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Lessons on ecosystem adaptation to climate change: dealing with climate variability, incomplete data and management decisions

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Abstract

Compensating for climate change effects by translocating southern tree populations is increasingly considered a feasible adaptation option in northern ecosystems. Here, we present lessons for future programs from two failed cases of tree populations translocated to more northern latitudes within their natural ranges. First, Iberian seeds of *Pinus pinaster* Ait. were planted in southwest France in the 1950s because large fires depleted the availability of local seeds. Extreme frosts in 1956, 1963 and 1985 decimated the introduced populations, inducing enormous economic losses. Second, seedlings of *Fraxinus excelsior* L. were imported from continental nurseries in Ireland in the 1990s because they were not available in the country. The trees soon exhibited bad form because of reduced frost resistance, and seed imports stopped. Bad form was more pronounced in trees introgressed with the sub-Mediterranean *F. angustifolia* Vahl, a usual candidate for temperate translocations. To avoid similar failures in the future, permanent monitoring is required, as maladaptation can remain cryptic for decades, and any early warnings should be given careful attention. Current policies recommend performing field tests before population translocations, but uncertainty will always be present because of the unexpected effects of the climate variability of target sites.

Keywords: decision making, extreme cold events, forest adaptation, climate change, early warning, cryptic maladaptation.

1. Introduction

Forest ecosystems are exhibiting shifts in species ranges[1,2], species turnover[3], changes in phenology timing[4,5] and changes in major vegetation types[6], all correlated to climate change. In the light of this evidence, the survival of many ecosystems will rely on migration, fast local adaptation and the phenotypic plasticity inherent to each species[7,8] as well as smart decisions from ecosystem managers to compensate for climate change effects. The consequences of an appropriate forest ecosystem adaptation policy will be far reaching because trees play a central role in ecosystem function and are considered founder species able to change local diversity[9] and provide ecosystem services such as regional climate stabilisation[10].

Strategies for adapting forests to climate change are framed as Sustainable Forest Management (SFM) practices. SFM generally includes increasing the genetic diversity of forest ecosystems to increase system resilience and adaptability to new climates[11–15], provided that the productivity of forests is not compromised[16–19]. To increase forest genetic diversity in temperate countries, managers may be tempted to use seeds from populations that are found at lower altitudes or at lower latitudes, to look for species that were historically present during warmer past geological periods (the so-called 'neo-native' forests) or to introduce species simply not native to the area. In general, the movement of populations has received different names, including assisted migration of populations, managed relocation, assisted migration, assisted colonisation and assisted translocation, which all refer to the intended translocation of biological units as propagules, individuals or populations to compensate for the negative effects of climate change[20].

Local extinctions due to maladaptation to climate change are expected in the future, and the search for populations that can survive future climate change[21] is essential to address the relocation of species. Lowland or southern populations are supposed to include enough genetic variation as a result of local adaptation[22] that they should provide 'pre-adapted' populations to cope with the warmer climates expected by the end of the 21st century. In general, we would expect that temperate trees living at the rear edge of their distributions would have increased mortality related to the augmentation of xeric episodes, whereas populations living at the northern edge of their distribution would migrate farther north with global warming. While the former is generally true and mortality is often related to drought events at the southern edge[23,24], there is less agreement regarding the latter statement. In the case of the US forests, for example, the migration rate based on the Forest Inventory Analysis records suggests that trees did not track climate change at the northern edge in the last few decades[25]. Such observations have promoted debate on whether the assisted migration of populations would be a smart alternative to maintain the health of the current forests[26–30]. To the best of our knowledge, the debate remains open, and only a few so-called experiences of assisted migration on trees have been set up[31,32], although these are too recent to provide insights about the long term benefits of such actions.

Here, we argue that the main barrier to climate change adaptation by translocating populations is the risk of cryptic maladaptation to target sites because of local, unknown climate variability. To demonstrate this barrier, we expose two failed experiences of tree plantations with more southern populations. These experiences illustrate the possible consequences of compensating for climate change effects by population translocation. We draw lessons from these cases to avoid similar failures in the future, and we identify possible situations to help decision makers when adapting forest ecosystems to climate change by population translocations.

