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Introduced forest tree species: some genetic and ecological consequences

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Introduction

Introduction of exotic resources is (and even more significantly, was) a wide-spread practice in almost every European country with a forestry tradition. It is especially so for the host country of this meeting, Great Britain, where introduced conifers play a predominant role in forestry (e.g. Samuel *et al.* this volume). The examples I will use in this paper, however, will be mostly drawn from French ecosystems and forests. They should be considered as models or case studies of a general European situation. I will very often use data from studies performed on *Cedrus atlantica* Carr. at INRA Avignon, France.

An introduced resource can be defined as a resource voluntarily or involuntarily brought by humans into an area where it was not present before. The introduction of forest trees is often the result of a voluntary germplasm (seed, cutting, graft) transfer. A forest resource can be considered introduced at several taxonomic levels—the most common levels considered are species and subspecies. The species *Pseudotsuga menziesii* (Mirb.) Franco was introduced to Europe from North America, the subspecies *Pinus nigra* subsp. *laricio* var. *corsicana* Hyl. was introduced to continental Europe from Corsica. The notion can be extended to further taxonomic levels. Plant material that comes from very different regions of provenance, new improved varieties or any plant material that presents identifiable genetic differences with the native populations of the same species, would qualify as introduced resources.

The concept of introduction should also be approached with space and time perspectives. Within a single country or region, resources can be both introduced and native. In France for example, *Larix decidua* Mill. is native in many mountain ecosystems, although its lowland forests are made of progeny introduced from the Sudeten and Poland. *Pinus pinaster* Aiton is introduced in the inland part of the Landes region (19th century plantations), and native to parts of its coastal dunes. As for time, the further we are from the actual introduction, the more we tend to consider a resource as native. At the scale of the last 15 000 years, almost no forest tree is native to its current distribution area in Europe. At human scale, it seems that a few human generations are sufficient to accept an exotic species as part of the natural landscape, and consider it as native. The acceptance threshold might be when we have no more direct contact with, or no immediate memory of, the people who were responsible for the introduction. There is evidence that *Cupressus sempervirens* L. and *Pinus pinea* L. were introduced by the Romans in south-western Mediterranean Europe (Thirgood 1981), where they are definitely considered as native today. *Cedrus atlantica* was introduced into southern France during the second half of the 19th century. It is now often considered as a natural part of the landscape by city people who enjoy walks under its now closed-canopy forests, although at the same time it is considered as invasive by local natural land managers.

Thus, most conifer resources should be considered as introduced exotics in Europe. Seeds of forests species, such as *Larix decidua, Picea abies* Karst., *Pinus nigra* Arn., *P. sylvestris* L. and *P. uncinata* Ramond ex DC are known to have been moved over thousands of kilometres in huge quantities across the whole of Europe at the end of the 19th century and during the 20th century (see Bartoli and Demesure-Musch (2003) for France). In the following discussion, I will mostly consider introduced forest trees at species and subspecies levels. I will focus on the most recent and massive introductions that occurred during the 19th and 20th centuries.

Importance of introduced conifers in Europe and France

In Europe, only 27% of forests are considered undisturbed by humans and more than 30% of forests are regenerated by planting or seeding. Conifer forests represent 42% of all forests, and mixed forests 40% (MCPFE 2003). The potential for introducing conifers is thus quite high.

In France, introduced conifer species cover more than a third of all conifer forest surface (estimated to be 5 million ha, including pure stands, mixed conifer dominated stands and conifer dominated woodlands) and account for half the annual wood production (Table 1). Introduced conifers are thus economically valuable as they are significantly more productive than native conifers.

Table 1. Introduced conifer species in France: surface area covered and wood production

Taxon	Species status	Surface area covered (ha)	Total production (m^3 per year)
Abies grandis Lindl.	Exotic	26 000	522 800
Abies nordmanniana (Steven) Spach	Exotic	10 000	53 600
Cedrus atlantica Carr.	Exotic	20 000	34 800
Larix japonica Carr.	Exotic	13 000	176 000
Picea sitkensis (Bong.) Carr.	Exotic	50 000	726 000
Pinus nigra subsp. *nigricans* Host.†	Exotic	192 000	1 200 000
Pinus nigra subsp. *laricio* Maire † (continental France)	Exotic	151 000	1 200 000
Pinus pinaster Aiton ‡	Native	~ 1 000 000	12 500 000
Pseudotsuga menziesii (Mirb.) Franco	Exotic	340 000	4 250 000
Totals (introduced conifers)		1 802 000	20 663 200
Totals (all conifers)		5 000 000	42 000 000

Source: Inventaire Forestier National (http://www.ifn.fr)

† P. nigra subsp. salzmannii (Dunal) Franco is the only native black pine in continental France

‡ Total (introduced and local provenance) Pinus pinaster forest surface area is 1 360 000 ha in France

