*, 2013). In this situation, there are options to source proportions of material which contain genetic variation for drought tolerance, due to historic adaptation to drier conditions than currently exist in GB. In other areas, increased temperature and longer growing seasons may actually lead to greater growth rates of tree species (Saxe *et al.*, 2001). In this case, existing populations may not be optimally adapted to make full use of increased temperature and longer growing seasons. However, in the absence of individuals who are able to take advantage of longer growing seasons, this will not necessarily have an impact on their survival, and conservative growth of indigenous populations will minimize the risk of frost damage and severe climatic episodes. Furthermore, there will be a greater contribution to regeneration from those genotypes that respond best to the environmental change, and a lagged evolutionary response to the change is expected in subsequent generations if natural regeneration is able to occur. So long as the novel climate remains within the total envelope occupied by the species within its current range, adaptation to the environmental change over many generations is a realistic outcome. Most native species within the UK have distributions elsewhere in Europe which encompass much warmer and drier conditions, so ultimately adaptation to such environmental change appears entirely feasible.

Practical implementation in GB forestry

For successful implementation of a ‘currently adapted’ strategy in response to climate, the first requirement is a mechanism that allows currently adapted seed sources to be correctly identified for planting. There is already a system of seed transfer regulation in GB forestry that goes some way to achieving planting of currently adapted seed sources across most native tree and shrub species (Herbert *et al.*, 1999). In this system, four regions of provenance are delineated within Britain and these are subdivided into a total of 24 fixed boundary seed zones. Delimitation of the common seed zones is based not on patterns of adaptive variation of trees but on proxies for this; geomorphology and major watersheds together with an additional altitudinal discriminant factor whereby seed lots are described as having been collected either above or below 300 m. The system was devised by Herbert *et al.* (1999) to encourage the use of local stock at planting sites as an extension to earlier administrative systems for identification and certification of seed lots under the Organisation for Economic Co-operation and Development (OECD) (Gordon *et al.*, 1992).

Following adoption of this system in the 1999, adherence to local provenance became a stipulation for receipt of government grant support for native woodland creation, at least when seed can be obtained without excessive difficulty (Buckley and Blakesley, 2008). A major achievement of the current system of seed zoning is that it has generally prevented grant support being provided for use of stock of non-GB provenance, much of which has been shown to survive for shorter periods or grow less well than GB provenances in Britain, including silver birch *Betula pendula* Roth (Worrell, 1992; Worrell et al., 2000); Scots pine *Pinus sylvestris* L., alder *Alnus glutinosa* (L.) Gaertn. and sessile oak *Quercus petraea* (Matt.) Liebl. (Worrell, 1992); hawthorn *Crataegus monogyna* Jacq. (Jones et al., 2001); ash *Fraxinus excelsior* L. (Cundall et al., 2003); and for sessile and pedunculate oak *Quercus robur* L. (Hubert, 2005).

It was recognized from its inception that the seed zone system for encouraging currently adapted seed sources in GB was no more than a first attempt which would require refinement as more knowledge became available. In the course of the last 15 years, a number of shortcomings in the system have been recognized, the first of which is that the regions of provenance and seed zones specified do not accurately reflect geographic areas with uniform environmental conditions for tree survival and growth in GB (Salmela et al., 2010).

In upland regions, the current seed zones contain within them a high degree of climatic variation (Salmela et al., 2010). Where climatic conditions are not uniform within seed zones, fine scale patterns of adaptive variation may be overlooked, such that the seed zones do not consist of populations which are adapted to similar environmental conditions (Salmela et al., 2011, 2013). Therefore, adhering to local seed zones in a heterogeneous landscape does not necessarily guarantee a local fitness advantage as plants from a geographically proximal location may be adapted to very different temperature, moisture and exposure regimes (Bischoff et al., 2006).

On the other hand, in more topographically homogenous lowland regions such as central and eastern England, seed zones could justifiably be enlarged. Seed zones that are smaller than necessary may make seed collection and stock management more laborious and complicated than necessary without any clear fitness advantage to planted stock (Hubert and Cottrell, 2007; Buckley and Blakesley, 2008; O'Neill et al., 2014). An example of excessively conservative seed zoning has been found for alder *A. glutinosa* in Belgium where assessment of patterns of molecular and adaptive variation demonstrated that material from each of the five seed zones could be exchanged with little risk of maladaptation (De Kort et al., 2014).

