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Is local best? Examining the evidence for local adaptation in trees and its scale

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Abstract

Background: Although the importance of using local provenance planting stock for woodland production, habitat conservation and restoration remains contentious, the concept is easy to understand, attractive and easy to 'sell'. With limited information about the extent and scale of adaptive variation in native trees, discussion about suitable seed sources often emphasises "local" in a very narrow sense or within political boundaries, rather than being based on sound evidence of the scale over which adaptation occurs. Concerns exist over the actual scale (magnitude and spatial scale) of adaptation in trees and the relative dangers of incorrect seed source or restricted seed collection, leading to the establishment of trees with restricted genetic diversity and limited adaptive potential. Tree provenance and progeny field trials in many parts of the world have shown the existence of genotype by environment interaction in many tree species, but have not necessarily looked at whether this is expressed as a home site advantage (i.e. whether provenance performance is unstable across sites, and there is better performance of a local seed source).

Methods/design: This review will examine the evidence for local adaptation and its scale in a number of native tree species from different trial sites across the globe (e.g. tropical, Mediterranean, temperate). These trials have been measured and in some cases results published in a range of formats. The data have, however, usually been presented in the form of which provenances grow best at which sites. The review will examine existing data (published and unpublished) in the context of the scale of local adaptation, with the results being presented in two formats: (a) relating survival, performance of provenances (classified by seed zone/provenance region of origin) to seed zone/provenance region of the planting site; (b) plotting survival, performance provenances against the distance (Euclidean/ecological) between the provenance and the trial site.

Keywords: Provenance trial, Reciprocal transplant experiment, Fitness, Seed source, Local adaptation, Restoration

Background

Trees are key components not only of forests and woodlands, but also of diverse agro-ecosystem landscapes, offering numerous and varied opportunities for both the use and conservation of native species (e.g. [1]). Planting of native tree species for forest or habitat restoration and other purposes on farms depends on a ready supply of germplasm (seeds or vegetative material), which in turn requires consideration of what is the best or most appropriate source of seed. Although 'what was available' often determines what is planted [2], choice of seed source, both in terms of its location and genetic composition, can have important consequences for the immediate success and long-term viability of plantings. Choice should be influenced by the objective of planting (e.g. for restoration or production, future adaptability or past adaptation) and the risks associated with particular seed sources (e.g. loss of adaptation, outbreeding depression, loss of diversity—genetic bottlenecks, or contamination of native gene pools prioritised for conservation). The mantra of local adaptation is one that has been widely spread and practically invoked in issues of habitat restoration and more general seed sourcing. Local genotypes are assumed to be better adapted to local conditions, as natural selection over time increases the frequency of

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genes that improve fitness; selecting for variation that is adaptive. Forest certification and timber labelling standards require action to conserve genetic diversity and to use local provenances (e.g. [3, 4]), while in some countries grants for tree planting may require the use of local material (e.g. [5]). The concept is easy to understand and the message is therefore attractive and easy to 'sell' (e.g. [6]).

The importance of local provenance in sourcing planting stock for forest production, habitat conservation and restoration does, however, remain contentious (e.g. [7, 8]). Concerns exist over the actual scale (magnitude and spatial scale) of adaptation in trees and the relative dangers of incorrect seed source or restricted seed collection, leading to the establishment of trees with restricted genetic diversity and limited adaptive potential. An undue emphasis on local seed sources or poor practice in seed collection may drive sourcing from small populations or a limited number of trees, producing populations that are unlikely to be both adapted and adaptable and therefore with limited potential for long-term persistence [9].

The relative degree to which morphological and growth differences in plants are under genetic or environmental control has been a fertile area of study. Ecologists are generally familiar with the classic genecology "common garden" transplant experiments that showed widespread occurrence of intraspecific, habitat-related, genetic variation in herbaceous species [10]. Clausen et al. [11] extended study of the expression of population adaptation to environmental differences, by using climatically different sites over a range of altitudes. Subsequent research has shown that such genetically related adaptive variation is widespread in herbaceous species with low levels of gene flow under strong selection pressures (summary in [12]).