Consequences of introductions for native forest ecosystems

Exotic forest resources have often been introduced for ecosystem rehabilitation when authorities in charge of forest management considered an area degraded, i.e. depleted of forests (for example after fire or over-grazing). This was particularly the case in the 19th century in many countries where introductions were part of massive reforestation programs for watershed management and erosion control after severe floods caused serious damage. The Mountain Rehabilitation Programme (French acronym RTM) which started during the second half of the 19th century in France is a good example (Bartoli and Demesure-Musch 2003). Exotic tree species were used because they were often proven to be better colonizers then autochthonous species in localized arboretum-like experiments. In France, *Pinus nigra* subsp. *nigricans* var. *austriaca* Loud. demonstrated better survival and growth than several other tree species in eroded Alpine regions and after several waves of plantations, now covers extensive areas (Table 1). These reforestation programmes continued well into the first half of the 20th century (Bartoli and Demesure-Musch 2003). Later reforestation programmes were based on more sophisticated scientific background, such as national and international networks of common garden species and provenance comparisons. More recently, exotic forest tree species have been used to reclaim forest areas destroyed by intense industrial air pollution in Central Europe (Küssner and Mosandl 2002).

Other cases of introduction might be linked to religious, agronomical value or a combination of several interests. For example, *Cupressus sempervirens* can be found near churches in the Mediterranean basin or as wind-breaks in southern France. *Pinus pinea* was introduced in the Mediterranean basin for its edible seeds, its value for landscaping, timber and resin production (Prada *et al.* 1997) and used as a landmark for Protestants in France during periods of religious persecution.

Two main types of impacts can be expected to occur because of the introduction of forest tree species: ecological and genetic.

Ecological consequences of exotic conifer introductions

Effects on soil and ecosystem functioning

Because introduced conifers are generally strong competitors for all environmental resources, their plantation can lead to colonization and invasion (*sensu* Richardson *et al.* 2000) of native ecosystems. Exotic conifers that become invasive can seriously affect water flow in rivers, as demonstrated by exotic pines in South Africa (Richardson and Higgins 1998).

Conifers are also notorious for decreasing litter and soil pH; for example, see Scholes and Nowicki (1998). This can alter carbon, nutrient and water cycles and soil biodiversity. Effects on biogeochemical cycles can be especially strong for those species that are planted or colonize acidic or neutral soils, e.g. *Pinus nigra* (Guende 1978). On calcareous soils, however, introduced conifers have demonstrated a positive influence for ecosystem functioning. In mountains of the Provence region of France, for example, recolonization by autochthonous species is facilitated by introduced pines (Guende 1978). These artificial ecosystems are now recolonized by native species and very strong natural recruitment dynamics can be observed (Figure 1).

Figure 1. Introduced species can facilitate recolonization by native species. Recolonization by *Fagus sylvatica* under a 19th century ecological restoration *Pinus uncinata* forest, Mont Ventoux, France. Photo: INRA Avignon.

Effects on landscape and biodiversity

Exotic conifer colonization and invasion can lead to the fragmentation, decrease in size and destruction of native ecosystems. In South Africa, invasive exotic pines have displaced native species and invaded conservation areas (Richardson and Higgins 1998). Although examples of high impact conifer invasions in Europe are as yet lacking, local cases may be found. For example, *Cedrus atlantica* is now rapidly invading native *Quercus pubescens* Willd. coppices in southern France where it was planted in relatively low numbers in the late 19th century. In Mediterranean countries, one of the main outcomes of forest colonization (and invasion) is the shift from open lands to closed canopy communities (e.g. *Pinus halepensis* Mill. or *Abies alba* Mill. (Figure 2) 'invading' abandoned cultivated or pasture lands in the northern Mediterranean). In addition to homogenizing natural landscapes towards continuous forest cover (which has a definite negative psychological dimension), this process reduces the very rich biodiversity open communities contain (Blondel and Aronson 1999). Conversely, introducing forest tree species in well-confined agricultural-like plantations can help reduce the economic pressure on native forest ecosystems and conserve biodiversity. In New Zealand for example, 99% of harvested wood comes from exotic plantation forests (of which 91% is *Pinus radiata* D. Don) that represent 21% of all forest cover (data from New Zealand's official statistics agency).

Figure 2. *Abies alba* colonizing pasture lands using juniper bushes as facilitators in the Lure mountains, southern France.

Introduction of exotic tree species can lead to pest invasions, as introduced pests can sometimes shift their habits. Seed insects are notorious for spreading from their introduced host to native populations of a phylogenetically related potential host species. For example, *Megastigmus rafni* Hoffmeyer—a seed insect found on several fir species in North America—was identified in France in 1990 on the native *Abies alba* (Roques and Skrzypczynska 2003).

Finally, introductions can become health problems to humans. Millions of the Mediterranean cypress, *Cupressus sempervirens* were planted as wind breaks during the 19th century and for landscaping during the 20th century in Provence, France (Fady 2000). Cypress is a very efficient producer of very small highly allergenic pollen grains. After more than one century of contact, approximately 10% of human populations in that region suffer from severe pollen allergy (Charpin 2000).