The second shortcoming of the seed zone system in GB is that (with the exception of Scots pine *P. sylvestris*) it is applied uniformly to all native species on the assumption that they show equivalent patterns of adaptive variation across the landscape, which is unlikely to be the case (Rehfeldt, 1994; Boshier and Stewart, 2005; Cavers and Cottrell, 2015). There is good evidence that this assumption is unlikely to be warranted. For instance, Vitasse et al. (2009) observed opposing adaptive clines in the phenological response of beech *F. sylvatica* to those of ash *Fraxinus excelsior* and sessile oak *Q. petraea* in the Pyrenees. In multiple common garden experiments established along an altitudinal cline, beech populations from a higher altitude were found to be the earliest to flush, whereas the opposite trend

was recorded in ash and oak. Moreover in the same trial, it was shown that for three other species, sycamore *Acer pseudoplatanus* L., holly *Ilex aquifolium* L. and European silver fir *Abies alba* Mill., there was no evidence of adaptive differences in phenology in response to altitude (Vitasse et al., 2009).

From these considerations, it is clear that if the 'currently adapted' seed sourcing policy is to be adopted, the present seed zone system in GB requires refinement. To do this, basic information is essential on the patterns of adaptive variation for different native tree species across GB to determine the critical environmental factors to which they are adapted. Using this information, it would be possible to modify the seed zone approach that already exists to tailor it to fit particular species or groups of species. Such species-specific guidelines are already in place in a number of other European countries (see Table 2 in Alia et al., (2009) which summarizes approaches to provenance choice in different European countries). Alternatively, seed source selection could be based not on proximity of source and planting site, but instead on ecological matching of these sites.

The Forestry Commission's Ecological Site Classification (Pyatt et al., 2001) provides a decision support system for species choice which uses soil characteristics and indicator plant species to determine an ecological profile for a planting site. Extending these methods to provenance choice, whereby registered seed stands would have an ecological profile which could be matched to the planting site would be useful but not without limitations, because as yet unforested sites will necessarily differ in their ecological characteristics from possible seed source sites, and it may be complex to ensure that ecological profiles were compiled with standardized methods.

A simpler approach might be to consider climatic similarity alone, using multivariate site similarity indices (Ying and Yanchuk, 2006). Natural Resources Canada operate a system called 'SeedWhere' (McKenney et al., 1999), which uses a statistical similarity metric to determine the extent of climatic similarity between conditions at the planting site and those at a range of possible seed source locations. In the USA, the 'Seedlot Selection Tool' (Howe et al., 2009) is a GIS tool which matches sites climatically and also allows the user to select a climate change model to identify areas which currently match predicted future climate at planting sites.

Once currently, adapted seed sources have been identified, guidelines need to be in place to ensure that the seed collected from the identified population is sufficiently genetically variable to allow evolutionary adaptation to environmental change to occur. It is generally accepted that seed collection should be based on even sampling of a minimum of 20–30 well-spaced seed trees to ensure sufficient variation in the planting material (Thomas et al., 2014). This is recommended in British guidance as a rule of thumb (Herbert et al., 1999), although it is worth noting that the number of parents required to sample large proportions of the genetic variation in natural populations will depend on the reproductive biology of the target species, notably the prevalence of self-fertilization and dispersal mechanisms (Hoban and Strand, 2015), and that the numbers required for British native species have not been investigated. The inclusion of high amounts of adaptive genetic variability in seed collections is aided by the high rates of pollen flow generally found in trees (Savolainen et al., 2007; Kremer et al., 2012). This means that seed sampled from a tree population contain a significant

proportion of genes that have been derived from other populations in the landscape, thereby broadening the genetic base (Bacles *et al.*, 2006).

The critical feature of the ‘currently adapted’ strategy for seed sourcing is that it is reliant on the operation of natural selection rather than human intervention to achieve adaptation to future environmental conditions. Thus, if this policy is adopted to create new native woodland, the management must be suitable to allow natural selection to be effective. This means that the initial population must be sufficiently large that even if there is strong selection in the novel environment at the end of the first generation, there is nevertheless sufficient reproduction among the survivors to allow natural regeneration to occur. Conditions such as level of herbivory must be sufficiently low at that time for natural regeneration to take place. If this is not the case then a possible alternative is collection of seed from the best-performing individuals that have been selected for adaptation to the new environment to be raised for supplementary planting in the same location.