Discussion about suitable seed sources often emphasises "local" in a very narrow sense or is based on political boundaries, rather than hard evidence for the scale of adaptation [13]. Across Europe countries are divided into provenance regions and/or seed zones, though the scale and number varies from country to country, rather than directly with variation in climatic factors. The delineation of Britain into four provenance regions and smaller seed zones took a pragmatic approach based on accumulated summer heat, mean annual rainfall, ecological and physical boundaries [14]. The adjustment, within the same region, of seed zone size to account for species differences in scales of adaptation and relationships to climatic factors, such as in the north-west USA [15] is rare. In Australia no such boundaries exist, but application of the precautionary principle regarding seed movement prevails and quarantine regulations limit the unrestricted movement of germplasm between some states.

Consideration of some basic genetic concepts can help understand the extent and scale of local adaptation that may apply to tree species. Natural selection may vary across a species distribution (divergent selection), causing each local population to evolve traits that provide an advantage under its local environmental conditions (i.e. its habitat), regardless of the consequences of these traits for fitness in other habitats. What should result, in the absence of other forces and constraints, is a pattern such that resident genotypes in each population have on average a higher relative fitness in their local habitat than genotypes from other habitats. This pattern and the process leading to it is known as local adaptation [16]. However, local adaptation may be impeded by gene flow, countered by genetic drift or natural selection due to temporal environmental variability and limited by a lack of genetic variation or by the genetic structure of underlying traits. Thus, although divergent natural selection is the driving force, these other forces, in particular gene flow, are integral to the spatial distribution of genetic variation and local adaptation is not an inevitable outcome of evolution under spatially divergent selection [17]. Environmental heterogeneity also favours evolution of adaptive phenotypic plasticity. Where there are no costs of and constraints on plasticity, a genotype that produces a locally optimal phenotype in each habitat should become fixed in all populations. Adaptive phenotypic plasticity would lead to adaptive phenotypic differentiation, but without underlying genetic differentiation [17].

In summary, factors predicted to promote local adaptation include: low gene flow (i.e. restricted pollen/seed dispersal or strong habitat fidelity), strong selection against genotypes optimally adapted to other habitats but moderate selection against intermediate genotypes (most likely under moderate differences between habitats with respect to traits under selection), little temporal variation in the forces of selection, small differences between habitats in quality (e.g. the amount of resources), and costs of or constraints on adaptive plasticity [17].

Most evidence of local adaptation comes from herbaceous plants with low levels of gene flow under strong selection pressures (e.g. heavy metal soil tolerance; [12]), factors which seem less likely to be present in the context of many tree species. There are many key differences between herbaceous plants and trees, where long life cycles, wide distributions and extensive gene flow (pollen and seed dispersal) tend to suggest more extensive scales and patterns of adaptation, and that local adaptation over a small geographic scale is unlikely unless selection forces are very strong e.g. very high environmental variation in frost resistance in *Eucalyptus urnigera* over a 450 m altitudinal transect on Mount Wellington, Tasmania [18, 19]. The prevalence of extensive gene flow may counteract selection, while temporal variation in selective forces that trees experience (e.g. yearly variation in temperature, rainfall, frosts) may have a stabilising effect rather than directional selection that would lead to highly localised adaptation. Given the long life of trees, the environment is also likely to have altered such that a particular site no longer experiences the same conditions under which the trees originally evolved. Such temporal variation in environment may be particularly important for trees, not only with respect to past adaptation but also in the context of climate change requiring more adaptive sourcing strategies [20].

As early as 1759 Linnaeus observed that yew trees from France grown in Scandinavia were less winter hardy than indigenous Swedish yews, while du Monceau planted different pine sources at common sites from 1745 to 1755, motivated by a need for material for shipbuilding rather than scientific insights into intraspecific variation of pines. Such utilitarian motives led to the establishment of formal common garden forestry experiments (provenance trials) in Europe from the 1890s. Such provenance and also progeny trials can provide information about levels and patterns of quantitative genetic variation and the extent of genotype-environment interaction for tree species. In temperate trees most morphological genetic variation occurs within rather than between provenances, but there is evidence for adaptive variation in a number of tree species in North-West America, owing to features such as aspect and altitude (e.g. [21–23]). The degree of risk in transplanting across a species' distribution is correlated more with environmental changes than with the geographical distance moved [21]. Geographical proximity may be a poor indicator of adaptive fitness (e.g. *Betula* spp. [24]) and also stability, with some provenances which show stable performance across sites located adjacent to unstable performers (e.g. [25]). Provenance and progeny field trials in many parts of the world have shown that while genotype by environment interaction occurs in many tree species, this may not be expressed as a home site advantage: i.e. provenance performance is unstable across sites, but not from better performance of local seed source [26].