Genetic consequences of exotic conifer introductions

Two main mechanisms can impact the genetic structure of native populations confronted with introduced resources: 1) fragmentation of native ecosystems and 2) gene flow and hybridization.

Fragmentation of native ecosystems

Forest resources introduced in high numbers and over large areas can lead to fragmentation in native ecosystems. Fragmentation increases geographical subdivision and imposes barriers to gene flow among populations. If native populations are still abundant and cover extensive areas, fragmentation will lead to independent local adaptations and geographical structuring with possible beneficial consequences in the long run. However, fragmentation may promote local extinctions either because of strong genetic drift followed by consanguineous mating or because of an increase in ecological pressure linked to the edge effect. These problems may arise when native resources are already significantly depleted. An example of this fragmentation process is well-illustrated in France by the spatial structure of native populations of *Pinus nigra* subsp. *salzmannii* (Dunal) Franco. Unlike in Spain, this black pine occurs in the Cévennes and Pyrenees in small populations localized on poor dry soils (Quézel and Médail 2003), possibly the remnants of much larger forests cut down for timber and to make way for agriculture and grazing lands. These forests are surrounded and fragmented by very large *Pinus nigra* subsp. *nigricans* and *P. nigra* subsp. *laricio* plantation forests.

Gene flow and hybridization

Introduced resources may also exchange genes with native ecosystems. Within a species, all subspecies intermix and varieties created from a breeding programme will be capable of fecundating wild-type populations. Further, reproductive isolation is often not achieved within wind-pollinated conifer genera. What we call species are often species complexes, within which extensive gene flow can occur under experimental conditions or when geographic barriers are removed. For example, Euro-Mediterranean *Abies* Mill. species intermix (Kormutak 1985) and so do Mediterranean *Cedrus* Duham. species (Fady *et al*. 2003). Genes might thus be easily passed from introduced resources to native populations of the same species and genus. If introduced resources are very numerous and/or possess genes that can quickly invade a gene pool, impacts are potentially strong and deleterious for local native resources (Lefèvre 2004). Genes with strong fitness will be passed along generations and create a new resource in replacement of the native one. The new resource could be better adapted than the replaced one if the genes passed along concern general adaptation such as better plasticity, increased tolerance to pests, frosts, drought, etc. However, if only genes linked to a very specialized and/or local adaptation are passed along and if the genetic background of the introduced resource is not polymorphic (e.g. clones), the advantage could be short-lived and the replacement of the old resource deleterious for the ecosystem—a consideration we should keep in mind in the era of genetically modified trees. Again, *Pinus nigra* subsp. *salzmannii* populations in France are a good example of this phenomenon. Not only do the very large *P. nigra* subsp. *nigra* and *P. nigra* subsp. *laricio* plantation forests reduce gene flow between its populations, but they can also be significant gene 'polluters' for this native resource, as all black pine subspecies have been shown to readily hybridize experimentally (Vidakovic 1974). *P. nigra* subsp. *salzmannii* is thus doubly threatened: by fragmentation and by exotic gene flow. This taxon is one of the few conifers recognized as constituting a high priority habitat under the EC Habitats Directive (Council Directive 92/43/EEC).

In conclusion, it is evident that introduction of forest resources can have a very significant impact on native resources and must be carefully monitored. The greater the number of the introduced resource there is, the stronger the potential effect on native ecosystems will be.

Changes expected in introduced resources

After successfully passing through the different barriers of adaptation to their new environment, new introduced genetic resources can develop into stands of various sizes and shapes (e.g. *Cupressus sempervirens* wind-breaks, *Cedrus atlantica* patchy naturalized populations and *Pseudotsuga menziesii* large planted populations). They can also occupy many kinds of ecosystems (low to high elevations, open to closed landscapes and water-deficient to humid bioclimates). They often derive from limited sample sizes (e.g. *Cedrus atlantica* in France) but can also originate from large and/or multiple introductions (e.g. *Pseudotsuga menziesii* in Europe). All these different situations will have different consequences for the genetic and ecological structure of the introduced resource.

Changes expected in introduced resources from a genetic point of view

Introduced resources are characterized by two main genetic features: 1) they are isolated from their original population and can no longer exchange genes with it and 2) they are in contact with new populations with which they can possibly exchange genes. This leads to one major genetic event for the introduced resource: rapid evolution.

Ecological conditions are often different in the new environment from that of the original environment. Population structure of the introduced population may also be quite different from that of the forest(s) where it originates. The introduced population can either come from a very limited number of original seed trees or from seeds collected on trees belonging to several different populations. Mechanisms such as genetic drift, genotypic recombination, selection and variation in the mating system, can be expected to play a strong role in the genetic make-up of the new introduced resource. The impact of mutations requires longer time scales and much larger sample sizes to be really effective; therefore, they are not generally considered as a major factor affecting the genetic make-up of these populations. However, it should be noted that mutations may have a significant effect in extreme environments such as those suffering from industrial pollution.