2. Iberian populations of *Pinus pinaster* introduced in Aquitaine, France

The maritime pine is a common forest species in Western Europe, especially in the southwest of France (Aquitaine region) and northern Spain and Portugal, where it also has great economic importance. Populations of maritime pine present high levels of genetic differentiation between populations, phenotypic plasticity and local adaptation in adaptive traits across their natural range [33–36], and southern populations would be more adapted to drought than northern ones. In France, *Pinus pinaster* occupies up to 10% of the national forested surface. The first plantations of maritime pine in the Landes of Aquitaine, currently one of the largest forest plantations in Europe, date back to the years that followed the national law of 19 June 1857, which ordered the afforestation of the communal lands in the region[37].

The Iberian populations were imported into France following the great fires that happened in the Aquitaine region in the years 1949 and 1950, which contributed to the neglect of local seeds[38]. The introduced populations subsequently showed low resistance to the frosts that occurred in the region in 1956 and 1963, but these events were presumably considered not bad enough to revaluate the use of these southern populations. The last and strongest frost event occurred in 1985 and was followed by an increase in the mortality of the Iberian populations, whereas the local populations were far less affected (Supplementary Figure S1).

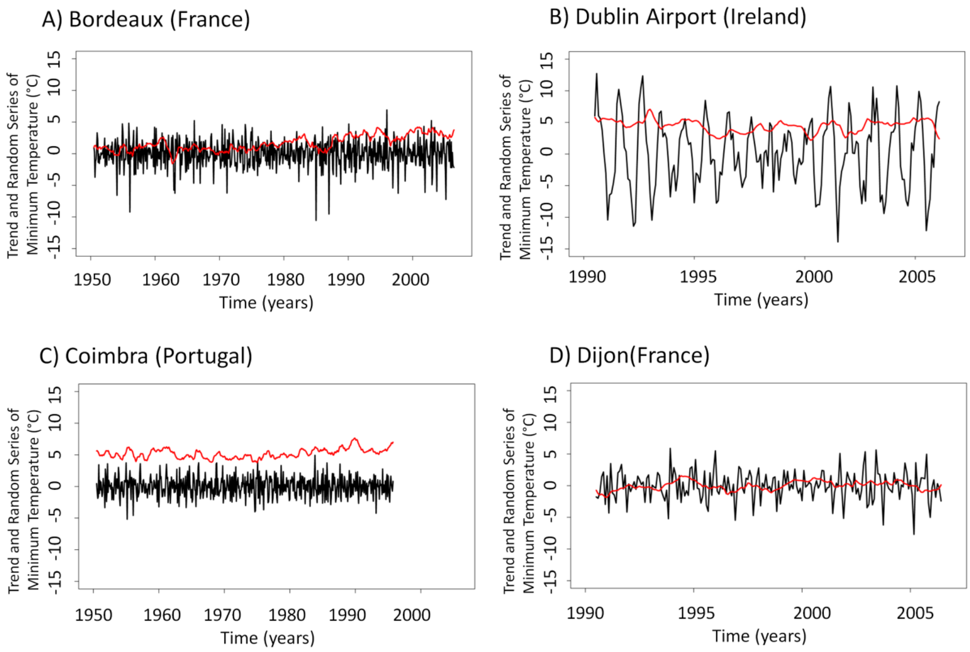

Illustration 1: Trend (red line) and extremes events extracted from the residual time series (black line) from the time series decomposition of the monthly climatic series of the minimum temperature recorded in the closest meteorological station to the source (C, D) and plantation sites (A, B) of both study cases. The original climate series (observed) was decomposed into its additive components: trend, seasonal and residual climatic series. Sources: Météo France for Bordeaux and Dijon series and European Climate Assessment Dataset for the Coimbra and Dublin Airport datasets (http://eca.knmi.nl/).

Aquitaine climate variability includes strong peaks of frost. The first recorded frost event occurred in 1709, and subsequent episodes were noted in 1729, 1756, 1766 and 1786[37]. Even if there is a general warming trend, the climatic series of Bordeaux from 1950 to 2006 shows minimum temperatures reaching -15ºC three times (Figure 1) and reaching -10ºC several times. For Landes, the most forested zone of Aquitaine, the recorded temperatures are even colder, down to -22ºC during 17 January 1985 in the more continental parts[38]. Coimbra is the nearest meteorological station to Leiria, the Portuguese location from which *Pinus pinaster* was largely planted in the Aquitaine region and that presented the highest mortality related to frost. Coimbra records show the coldest temperature was registered in 1941, with absolute minimums that fell to only -7.8 ºC (http://www.meteo.pt/pt/oclima/extremos/) in the last 60 years (Illustration 1 A, B). However, the climate averages of the last 30 years are slightly different in Leiria and Aquitaine, which suggests that provenances coming from Leiria would have survived in the Aquitaine region (Illustration 2A).