Predictive provenancing

Predictive provenancing uses planting stock raised from seed collected in an area that currently experiences a climate similar to that predicted for the planting site in the future. A pure predictive provenancing approach would involve the selection of a single seed source population which offered the closest match to anticipated climate at some time in the future (i.e., a space-for-time substitution), in place of local origin material.

An intermediate option is composite provenancing (Broadhurst *et al.*, 2008; Breed *et al.*, 2013). Under composite provenancing, proportions of the seed would be collected from multiple populations located in areas at increasing geographical distances from the planting site. The seed would be collected from populations in locations experiencing currently warmer conditions than the planting site and would be mixed with a proportion of local seed. For instance, under composite provenancing, a planting scheme in southern Scotland would be designed to include perhaps one-third of locally sourced seed, one-third southern English origin seed and one-third French origin seed.

The thinking underlying predictive provenancing approaches are that climate change is occurring quickly, and that by the time when trees currently being planted become mature and reproductive, they will be encountering dramatically different climates (Broadmeadow and Ray, 2005). Using climate projection models, it is assumed that we can predict these future climates. The assertion of predictive provenancing is that in these circumstances the best approach to seed sourcing is to collect seed from genotypes that are adapted not to the present climate, but to the future anticipated climate, giving trees the best possible opportunity to survive and reproduce at that time. It is worth looking in detail at the validity of this superficially appealing argument to determine whether it withstands close scrutiny.

It is firstly important to note that the arguments supporting predictive provenancing are expressed in terms of adaptation to one particular aspect of the environment, namely climate (Aitken and Whitlock, 2013). However, climate does not represent the full suite of environmental factors to which a tree

must be adapted. There is overwhelming evidence that local adaptation in trees occurs not only to climate but to many other aspects of the environment, particularly soils and soil biota, herbivores and pathogens (Ennos 2015; Kranabetter *et al.*, 2015; Pickles *et al.*, 2015). Lack of adaptation to these aspects of the environment may reduce the survival and growth of tree populations. Under predictive provenancing, seed would be moved to new environments solely on the basis of predicted future climate, taking no account of adaptation to any other aspect of the environment. It is therefore likely that the seedlings raised from translocated seed will be of lower fitness than locally sourced seed with respect to these other aspects of the environment. In recognition of the possibility of strong adaptation to non-climatic factors, Aitken and Whitlock (2013) make the argument that this approach should only be considered when populations of a species are known to show strong adaptation to climate but not to other aspects of the environment. However, this important point has been overlooked in current British guidance.

The second point to note is that under predictive provenancing, translocated seed will initially be ill adapted to the current climate. For example, with northwards movement of seed stock, there is an increased risk of exposure of buds and foliage to late spring and early autumn frosts compared with locally adapted stock, as the timings of leaf and bud emergence and senescence may not be phased to avoid frost, due to past adaptation to a longer growing season (Vander Mijnsbrugge *et al.*, 2015; 2016). Frost damage may reduce the chances of establishment of translocated seedlings, or adversely affect the form of trees if leading shoots are killed by frost, causing forking (Kerr and Boswell, 2001; Cundall *et al.*, 2003). Thus, maladaptation both to initial climate and to other important aspects of the environment is likely to result in lower initial survival of provenances translocated in anticipation of climate change. Under a pure predictive provenancing regime, this would lead to poor stocking of sites. Under composite provenancing, a possibility is that there will be high survival of the local component of the seedling population and low survival of the translocated stock, so that as the population reaches maturity there is the unintended consequence that the majority of the population that is exposed to the novel climate has actually been derived from local provenance.

While natural selection in the early stages of tree development ought to remove the most maladapted individuals as seedlings (Persson and Ståhl, 1990), it is also possible that maladaptation may not become apparent for several years, and possibly beyond the age at which individuals are reproductively mature. Exposure to relatively infrequent events such as harsh spring frosts after mild winters (Worrell *et al.*, 2000; Hubert, 2005; Benito-Garzón *et al.*, 2013a, 2013b), rare or seasonal flooding events (Linhart and Baker, 1973; Lenssen *et al.*, 2004), high winds (Pelham *et al.*, 1988) and droughts (Cavin *et al.*, 2013) may cause problems for established trees which are not adapted to such conditions. For instance, Worrell *et al.* (2000) found that silver birch *B. pendula* Roth. from Scandinavian origins which had shown good initial growth in Scottish provenance trials proved to be susceptible to damage by late spring frosts after mild winters as long as 10 years after planting and therefore eventually experienced substantially higher mortality than native origin material.