At this point, I will further describe the Mediterranean *Cedrus* species complex, which I have already used as model to illustrate several points on the impact of introduction on native resources. This species complex regroups three taxonomical units which colonize mountains at elevations between 800 and

2000 m: *Cedrus libani* A. Rich. in the Middle East, *C. brevifolia* Henry in Cyprus and *C. atlantica* in North Africa (Figure 3a). Although geographically distant, all Mediterranean *Cedrus* species are phylogenetically related (Figure 3b) and can exchange genes in plantation forests (Fady *et al*. 2003). *C. atlantica* from Algeria was used for reforestation in southern France ca. 1860 where it is now covering over 20 000 ha (Table 1).

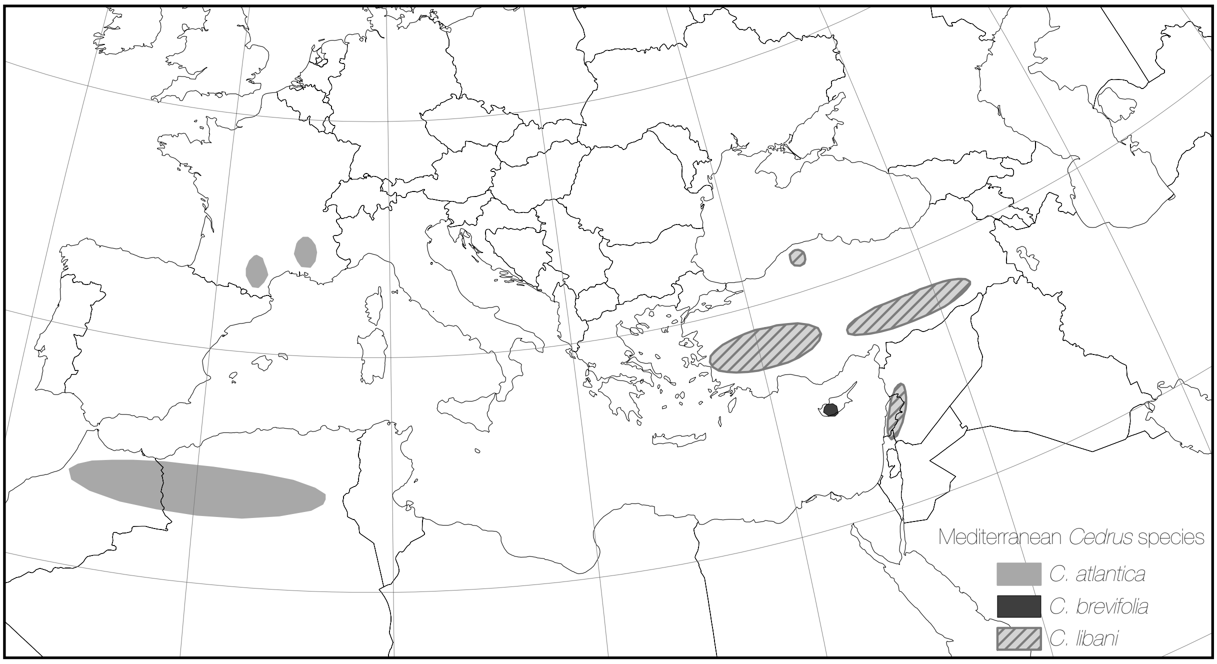

Figure 3a. The phylogenetically related and geographically separated Mediterranean *Cedrus* species: a model to study genetic and ecological consequences on introduced species. *Cedrus atlantica* is shown in solid grey (and is not native to France), *C. brevifolia* is shown in black and *C. libani* in shaded grey.