Reciprocal transplant experiments (RTEs), which test the performance of home and away genotypes within the sites from which the genotypes originate [27] are better suited to test directly for local adaptation to environmental heterogeneity in trees. The experiments can mimic natural regeneration by establishing in a wood, at close spacings to encourage early competition, and with minimal intervention (e.g. little or no weeding). In subjecting the plants to more natural conditions than in most provenance trials, it is possible to study responses to natural processes within the environment at each site, including competition with the native flora. They allow examination of how well the scale of adaptation relates to existing provenance zones and guidelines for sourcing and certifying reproductive material and whether the scale of adaptation under natural regeneration conditions is similar to that shown in plantation provenance trials. Although most RTEs of herbaceous plants have identified localised adaptation at the finest scale examined (e.g. [28–31]), there appear to be few truly reciprocal transplant experiments undertaken on trees (e.g. [32, 33]).

The question arises as to what empirical scientific evidence exists in trees for deciding whether the local seed source performs best, or how local a seed source should be? In other words, what is the geographic scale at which local adaptation occurs in trees? Should seed come from the same wood, forest, remnant, the same watershed, the same county or country? Is geographical or ecological distance more important? (e.g. [34]). There appears to be a rich literature, primarily genecological studies, that report variation in traits expected to be of adaptive importance in trees and factors that influence this variation. The assumption is that the adaptive traits measured reflect, or are correlated with, fitness, although they may not directly study adaptation (represented by long-term growth, survival, or fecundity), nor whether the local population performs best. Indeed, considering some adaptive traits maybe problematic, such as considering what date of budburst is best compared to that of other populations? The response function maybe linear, rather than curvilinear such as in growth or survival. One review suggests that there may be few direct empirical studies of local adaptation in tree species (e.g. [35]), although this appears to have avoided the 'grey' literature which is potentially rich in the reporting of provenance trials of native tree species.

Objective of the review

The primary aim of this systematic review is to review the evidence for local adaptation and its scale in native tree species in different parts of the world (e.g. tropical, Mediterranean, temperate, boreal). Thus we want to address the following primary and secondary questions.

Primary review question

Is local best—do local trees perform better than other trees?

Secondary question

Does local adaptation in trees vary with species' characteristics?

We take a broad view of "species characteristics" covering all aspects that are detailed as effect modifiers.

Methods

This systematic review will undertake an extensive literature search to assess the evidence for the existence and scale of local adaptation in tree species in different regions of the world (tropical, Mediterranean, temperate, boreal). Data will be extracted for meta-analysis of at least a sub-set of the review questions. Findings are expected to help inform current and future policy on seed sourcing for tree planting and forest restoration in a variety of contexts. In particular it should provide an evidence-base for examining practice in developing seed zones, the extent to which the scale of adaptation relates to existing provenance/seed zones and guidelines for sourcing and certifying reproductive material.

Search strategy

Although the scope of this systematic review is relatively narrow, the precise nature and type of experimental data that address the question mean that it can be difficult to identify relevant studies solely from titles and abstracts. "Adaptation" for example is a broad concept which would produce many papers that discuss traits of potentially adaptive importance, but do not present evidence for or against the presence of local adaptation. Similarly, "provenance trial" is too broad, as it will produce a large number of papers that report results for species that are not native to the trial site (i.e. exotic species) and therefore say nothing about local adaptation. Such papers may also show evidence of genotype environment interaction, but the lack of any seed source that can be considered 'local' means that there is no evidence on local adaptation. These issues are expressed in the exclusion criteria below.

A subgroup of protocol authors tested different search strategies, using combinations of key words and phrases compiled in a two-day scoping meeting. These strategies were tested against a reference list of papers (see "Appendix") to refine the search and achieve a balance between extracting an unmanageable set of papers which 'might' contain a table of useful data and a narrow set with known useful data, but which might reflect the authors' bias and not represent the overall evidence base. Keywords and phrases for searches in the main bibliographic databases (indicated by an asterisk in Table 1) were derived from the PICOs listed below, with the terms and search logic shown below.