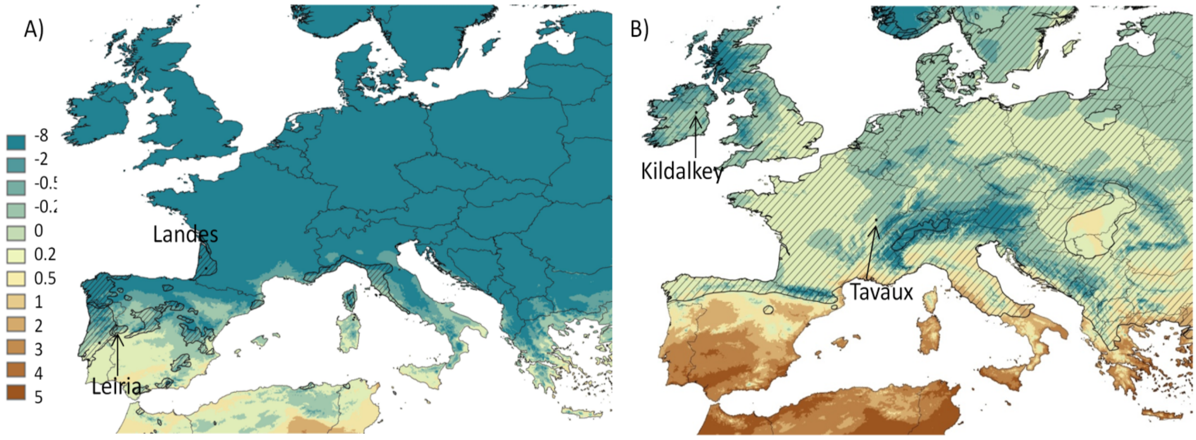

Illustration 2: Climate analogues from the plantation sites for the case of Pinus pinaster (A) and Fraxinus excelsior x F.angustifolia (B) using average climate analogues. Values different from zero indicate differences between the plantation and the origin of the species. The climate analogues were calculated by synthesizing five climate variables into a principal component analysis (PCA) as described in Supplementary Material and Methods. Here we show the first component of the PCA analysis that gathers 50% of the variance. The shaded areas show the distribution of Pinus pinaster (A) and Fraxinus excelsior (B) in Europe.

Field tests were designed to evaluate the extent to which populations were adapted to local conditions in maritime pine as a research response to guide future translocation programs, but no measures against the plantation of Iberian populations for commercial purposes were taken before the strong frost of 1985. The degree of acclimation of several seeds from different populations of *Pinus pinaster* from Europe and North Africa was tested by three population trial experiments in France in 1960, the last of which was set up 1981 (briefly described by Harfouche & Kremer[39]). The results revealed that the Portuguese populations, and to a lesser degree the Iberian ones, were indeed more sensible to frost than the local populations from Landes[38]. Less information exists on the two other experiments that were set up before (but see Supplementary Figure S1), which indicated a certain sensibility of the Portuguese populations to frost[40,41]. During the frost of 1956, it was not clear that the Iberian populations were more sensible to frost than the local ones[40]. During the frost of 1963, one publication linked the high mortality of the Iberian populations with the frost wave[41]. After the frost of 1985, the origin of the trees was determined by a terpenic analysis that allowed the post-mortem differentiation of female cones[38]. This analysis confirmed suspicions of links between Iberian origin and low frost resistance. Afterwards, only guaranteed seeds from local populations were used as a source, and no more seeds from Portugal or Spain were imported.