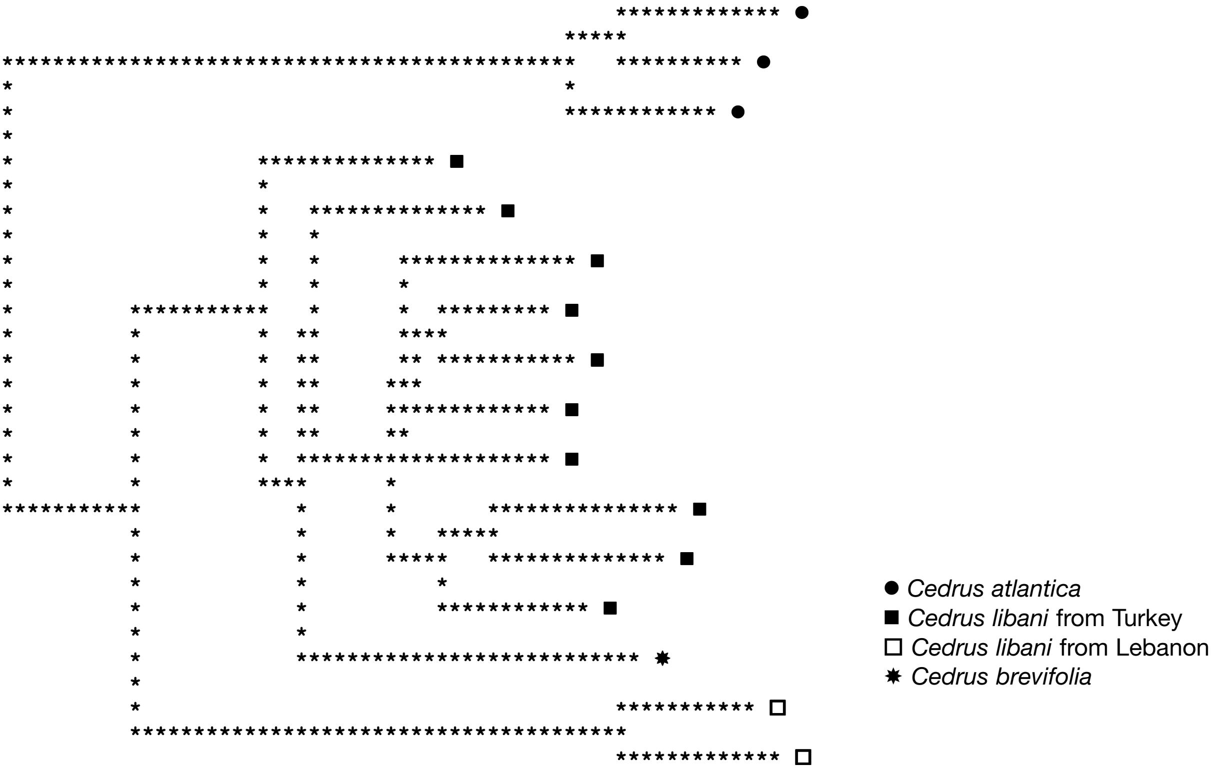

Figure 3b: Isozyme analysis of phylogenetic relationships among Mediterranean *Cedrus* taxa (Fady, unpublished data). Branch length in the dendrogram increases with genetic distance.

Genetic drift

When introduced resources are small isolated populations, or populations with very few reproducing adults, genetic drift can be expected, leading to a modification of the genetic make-up of the population. One outcome to expect in case of demographic bottlenecks is the random loss of alleles and reproduction among few trees, leading to the rise of a consanguineous, excessively homozygous first generation population. In wind-pollinated tree species, studies indicate that such extreme bottlenecks only occur when populations are founded by one or very few seed trees, e.g. Sagnard (2001) for *Abies alba* and Ledig and Conkle (1983) for *Pinus torreyana* Parry ex Carr. (but see Ledig *et al.* (1999) for a counter example with *P. maximartinezii* Rzed.). Genetic drift is thus to be expected when arboreta or *ex situ* collections are the starting point of a new forest stand, either through natural regeneration or plantation. It might also be expected when forest management removes significant numbers of first generation adult trees in an introduced stand. Irregular flowering may increase the effect of drift by promoting reproduction among a limited subset of adult trees (Krouchi *et al.* 2003). Drift can be one of the reasons why introduced resources diverge genetically very quickly from their parent populations. This was postulated for some of the French cedar forests which have a reduced diversity compared to their parent populations in Algeria (Figure 4).

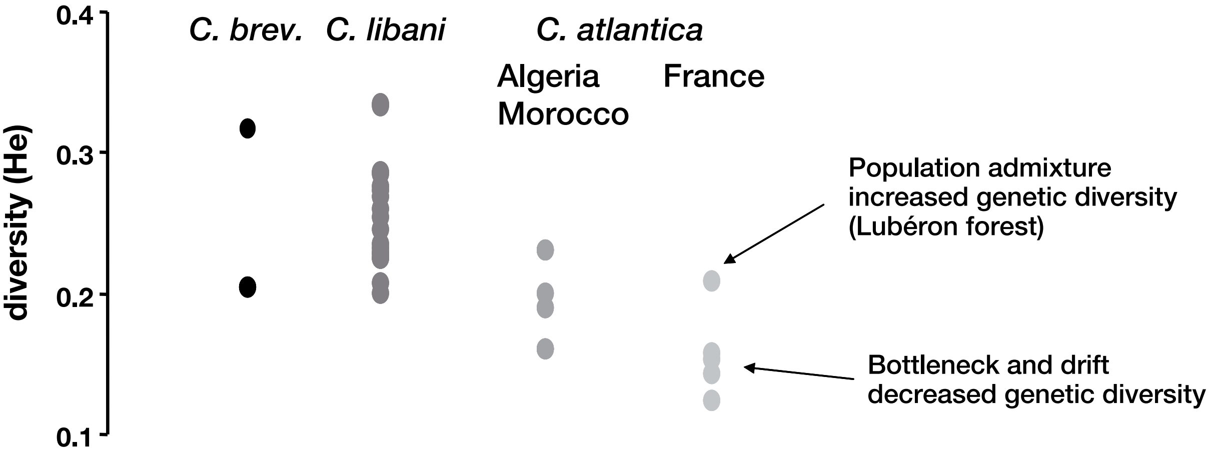

Figure 4. Effect of population admixture versus drift on the genetic diversity of *Cedrus atlantica* populations introduced in France. Data source: Fallour (1998).