Thus, where local and non-local provenances are mixed in composite provenancing, there is a risk that vigorous non-local

material from benign climates may survive and grow quickly for a period of time during which it outcompetes the more conservative local provenance. In extraordinary circumstances, a possible scenario is that a rare event which later kills the non-local provenance material would result in the absence of woodland cover, as the local outcompeted provenance material would no longer exist to replace the dead non-local material.

Apart from these considerations, it is also important to investigate two assumptions crucial to the validity of the predictive provenancing approach; that we can predict with some certainty the future climate, and that analogues of these future climates can be found today within the range of our native tree species. Several problems limit our ability to predict future climate in GB. Firstly, the environment, particularly in upland regions, is heterogeneous at a fine geographic scale. Interpolated climate projection models are insufficiently fine grained to take strong microclimatic influences on biota into account (Suggit *et al.*, 2011). For instance, the UKCIP02 models (Hulme *et al.*, 2002) which are applied in Broadmeadow and Ray (2005), treat the UK as a series of 50 x 50 km grid squares and are likely to underestimate climatic complexity by reporting smoothed values over large and complex areas. Approaches to enhancing the precision of climatic projections have advanced since 2002, and decision support systems now include 5 x 5 km gridded projections (Jones *et al.*, 2009). Nonetheless, even these are likely to be too coarse-grained to be used for certain aspects of site-scale planning, especially in heterogeneous environments and are themselves, not free of uncertainty. Secondly, British weather and ecosystems are strongly influenced by the North Atlantic Oscillation, which causes variable winter weather conditions (Ottersen *et al.*, 2001; Stenseth *et al.*, 2002). In some years, changes in circulation patterns may result in conditions that are very different from the averages predicted by long-term climate models. For translocated material, timing of phenological events such as bud burst and bud set may be asynchronous with the beginning and end of the local growing season. This phenological mismatch could lead to frost damage at times when translocated material is not dormant (Vitasse *et al.*, 2009; Cavers and Cottrell, 2015). Trees which are under stress because of maladaptation are less well equipped to resist pests and pathogens (Telford *et al.*, 2015), some of which are also expected to increase in frequency and severity under climate change (Battisti *et al.*, 2005; Sturrock *et al.*, 2011). These differences in phenology could also have negative impacts on associated species if, for example, earlier bud burst reduces the time and capacity of vernal plant species to reproduce (Buckley and Blakesley, 2008; Roberts *et al.*, 2015).

A final concern is that while studies demonstrate poleward, or up-slope migration of some species in response to warming or drying (Parmesan and Yohe, 2003), this cannot be expected to be a universal rule. The consequences of climate change are likely to be more complex than poleward movement of conditions, as some aspects of the current environment, such as photoperiod, which can also be linked to phenological activity (Koski and Sievanen, 1985) and continentality will be held constant (Aitken and Whitlock, 2013). Other climatic factors, such as windiness and cloud cover, will not change in a directional manner. There is, therefore, no present-day analogue of future climates, and so treating space as a substitution for time is problematic (Williams *et al.*, 2007; Benito-Garzon *et al.*, 2013b;

Nagamitsu *et al.*, 2014). A more likely scenario is that future conditions will involve increased inter- and intra-annual climatic variability, leading to wider extremes (IPCC, 2013), which adds further complexity to efforts to predict the direction and strength of change.

Practical implementation in GB forestry

On the basis of the considerations given above, it is reasonable to make use of predictive provenancing only under a restricted set of conditions (Aitken and Whitlock, 2013). These are where future climate predictions are robust, climates analogous to the future predicted climate exist within the range of a native species and environmental heterogeneity for parameters other than climate is low. In GB this restrictive set of conditions is most likely to apply to seed sourcing in lowland southern England. The inclusion of varying proportions of southerly provenances alongside local provenance material in new plantings has been recommended as an adaptation strategy in England by Forestry Commission England (Broadmeadow *et al.*, 2005; Forestry Commission England, 2010; Morison *et al.*, 2010; Weir, 2015), as well as by Natural England and the RSPB (2014). A recommendation is to use a mixture of planting material derived from seed from multiple provenances located 2–5° further south than the planting site, provided that distance from the Atlantic Ocean of seed sources is similar to that of the planting site. Recommendations suggest that these should be used in addition to at least one-third local provenance material (Forestry Commission England, 2010), although these guidelines are rather general and open to interpretation. An aspect that appears to be missing from the guidelines is a recommendation to match as far as possible the edaphic and biotic components of the environment at the planting and source sites.