The frost of the 1985 winter affected 300 to 400 km² of the Landes forest in southwestern France, impacting approximately 1 400 000 m^3 of wood [42]. This enormous economic loss led to the only case where the use of foreign tree populations was prohibited by the European Union, which otherwise promotes the free exchange of seeds between ecological matching sites (EU Council Directive 1999/105/EC of 22 December 1999). In 2005, the

Illustration 3: Example of the bad form exhibited by the planted ash in Ireland (Photo: Juan Fernandez-Manjarres)

European Commission authorised France to prohibit the marketing (with a view to seeding or planting in France) of reproductive material of *Pinus Pinaster* of Iberian Peninsula origin to end users, arguing that it was unsuitable for use in such territories under the Council Directive cited above.

3. *Fraxinus excelsior* populations introduced in Ireland

At the beginning of the twentieth century, only 1% of Ireland's surface was covered by forests[43], but the recent afforestation efforts of the government and the European Union have significantly increased the surface of forest plantations. Ireland benefited from three afforestation programmes from the mid-1980s to 2006, encouraged by governmental and European grants[44] to turn farmland into forests[45]. As a result, forests covered 10% of Ireland's surface by 2007. At the beginning of the afforestation, most of the species were conifers intended for wood harvesting, but in the latter years of the programmes the use of broadleaf forests became more common in an effort to conserve the native species of the country. Ash also became a major species in Ireland, with 19,200 ha of land covered[45].

The government-funded afforestation program in the 1990s led to a high demand for seeds that could not be completely sourced in the country. Hence, seeds from commercial nurseries were imported from continental Europe, mostly from France and the Netherlands. Within the imported seeds, natural hybrid populations of common ash and small leaved ash (*Fraxinus excelsior* x *F. angustifolia*) were unintentionally mixed with common ash (*F. excelsior*), the only species native to Ireland. Incidentally, *F. angustifolia* was regarded as a candidate species for increasing the genetic diversity of forests in the British Isles because of its sub-Mediterranean distribution, so its accidental introduction is not completely contrary to current propositions to adapt forests to climate change[46]. In contrast to *F. excelsior*, which is mostly temperate, *F. angustifolia* is a circum-Mediterranean species that reaches its northern edge in France, were hybrid zones between both *Fraxinus* have been found[47]. At the time the seedlings were introduced to Ireland, the natural hybrids between the two Ash species were poorly known and were handled indistinctly in nurseries. A few years after plantation, many trees exhibited irregular branching, as leaf buds were often lost to frosts, changing the physiognomy of trees. This effect was more pronounced on the suspected hybrids. More importantly, it is suspected that the presence of these hybrid trees posed the risk of genetic contamination of local populations[48]. In addition, the target and original locations of *Fraxinus* are climate analogues (Figure 2B), indicating that both sites have similar average climates and suggesting that the species would likely have survived in the plantation site.

The problems generated by *Fraxinus excelsior* x *F. angustifolia* translocation started an intra-community international trade dispute, and Ireland stopped buying Ash seeds from France, the Netherlands and Hungary for some time. We believe that up to 14 million trees may have been involved (G. Douglas, pers. comm.), but the actual proportion of hybrid trees remains unknown to date. The Irish government supported research to verify the origin of the problems associated with maladapted populations of *F. excelsior* in general (RAP: Reassessing Ash Potential) and of the risks of maladaptation because of hybridisation in particular (Ashgen: identifying the scale of suspected hybrid ash in Ireland). Currently, managers avoid the use of imported seeds from ash, even if the market with continental Europe has been reopened and most plantations will be harvested 20 years from plantation time when the subsidies end.

4. What Lessons can be learned?

Several lessons can be learned from these two failed cases of translocations from climatic, policy and decision making perspectives. Although our example is based on tree populations, we think the lessons are also applicable to other organisms, including endangered species with some restrictions.

Look at the climate variability and not merely the mean climate. If we look at the average weather, the translocations from Portugal to southern Atlantic France and from eastern France to Ireland are within expected climate boundaries when calculated on mean temperature and precipitation variables (cf. Fig. 2). Moreover, they largely correspond to what would be expected if we want to compensate for future climate change effects. However, things went wrong in both cases, and the proximal cause seems to be the lack of frost resistance of these southern populations subject to extreme weather events (Illustration 1, 3 and Supplementary Figure S1).