Gene pool recombination (admixture)

When introductions are made from larger gene pools, and using large sample sizes, genetic drift is less likely to happen. In these populations, disappearance of the neighbourhood structures of the original populations might be expected. Unrelated trees will mate in the introduced stand, which will reduce the genetic load linked to consanguinity. Introductions can also be made from several seed sources and/or over several introduction waves; in these circumstances some level of heterosis or admixture effect can be expected. The Lubéron *Cedrus atlantica* forest in France provides an example of this phenomenon (Figure 4). Its increased diversity compared to its Algerian parent populations was explained as a result of admixture (Lefèvre *et al.* 2004).

The spatial structure of reproducing trees is of importance as it will affect their mating system (how a progeny is created) and, consequently, spatial genetic structure of the new generation. This effect will be stronger when few reproducing adult trees are contributing to the next generation.

Figure 5 illustrates this effect using a simulated tree population (Sagnard 2001). When the seed trees are randomly or regularly arranged, the seedlings they produce will show a significant spatial family structure, i.e. related seedlings will tend to be closer to each other than expected by chance alone. Such a structure will not be observed if seed trees are clumped together, as the stand will behave as one gene pool and disperse its seeds randomly in all available favourable microsites.

Such spatial genetic structures can be created when the introduction is made from a small gene pool, when strong selection or forest management has left very few trees, or when only a subset of the adult trees participate in the mating. This latter reason may explain why neighbourhood structures are found in native stands. Consequences are increased consanguineous mating and the development of a new generation of trees that might be less fit than their parents.

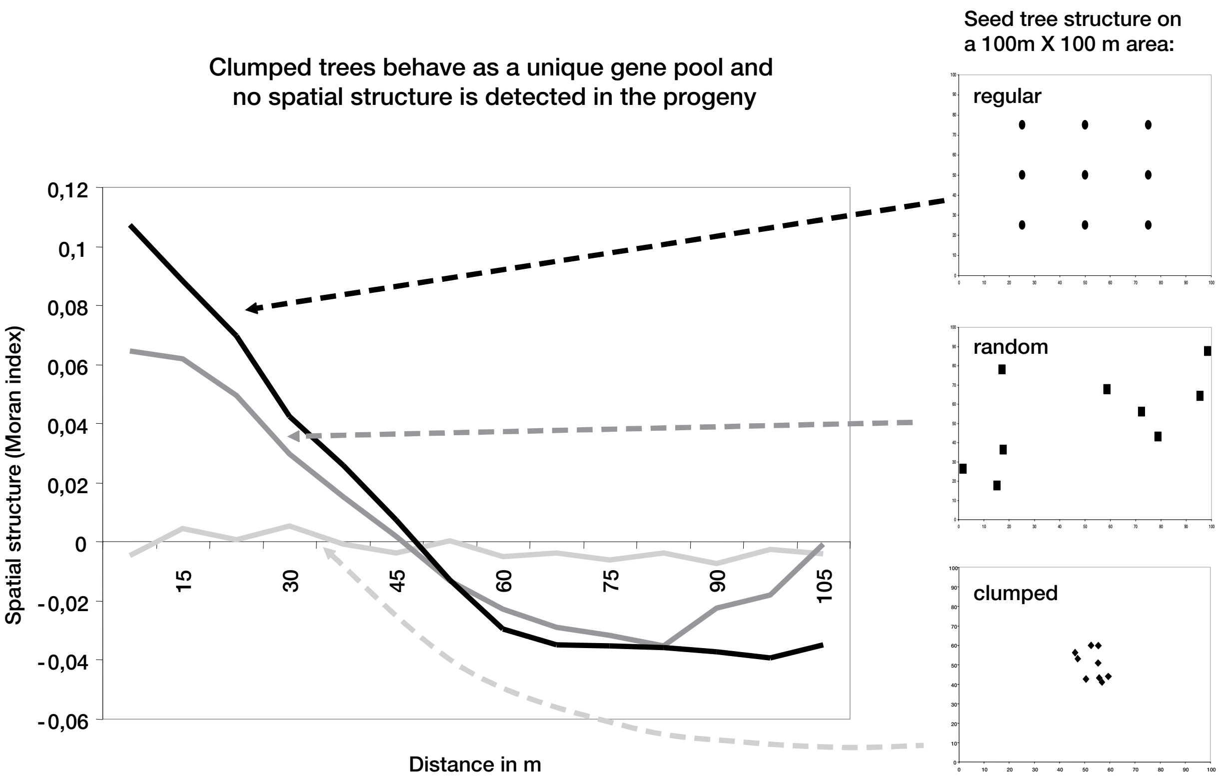

Figure 5. Effect of seed tree structure on the seedlings they produce: a simulation using a single bi-allelic locus. A positive Moran index indicates that genetically identical seedlings tend to be spatially grouped at certain distances from seed trees.