It is vital to consider studies published in languages other than English and so the search strategy will be applied (and documented carefully for peer review) to the following languages: English, French, Spanish, Portuguese and German, subject to time and resources but excluding Russian, Chinese, Japanese, except where they have good English summaries or tables/figures with English captions. Given the reporting of many field trials in non-peer reviewed technical reports, there will also be a heavy emphasis on the use of grey literature. Criteria for selection will be based on documented quality of data collection, rather than source of the data and will include consideration of suitable replications, accuracy and reliability of data analysis.

Table 1 Databases and websites

Bibliographic databases	Grey literature
Web of Science[a]	Institutions
CAB Abstracts (with particular focus on the Forestry & Forest Products Abstracts subset)[a]	Bioversity-EUFORGEN network
Scopus[a]	FAO
Agricola	USDA Forest Service
Agris	ICRAF
JSTOR	CIFOR
Web searches	CATIE
Google	IUFRO
Google Scholar	

[a] Relate to sources which will be searched using strategy

PICOs: components of the primary question

Population undomesticated indigenous forest trees (results of trials are a function of natural selection and not human selection).

Intervention selecting/using local trees.

Comparator selecting/using non-local (distant) seed sources (measured by either geographic/euclidean or environmental distance).

Outcomes measures of performance (survival, growth, productivity).

Relationships between PICOs are shown in Fig. 1 which presents a 'theory of change' showing how interventions are thought to have an impact or cause a change in the population's performance, depending on whether or not local adaptation exists. Thus where local adaptation exists use of non-local material in habitat restoration will lead to sub-optimal results. Changes in climate are viewed as an effect modifier in a similar context to movement of a population, as it may place a population in a new environment and hence reduce the previous importance of local adaptation. The effect is however not measurable owing to the uncertainty of future climates.

Definitions

Local although central to the question, a definition of 'local' is problematic. One of the expected outcomes of the review is to be able give a more reasoned definition of what constitutes a local seed source and this will be an iterative process. Initially we will test use of the following definition or criteria to decide if 'local' material has been

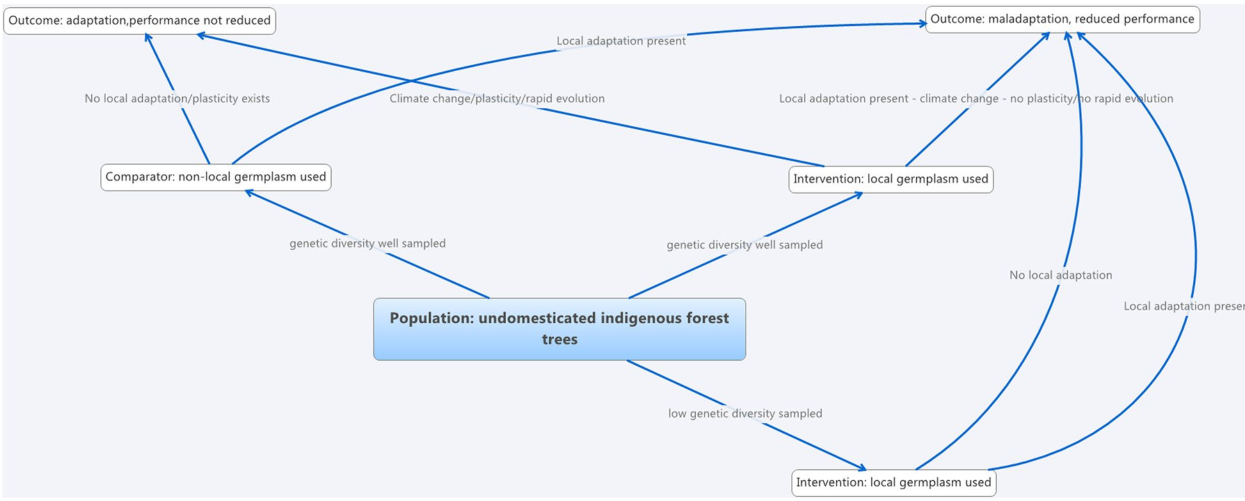

Fig. 1 Theory of change showing how interventions may impact on or change a population's performance, depending on whether or not local adaptation exists

included in a trial: (1) if the authors give a definition or state that a particular seed lot was included as local material or as a control, (2) if a trial contains a seed lot from the same seed zone/provenance zone as the trial site location (applicable where a country has defined seed/provenance zones), (3) if a trial contains a seed lot from a site with similar soil/climatic conditions to the trial site and within a distance over which there is evidence of extensive pollen flow for the species.