Know the genetic constitution of the translocated populations. In the case of *Fraxinus* in Ireland, the failure was due to a lack of knowledge of the biology of the species (most hybrids are cryptic and require molecular and morphological data to be detected), and the community was not aware of the extent of the hybrid zone, which proved larger than expected[49]. Nevertheless, the overall plantation form was bad, suggesting that even non-introgressed trees of *F. excelsior* were simply not adapted to the harsher Irish conditions. More importantly, however, the issue could have been avoided if field trials had been set up in Ireland before implementing large scale afforestations (see below). In the case of maritime pine, the issue of maladaptation is also clearly related to the lack of information about the distribution of the adaptive variation of the species, information that became available some 30 years after the introduction of the species in the 1950s, which confirmed suspicions.

Establish field trials first and pay attention to early warnings of maladaptation. In both cases, different population choices would have been made if the field trials had been performed before actually proceeding to afforest thousands of hectares. Although trials are possible for plants, this step is more critical for animal species because, in most cases, it is the individuals and not the propagules that would be translocated. A related issue to be decided when establishing trials is how long they should be. In the case of maritime pine, the first signs of maladaptation appeared only 7 years after the plantations were established, but were deemed not bad enough. In the case of Ireland, tree form was blatantly bad in the first years, despite that the initial growth was vigorous, setting off alarms.

Maintain long-term monitoring programs to detect cryptic maladaptation. Not observing the maladaptation of an introduced population in the first years does not necessarily guarantee that things can go wrong later. This issue will become more important in the face of climate change as new climates may have no analogue with the climate at the target site or with the climate from the source population[50].

Be ready to making rapid decisions to stop programs even with incomplete evidence. Legal constraints preventing the introduction of populations will necessarily come late as the process of producing management regulations is long and difficult and requires conclusive evidence to convince policy makers. In the case of maritime pine, the EU regulation was enacted in 2005, approximately 20 years after the signs of maladaptation were clear and most likely approximately 10 years after the evidence of the field trials confirmed the lack of frost resistance of southern populations.

Trust the opinion of local managers. Managers and practitioners who know their ecosystems well are an important source of knowledge on the state of the programmes, and following their recommendations can not only save time and money but also prevent irreversible cases of genetic contamination or species invasions, as occurred in both cases presented here. *Fraxinus* plantations were eradicated soon after the bad forms in the trees were found. In the case of *Pinaster*, managers only reacted after the great mortality event occurred in 1985, even though it was 20 years before the EU regulation was enacted (see the previous lesson).

5. What possibilities and decisions can be expected when compensating for climate change effects by population translocations?

The two cases discussed above illustrate only two of several plausible possibilities for ecosystems subject to translocating populations in their management plans. Figure 4 summarises the alternatives. Awareness of these schemas should be incorporated within SFM programmes to allow managers to be prepared with alternative plans if any signs of failures become apparent. Depending on the possibilities and the degree of climate change, we can identify at least three management options:

i) *No need for the introduction of new populations* (schemas A, B, and E; Figure 4): local species maintain their fitness by adapting to new climates, and translocations are not needed (schema A). Early warnings of climate maladaptation are detected in the short-term, indicating that introduced populations will perform worse than the local population (schema B). Climate-related cryptic maladaptation is only detected after many years as a consequence of unexpected extreme events (schema E).

ii) *A mix of introduced and local populations is the best option for minimising population decay* (schema D; Figure 4). Translocated populations that compensate for local fitness decrease even if compensation is not optimal with respect to the pre-climate-change fitness of the local population.

iii) *Better performance of the introduced population compared with local populations* (schema C; Figure 4). In the most radical case, where climate change would induce the perishing of local populations, the translocation of new populations would help maintain the ecosystem function, even if compensation is not optimal with respect to the pre-climate-change fitness of the local population.

The pace of climate change implies that these decisions are likely to be made before complete scientific information on the survival capacity of trees is gathered in the population trials. Moreover, the responses of local and introduced populations will be different depending on the degree of maladaptation of local and introduced populations over time. Whereas early warnings would prevent great economic risks on some plantations (schema B), in other cases maladaptation is visible too late (schema E). Only constant monitoring can tell which type of schema the target populations will face.