Conversely, disruption of consanguineous mating can explain why the progeny of introduced resources perform better than that of their original parent populations. Following plantation in the 1860s, very few introduced *Cedrus atlantica* trees survived. A reduction of consanguinity (mating among unrelated first generation survivors) was found to be one of the likely hypotheses to explain why the progeny of introduced stands perform significantly better than that of native North African populations in common garden experiments in France (Figure 6).

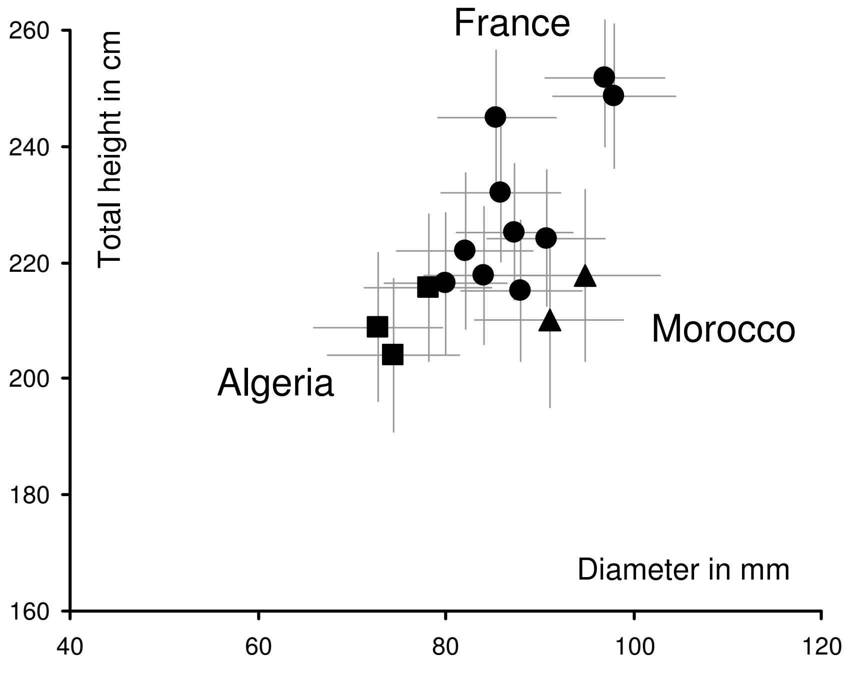

Figure 6. Possible effect of disruption of consanguineous mating on the genetic diversity of introduced populations: French *Cedrus atlantica* populations grow better in their new environment than their natural counterparts (Lefèvre, unpublished data).

Selection

When new environmental conditions differ from the original ones, the introduced resource will undergo a selection process to adapt to these new conditions. If the new environment is too different from the original one, the introduced trees will not survive. In France for example, 30 000 ha of north-western Iberian *P. pinaster* provenances introduced decades earlier in the Landes region were destroyed by the 1984–1985 winter frosts (Riou-Nivert 2002). Arboreta and common garden experiments are designed precisely to avoid introducing ill-adapted genotypes, as they test such adaptive traits as frost, water and pest resistance over decades and several environmental conditions before a resource is introduced. Although expensive to install and maintain, they provide precious safeguards over inappropriate introductions and constitute networks of high biodiversity value that should be under high priority conservation.

When adaptation is possible, divergence from the original population will be achieved faster with increasing selection pressure. A rapid adaptation and differentiation process, sometimes over a single generation, has often been observed for introduced resources. For example, first generation progeny of *Picea abies* introduced into Norway from Germany had a bud set date identical to the native local Norwegian resources, but significantly different from their original German parent populations (Skrøppa and Kohmann 1997). Selection is also a likely hypothesis for the better growth performance of the progeny of introduced *Cedrus atlantica* over that of the original populations from Algeria in southern France (Figure 6).

Hybridization

Just as introduced resources can hybridize with autochthonous and locally adapted species, native species can hybridize and modify introduced resources. Reproductive barriers are often weak between taxonomic units within genera because of insufficient elapsed time since geographical or ecological separation and because the mating system seems not to be the primary target of genetic changes that occur through evolution (Avise 1994). When introduced resources constitute small populations, the impact of hybridization can be strong. For example, hybridization has been shown to be very common when *C. libani* and *C. atlantica* are grown together—in some cases, up to 80% of the progeny was made of hybrid seeds (Fady *et al*. 2003). Acting in a similar, although more radical way, as admixture, hybridization can significantly contribute to the rapid emergence of a new resource. For example, the hybrid progeny of *C. atlantica* demonstrated increased resistance to aphids in experimental conditions, a trait transmitted from *C. libani* (Fabre and Chalon 2005), and is of significant interest in southern France.