Species change

As a consequence of environmental change, predictions may indicate that a species will no longer be able to survive in its present site, no matter where it is sampled from in its natural distribution. This would be the case if a species were present at the trailing edge (southern margin of the species range exposed to currently warmer conditions) of its distribution and predicted climate fell outside the envelope currently occupied, an uncommon situation in British native trees. Alternatively, a species may be threatened with extirpation by a novel introduced pathogen to which it possesses no resistance (Anagnostakis, 1987). In both of these cases, the only remaining strategy would be replacement with an ecologically similar species, in the second instance by one unaffected by the exotic pathogen (Mitchell *et al.*, 2014). In the context of new native woodland creation, this would only be appropriate if the replacement species was native and capable of sustaining native biodiversity. Thus, typical replacement species that would not otherwise naturally colonize the site would be ecologically similar native species with a restricted current distribution and limited dispersal abilities, but with the possibility of assisted range expansion under climate change. In this scenario, it may also be appropriate to allow for natural colonization by other native species in existing stands, or to buffer the absence with multiple native species (Mitchell *et al.*, 2014).

A more radical suggestion that has been proposed in situations where native species are threatened with extirpation by introduced exotic herbivores and pathogens is the replacement of a native species by a closely related exotic species resistant to the threat organisms. A case in point is the proposed replacement of ash that is susceptible to *Hymenoschyphus fraxinea* (T. Kowalski) Baral, Queloz, Hosoya by a resistant exotic ash from Asia (Boshier and Buggs, 2015; Harper et al., 2016). The exotic species would be used in the expectation that it would take over the ecological role of the threatened species.

There are a number of important objections to this proposal. Firstly, while exotic forest plantations have been shown in some cases to provide habitat for a comparable total number of native species to semi-natural woodlands (Sax et al., 2005; Quine and Humphrey, 2010), community composition is not the same (Quine and Humphrey, 2010). Changes in composition are likely to have the greatest effect upon species which are strongly associated with particular native host species, for example, epiphytic lichens, which may fail to establish in the novel environment or be displaced by generalist taxa (Mitchell et al., 2014). It is, however, very difficult to generalize about the possible complex effects of exotic vs native forests on biodiversity but a useful discussion is presented in Carnus et al. (2006). Secondly, although there are many examples of tree species introductions being considered 'successful' from an economic perspective (Koskela et al., 2014), many introductions have proved to be failures or have had profound ecological consequences, at least at local scale (Peterken, 2001). A good example of introductions that held initial promise, albeit not for nature conservation objectives, but ultimately failed is that of the five-needle pines *Pinus monticola* Douglas ex D. Don. and *Pinus strobus* L. that are currently being promoted for planting in GB (<http://www.silvifuture.org.uk/species>). Previous introductions of these species to GB failed because both are susceptible to white pine blister rust *Cronartium ribicola* J.C. Fisch. which causes debilitating girdling cankers (Pawsey, 1963; Geils et al., 2010).

Even if introduced species do survive, in the absence of long-term provenance trials with the exotic species, it would be difficult to match seed sources to site. The resulting stressed trees may either not survive or act as a susceptible host to native herbivores and pathogens with which they had not co-evolved (Watt, 1986; Peterken, 2001; Castagneyrol et al., 2014), allowing the pest and pathogen populations to increase and put further pressure on the already threatened native species (Ennos, 2001, 2015). For example, Corsican pine *Pinus nigra* subsp. *laricio* Maire is a widespread exotic in GB that has recently proved highly susceptible to *Dothistroma* needle blight, *Dothistroma septosporum* (Dorog) Morelet and generated inoculum levels that are sufficient to threaten native Scots pine, *P. sylvestris* (Brown and Webber, 2008). Additionally, the planting of new exotic species could act as a conduit or foothold for entry of exotic herbivores and pathogens capable of switching to the native species.