One alternative to decrease the uncertainty of the decisions with incomplete information would be to simulate translocations of populations based on field trials to minimise the risk of maladaptation of outsider populations in a territory at small scales of translocation[21,51]. Next, new field trials at the target sites would be set, a time frame would be defined (approximately 20 years for trees) and an accepted degree or tolerance of maladaptation would be identified, as shown in Figure 4. If the field trial is accepted by stakeholders (no signs or acceptable levels of maladaptation), a larger program would be defined; if it fails, alternative populations could be searched for or it could start again with a new species, resulting in costly processes of trial and error that seem unavoidable in many cases. Testing for the best-suited translocated populations could be afforded up to certain limits with non-endangered commercial populations such as widespread trees, which is not the case for endangered species for which translocation failure is not an option.

6. Conclusions

The transition from the relatively stable climate of the Holocene towards the Anthropocene[50] has spurred a rethink of ecosystem management. Helping species adapt to the new climates of the Anthropocene involves not only dealing with a global increase in temperatures, but also a higher climate variability and frequency of extreme events [52,53]. Newly emerging climates[50,54] and the uncertainty related to climate change[55], especially regarding extreme events, will make the search for southern locations with similar climatic conditions to those of the northern populations extremely difficult (Figure 2A, 2B). Extreme cold events, such as those reported here, highlight the danger of translocating southern tree populations into northern locations. The current focus on extreme climate-related risks concerns the increase of heat waves[53] and flood-causing precipitation extremes[56]. Extreme cold events appear less worrisome because they are expected to decrease in frequency and intensity in the future[55]. Our work is a reminder that policies of forest adaptation to climate change should account for extreme cold events in the target and source populations, ensuring that target locations will resemble source locations not only in the climate average[57] but also in the frequency and intensity of extreme cold events.