Other

In addition to systematic searching (as above), references in relevant books will also be searched as time and resources permit with supplementary searches such of bibliographies and literature provided directly by stakeholders/review authors. Unpublished data from trials the review authors know exist that fulfil all the criteria, but not currently publically available will also be accessed.

Search terms and Boolean logic

Following scoping trials, searches in CAB Abstracts, Web of Science and Scopus will be based on the logic A AND B AND C AND D, where A,B,C,D are the sets of terms listed below. nb CABICODE will only be used in CAB Abstracts. In Scopus and Web of Science this will be omitted.

A: (tree or shrub or forest or woodland or woods) or KK*.cc. [CABICODE for 'forests and forestry]).

AND

B: (local or reciprocal or natural or native or reciprocal or transplant or translocation).

OR

(provenance).

OR

(native or endemic or local or reciprocal or natural or transplant or translocation).

AND.

C: (plasticity or Adaptation or Ecotypes or "genetic diversity" or "genetic parameters" or "genetic variability" or "genetic variation" or "genotype environment interaction" or genotypes or "genotypic variability" or "genotypic variation" or "geographic distribution" or "geographical distribution" or "geographical origin" or "geographic origin" or "geographical races" or "geographic races" or "geographical variation" or "phenotypic variability" or "seed sources" or "genetic differentiation" or "geographic variation").

OR

(Adaptation or Ecotypes or "genetic diversity" or "genetic parameters" or "genetic variability" or "genetic variation" or "genotype environment interaction" or genotypes or "genotypic variability" or "genotypic variation" or "geographic distribution" or "geographical distribution" or "geographical origin" or "geographic origin" or "geographical races" or "geographic races" or "geographical variation" or "phenotypic variability" or "seed sources").

AND

D: (variety trial*" or "field experiment*" or "field test*" or "provenance trial*" or "provenance test*").

Tested on 4/3/2015–yielded 4497 records.

Article screening and study inclusion criteria

The review will involve the identification of field trials that fulfil the criteria to yield suitable data. This review will use existing data from established provenance trials to examine the evidence for local adaptation and its scale in a number of native tree species in different parts of the world (e.g. tropical, Mediterranean, temperate, boreal). These trials have been measured and in some cases results published in a range of formats. The data have, however usually been presented in the form of which provenances grow best at which sites. Studies will be included if they are of tree species within their indigenous range and include information on the interventions and outcomes set out in the PICO list above. Consequently, a complete list of interventions and outcomes will be documented iteratively as these emerge. A subgroup of authors will select papers retrieved from the searches, following removal of duplicates. The first stage of inclusion/exclusion will entail screening for relevance of articles by title followed by screening using titles and abstracts together; finally the assessment will be based on reading the full text. At each stage, studies will remain in the set to be included if they MAY contain relevant information about the interventions or outcomes. This will help reduce the possibility of being overly-restrictive about relevant outcomes at the outset. Assessments of randomly selected sets of 100 articles will be conducted to test consistency between researchers' screening judgment at each stage of the inclusion/exclusion process. Cohen's Kappa metrics will be used to indicate a measure of consistency, with a consistency co-efficient of $\geq$0.6 usually accepted as adequate [36]. Results of screening will be documented (including reasons for exclusion) and available as supplementary material to the systematic review paper.

Exclusion criteria

Papers will be excluded if the reported study/field trial is:

- of an herbaceous species, bamboo i.e. not a tree (palm 'trees'/shrubs >3 m will be included).
- of an exotic species. i.e. the species is not indigenous to the region where the trial is established.
- of an indigenous species but the germplasm sources are of domesticated, selected, or cultivar(s), varieties.
- of an indigenous species, but there is no valid *local* seed source in the trial.
- of an indigenous species and there is a valid local seed source in the trial, but there is no other source with which to compare.
- no data on performance traits.

Effect modifiers

The following will be recorded, where available as potential effect modifiers and sources of heterogeneity. These will in turn allow assessment of the relative scale of distances between the Intervention and Comparators (strength of effect modifiers) and the scale of responses.

Species distribution (latitude, longitude range, then classified as widespread, narrow, continuous, disjunct, soil types).

Scale of sampling of the species distribution.