A final objection to the introduction of exotic species is the possibility that the exotic species, released from its natural enemies may become invasive (Reinhart et al., 2003). There are many (hundreds) examples on a global scale, of introduced woody plants becoming invasive (Richardson and Rejmánek, 2011). In some instances, these can have unforeseen interactions with other introduced species, leading to multiple negative feedbacks—or 'invasion meltdown' *sensu* Simberloff and Von

Holle (1999). For instance, in Patagonia, introduced red deer *Cervus elaphus* L. were found to graze native vegetation preferentially, which in turn favoured the continued invasion of native habitats by introduced Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco (Relva et al., 2010). Thus, before the hasty introduction of new exotic species on a wide scale, attention must be paid to the possibility of highly undesirable ecological interactions involving these exotic species and related native trees and their pests and pathogens (Castagneyrol et al., 2014; Branco et al., 2015; Ennos, 2015). Multiple simultaneous introductions of exotic species to Britain for any purpose have the potential to cause a host of unforeseen and complex ecological problems

Practical implementation in GB forestry

In the UK, there are very few examples of native tree species at the trailing edge of their distributions which are likely to find themselves outside the species' climatic envelope within the next generation. Therefore, as a putative climate change adaptation strategy, there appears to be no necessity for species change caused by this phenomenon. On the other hand, there are a number of species that are at the leading edge of their distributions (northern range margins) with the possibility of expansion to the north under climate change. Some obvious examples are hornbeam, *Carpinus betulus* L., black poplar *Populus nigra* L. and the two limes, *Tilia cordata* Mill. and *Tilia platyphyllos* Scop. Adding these species to planting schemes taking place outside their current range affords the opportunity to enhance their natural rate of northward spread under climate change which may otherwise be inhibited by habitat fragmentation. While these activities are rather more aligned to species conservation programmes, than ecosystem-oriented restoration (Sansilvestri et al., 2015), encouraging diversity of native species in new plantings may confer additional biological resilience to climate change, but is only appropriate in situations where appropriate seed sources can be identified.

A case where rapid change in the biotic environment suggests the implementation of a species change policy is that triggered by the introduction of the exotic pathogen *Hymenoschyphus fraxineus* into Britain. Species change to an ecologically similar native species, such as aspen, *Populus tremula* L. which is unaffected by the pathogen, is currently one of the options being pursued, as well as attempting to account for the loss of ash by using a range of other native species (Mitchell et al., 2014). It is worth noting, however, that to discontinue the use, including management designed to encourage regeneration of any species for plant health reasons would necessarily reduce its capacity to evolve resistance to the pathogen or adapt to environmental change.

Conclusions

Climate change is just one of many challenges to the maintenance and expansion of woodland cover in GB. Other factors include high herbivore density, patterns of land use and ownership, infrastructure development, pests and diseases. The threat posed by these multiple pressures and the interactions between them highlight the need to recognize that there is no 'quick fix' for adaptation to climate change and no single seed sourcing strategy can be seen as a surrogate for sound, continued

woodland management, including that which aims to encourage natural regeneration and colonization. Several potential problems have been identified with intervention strategies. However, maintaining the *status quo* may also be problematic. A moderate approach might involve updating or extending the *status quo* in order to improve knowledge and make better use of existing genetic resources and evolutionary processes, thereby ensuring that native tree seed sourcing is better grounded in biological principles. In the short term, this would involve using environmental information to better match seed sources with planting sites, rather than focusing strictly on the current system of seed zones while continually monitoring populations further south which are likely to experience climate change related problems before they occur in Britain. However, in the longer term, this ought to be informed by a more detailed understanding of the responses of tree species and the populations within them to different environments. To achieve this, we firstly need information from a range of populations on their ability to acclimate to novel environmental conditions. Secondly, we need information on the pattern of adaptation of trees across the landscape in response to environmental factors, so that presently adapted seed sources can be identified for any particular planting site. Thirdly, we need a better assessment of the extent of genetic variability in standing tree populations. Although adaptation will depend on a whole range of factors, for some traits a measure of the extent of heritable genetic variation in populations can be obtained from progeny trials. This will allow an indication of likely rates at which populations might adapt to a novel environment if natural regeneration occurs. Finally, we need to know the limits of adaptation or tolerance of the species as a whole. This will determine whether a population of the species can realistically be expected to adapt to and survive in changed conditions. In the immediate absence of this information, it is necessary to pay close attention to the risks identified in this article before exposing newly established woodlands to the many uncertainties in the implications of predictive provenancing and species change. Any such efforts must initially be conducted conservatively and treated as long-term experiments until sufficient evidence can be found which suggests that these strategies are necessary, effective and can be implemented practically.

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Conflict of interest statement

None declared.

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