Changes expected in introduced resources from an ecological point of view

Once planted and successfully adapted to its new environment, the introduced resource can create, or become part of, a new ecological community. Its size and spatial structure will determine whether or not it will be able to successfully reproduce and whether or not it will be colonized by members of the surrounding communities. This in turn will determine its biodiversity value in the long run.

Because they are usually introduced without their native co-adapted community of insect predators and parasites, exotic forest stands are particularly susceptible to insects, both the local ones that can modify their feeding habits and their original ones when accidentally introduced. Strong insect damage might occur several decades after introduction because resistance to insect predation will not be a primary determinant to adaptation at the time of introduction. It may take time for the local insect community to adapt to this newly available food supply, or for the original insect community to be introduced and adapt to its new environment. For example, in France, the introduced seed insect *Megastigmus spermotrophus* Wachtl has only recently started to significantly decrease seed set in Douglas-fir although it may have been introduced as early as a century ago (Rappaport and Roques 1991). A counter example is provided by *M. schimitscheki* Novitzky which was only discovered in 1994 and is already significantly reducing seed set in cedar forests in southern France (Fabre *et al*. 2004). As an example of insect adaptation to new resources, the pine processionary caterpillar, *Thaumetopoea pityocampa* Schiff., has adapted to numerous introduced conifers in France, and principally to the abundantly available *Pinus nigra* (Démolin 1969).

Native ecosystems, where phylogenetically related insect species exist along with their insect predator and parasite community, can buffer insect outbreaks in introduced forests (Roques 1983). For example, the native *Megastigmus suspectus* Borr. community found in *Abies alba* forests in France could provide such beneficial ecological buffer for the introduced *Abies* and *Cedrus* stands growing in their vicinity. When native ecosystems cannot be used for controlling insect outbreaks, collecting natural parasites and predators from the natural distribution area can be efficient. For example, the hymenoptera *Pauesia cedrobii* Starý and Leclant, collected in North Africa, significantly reduced the impact of the aphid *Cedrobium laportei* Remaudière on the French *Cedrus atlantica* forests (Fabre and Rabasse 1987). This aphid had been introduced accidentally from North Africa.

Introduced conifers remain ecologically vulnerable for a significant length of time after their first introduction, as the construction of a fully functional forest ecosystem takes at least several tree generations.

Conservation and sustainable management of introduced conifers

Introduced resources evolve very quickly. Over just one generation, they can constitute a gene pool that is quite different from their original seed stand(s) and after a few generations, they can constitute an ecologically sustainable resource. Sustainability could be considered to be effective once the second generation after foundation is in place and reproducing. Depending on the species, we can estimate the time frame for a sustainable conifer landrace to occur to be approximately 100–150 years after initial introduction.

Once ecologically and genetically sustainable, the introduced resource should be recognized (nationally and internationally) as a new gene pool—a landrace. An introduced resource will have different conservation values for the species, depending on whether it is threatened or not.

When the species is recognized as threatened in its native distribution area, the introduced resource can be used as potential seed source for ecosystem restoration. This will only be possible if interspecific gene flow does not occur, if the effective number of reproducing trees is high enough to avoid genetic drift and if ecological conditions (both biotic and abiotic) are not too different from those of the natural area. Thus, arboretum-type, garden-like or admixture-origin plantations should be avoided for seed collections, although large single-provenance *ex situ* conservation forests might be best suited.

If the species is not threatened in its original area, the ecosystems containing the introduced resource (which has now become a landrace) can be considered as an addendum to the distribution range of the species. An *in situ* approach to resource management will be best suited, in close collaboration with countries throughout the species' range. Forests chosen as part of the *in situ* conservation network should be naturally regenerated, or artificially regenerated using only local seed trees. Their reproducing population size should be large enough—optimally several thousands (Lande 1995). Populations originating from large seed collections and occupying large areas, possibly over several environmental conditions, could qualify for this *in situ* management. But forests originating from very limited gene pools or admixtures, or where interspecific gene flow occurs, could also qualify. In this case, population origin matters less than whether or not they constitute an original and sustainable genetic and ecological resource.

Conclusions

In conclusion, introducing exotic forest trees should be undertaken carefully. They should be tested over several environments and decades for adaptability in specifically designed common garden experiments. Gene flow to and from them should also be carefully monitored. Once introduced, forest management that aims to limit genetic family structures (i.e. consanguinity) and to accelerate the constitution of dynamic and functional ecosystems, should be adopted. Once introduction is successful, I suggest that introduced resources should definitively be included in gene conservation networks. Further, their genetic and ecological monitoring should provide helpful insights to understand the processes that govern evolution and speciation.

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