Sampling protocol for germplasm collection (genetic diversity well or poorly represented).

Trial site(s) geographical location (latitude, longitude, continentality).

Trial site(s) altitude.

Trial site(s) climate (rainfall, length of dry season).

Trial site soil type.

Nursery conditions.

Trial management.

Range of trial sites.

Family/genus.

Species dispersal syndrome (pollen and seed).

Species ecological guild (e.g. pioneer, climax).

Biome (e.g. boreal, temperate, tropical).

Study quality assessment

Studies included in the review after full text screening will be critically appraised for study design, the robustness of their study design and the extent to which authors have attempted to limit bias. Variables outlined in Table 2 will be used to construct a list from which the quality of individual studies can be assessed. Studies will be categorised as having high or low susceptibility to bias on the basis of presence/absence of replication, measures of variance and potential effect modifiers. Studies with high susceptibility to bias will not necessarily be excluded from the narrative review, but will be subjected to sensitivity analysis following Brooks et al. [37]. We are aware of the proposal by Bilotta et al. [38] that environmental systematic reviews should adapt the Environmental-Risk of Bias Tool and we will check the feasibility of this approach for our set of studies. Studies that are scored as 0 or poor for 'sampling of germplasm' and 'precision of measuring effects' (Table 2) will be excluded. Studies scored as poor for 'replication' will be excluded if they are the only study of that species, but could be included in meta-analysis where there are a number of studies of the same species.

Although our review will include a number of older studies, use of robust randomised complete block designs has been commonplace for a long time in forestry research, such that provenance trials have generally had good experimental design and replication. Bias is most likely in the process of seed collection through sampling a small number of trees within a population and in sampling a restricted part of a species natural range. Differential treatment of provenances within trial (e.g. management that lead to distortions, fertiliser,

Table 2 Criteria for critical appraisal and data extraction from studies selected after full text screening

Main sections	Criteria for critical appraisal	Assessment	Data extracted
Description of the study site(s)	Are the location of trial sites known?	If not then individual provenances or trial sites within studies excluded. Ultimately study excluded	Latitude and longitude of trial sites and germplasm sampling sites
Population	Are the location of the germplasm sampling sites known?	If not then individual provenances or trial sites dropped. Ultimately study excluded	Latitude and longitude of trial sites and germplasm sampling sites
Methods (clear and repeatable methodology)	Sampling of germplasm	0 = no info Poor <10 trees (individual provenances dropped) Good >10	Number of trees collected from in provenance seed sample
	Precision of measuring effects	0 = no info Poor <10 trees (individual provenances or trial sites dropped. Ultimately study excluded) Good >10	Plot size (no of trees)/shape, number of plots, treatments, blocks, replications and test sites (see also below)—number of trees that contributed to the mean
	Replication	0 = no info Poor <3 provenances and replications Good ≥3 provenances and replications	
	Outcome measured at relevant moment	0 = no information Poor–younger age than data extraction criteria Good ≥age for data extraction criteria	Phenology data ≥2 years after planting Survival data ≥2 years after planting Growth data 15–25 % rotation age
Results	Validity or reliability of data		Data for mean, SD/SE and or ANOVAR indicating significance of differences
	Variables measured allow relevance to performance to be deduced		Survival, growth (height, dbh, volume), disease/pest impact, frost damage, phenology of bud burst/set, flower/seed production
	Evidence of bias to estimates of means	Individual site or whole study excluded	Differential treatment of provenances within trial (e.g. management that lead to distortions, fertiliser, thinning)

thinning), while less likely would result in bias that would lead to a trial be excluded from the review (see Table 2).

Data synthesis and presentation

A narrative synthesis of data from all studies included in the review will describe the quality of the results along with the study findings. Tables will be produced to summarise these results. The review will reanalyse existing data in the context of the scale of local adaptation, the results being presented as:

1. plotting survival, performance (e.g. height, diameter, productivity—volume/ha, basal area/ha) of provenances against the transfer distance (Euclidean/environmental gradients) between the provenance and trial site (site minus source), for all combinations of sources planted at test sites. A transfer function approach gives an idea of the scale of adaptation as measured by the width of the function, as well as an effect size (e.g. 20 % decrease in height if a population moved 2 °C averaged over all test sites/provenance transfers).
2. pairwise comparisons—we will examine options: (1) pairwise comparisons of each non-local provenance to the local provenance, giving proportions of transfers where local are better/worse than distant sources; (2) measuring the effect size as distant minus local (standardized by local site mean).

Where studies report for species in the same; (1) climatic region (e.g. boreal, temperate, tropical), (2) genus (e.g. *Cedrela, Picea, Pinus*), (3) trial with assessments at different age, (4) dispersal syndrome (pollen and/or seed) meta-analysis may be possible. Specific details of the quantitative analysis will emerge once full-text screening has yielded a set of studies that can be assessed for content and quality. If meta-analysis is possible, it will take the form of random-effects models, and meta-regression where effect modifiers cause significant heterogeneity between studies in the context of (1) and (2) above.

Publication bias

There is evidence that in many research areas papers are more likely to be published if they demonstrate clear, positive results (or strong negative effects), and that papers that show little or no effect are less likely to be published. The use of published provenance trial results where the original objective of reporting was to identify the 'best' provenance in terms of growth, form and other variables, rather than identifying local adaptation makes the review less susceptible to bias than might normally be the case. To assess the possibility of such publication bias, we will compare studies in the 'grey' literature with studies in peer reviewed journals to assess whether there is evidence of publication bias [39]. If data allow, we will assess bias using sensitivity analyses [40].

Authors' contributions

All authors discussed the review title in a 2-day workshop, agreed the scope and extent of the review, and contributed to the draft. The full systematic review will be under the leadership of David Boshier. All authors read and approved the final manuscript.

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For the CAB Abstracts database, searching is limited to Title, Abstract and keyword fields using the field limiters shown in the Search terms section. Web of Science and Scopus have a default search mode that interrogates only those fields, which will be used. This eliminates papers that contain any of our keywords in, for example, journal titles, institution addresses, etc. KK100 and FF020 are two of a suite of CABICODES, which are applied as additional indexing categories by abstractors compiling CAB Abstracts. They relate respectively to: Forests and Forest Trees (Biology and Ecology), and Plant Breeding and Genetics. For a full list see http://www.cabi.org/Uploads/CABI/publishing/training-materials/additional-resources/cabi-code-guide.pdf.

Competing interests

The authors declare that they have no competing interests.

Appendix

Reference list of papers for testing adequacy of search strategy on local adaptation in forest trees

1. Alía R, Moro J, Denis JB. Performance of *Pinus pinaster* provenances in Spain: interpretation of the genotype by environment interaction. Can J For Res. 1997;27:1548–1559.

2. Boyle TJB Range-wide provenance tests of black spruce in Ontario. Can For Serv Petawawa Natl For Inst Inf Rep. PI-X-57; 1985.

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4. Cundall EP, Cahalan CM, Connolly T. Early results of ash (*Fraxinus excelsior* L.) provenance trials at sites in England and Wales. Forestry. 2003;76:385–400.

5. Eiche V. Cold damage and plant mortality in experimental provenance plantations with Scots pine in northern Sweden. Stud For Suec 1966, 36:1–218.

6. Eiche V, Andersson E. Survival and growth in Scots pine (*Pinus sylvestris* L.) provenance experiments in northern Sweden. Theor. Appl. Genet. 1974; 44:49–57.

7. Giertych M. Summary of results of the IUFRO 1938 Norway spruce (*Picea abies* (L.) Karst.) provenance experiments. Height growth. Silvae Genetica. 1976;25:154–164.

8. Giertych M: Report on the IUFRO 1938 and 1939 provenance experiments on Norway spruce / Picea abies / L./ Karst./. Polish Academy of Sciences, Kórnik, Poland. 1984.

9. Giertych M. Summary of results on Scots pine (*Pinus sylvestris* L.) height growth in IUFRO provenance experiments. Silvae Genetica. 1979; 28:136–152.

10. Hamann A, Koshy MP, Namkoong G, Ying CC. Genotype × environment interactions in *Alnus rubra*: developing seed zones and seed-transfer guidelines with spatial statistics and GIS. *Forest* Ecol Manag 2000;136:107–119.

11. Hansen CP, Dien PQ, Tung HV: Assessment and analysis of two Pinus kesiya provenance trials in Vietnam: Trial No. 1, Ba Vi, Trial No. 2, Lang Hanh. Danida Forest Seed Centre, 64 p. (Results and Documentation No. 17) 2003.

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