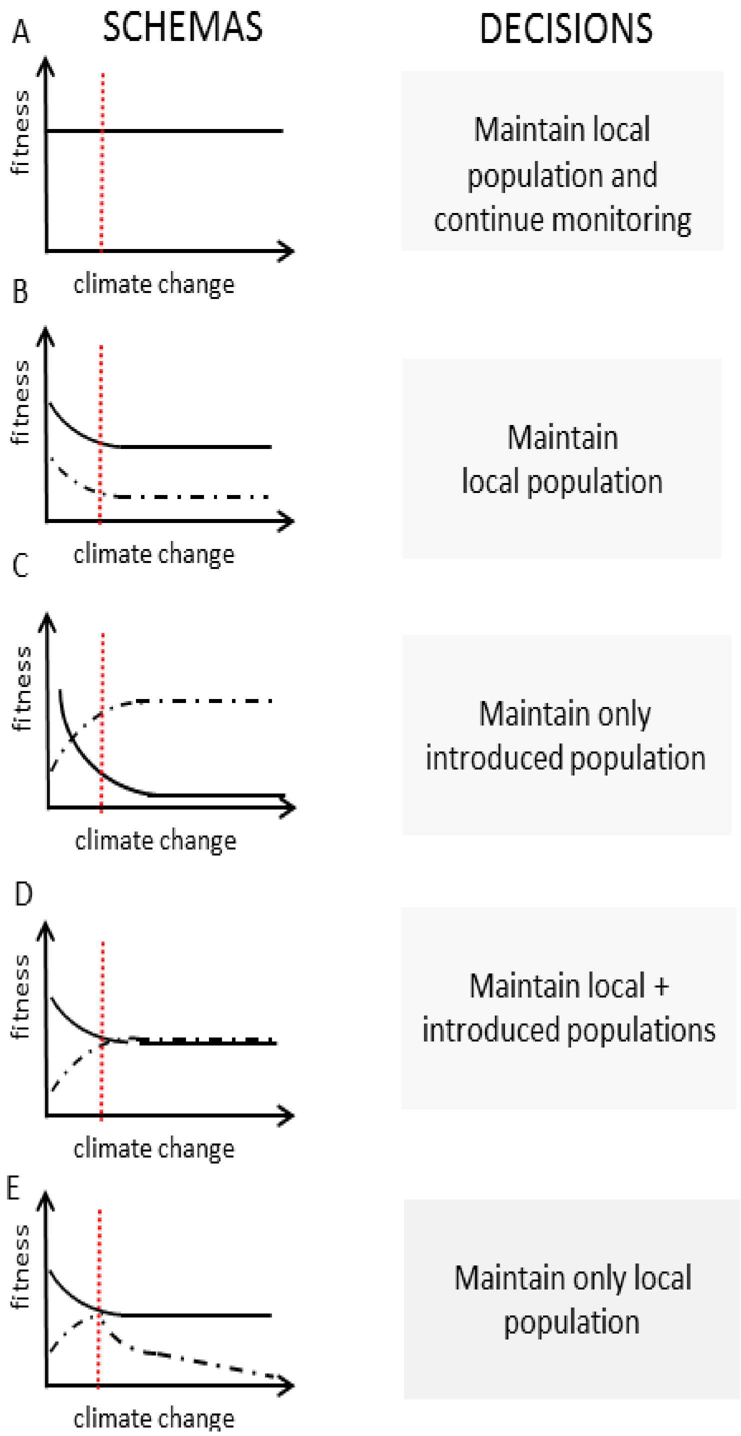

Illustration 4: Decisions schemes to adapt managed forest to climate change with population translocations. Decisions are based on sequential incomplete information gathered from provenance tests and/or simulations that allow the detection of early maladaptation. Schemas A, B, C, D, and E represent the adaptation possibilities of the local populations (continuous line) and the introduced populations (dotted line) under climate change. Schema B would have been the case of Fraxinus in Ireland if the field trials had been established before the introductions, whereas schema E corresponds to the Pinus pinaster case, where cryptic maladaptation is only apparent as a consequence of unexpected extreme events. The red vertical line indicates the time for a possible early warning.

Here, we describe two recent examples equivalent to compensating for climate change effects by population translocations in northern temperate ecosystems. These examples are expensive lessons on the inherent risk of such measures. In the case of maritime pine, the maladaptation remained cryptic for decades, despite some early warnings. In the case of ash, the early warnings were strong enough to stop all seed imports. Both cases are a reminder of the need for field tests before large-scale population introductions and for long-term monitoring and adaptive decision-making. Climate change will likely decrease the number of extreme cold events[55], yet they will most likely remain the hidden element behind the maladaptation of southern populations to northern locations.

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References

1. Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P. & Brisse, H. A significant upward shift in plant species optimum elevation during the 20th century. Science 320, 1768–71 (2008).
2. Chen, I.-C., Hill, J. K., Ohlemuller, R., Roy, D. B. & Thomas, C. D. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. Science 333, 1024–1026 (2011).
3. Hillebrand, H., Soininen, J. & Snoeijs, P. Warming leads to higher species turnover in a coastal ecosystem. Global Change Biology 16, 1181–1193 (2010).
4. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42 (2003).
5. Gordo, O. & Sanz, J. J. Long-term temporal changes of plant phenology in the Western Mediterranean. Global Change Biology 15, 1930–1948 (2009).
6. Beck, P. S. A. et al. Changes in forest productivity across Alaska consistent with biome shift. Ecology letters 14, 373–9 (2011).
7. Reusch, T. B. H. & Wood, T. E. Molecular ecology of global change. Molecular ecology 16, 3973–92 (2007).
8. Richter, S. et al. Phenotypic plasticity facilitates resistance to climate change in a highly variable environment. Oecologia 169, 269–79 (2011).
9. Ellison, A. M. et al. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3, 479–486 (2005).
10. Bonan, G. B. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320, 1444–9 (2008).
11. Thompson, I., Mackey, B., McNulty, S. & Mosseler, A. Forest Resilience, Biodiversity, and Climate Change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystem. 67 (Montreal, 2009).
12. Europe, F. RESOLUTION H1. General guidelines for the sustainable management of forests in Europe. http://www.foresteurope.org/eng/What_we_work_for/Sustainable_Forest_Management/ 5 (Helsinky, 1993).at <http://www.foresteurope.org/filestore/foresteurope/Conferences/Helsinki/helsinki_resolution_h1.pdf>
13. Verges, P. Plan Adaptation Climat. Rapport des groupes de travail de la concertation nationale. Ministère de l’écologie, de l'énergie, du développement durable et de la mer, en charge des Technologies vertes et des Négociations sur le climat. (2010).at <http://www.developpement-durable.gouv.fr/IMG/pdf/rapport_concertation_adaptation_17_06_2010.pdf.>
14. FAO Managing forests for climate change. Working Paper (2010).at <http://www.fao.org/docrep/013/i1960e/i1960e00.pdf>
15. IPCC IPCC Fourth Assessment Report. Working group III: Mitigation of Climate Change. (2007).
16. Innes, J. et al. Management for Adaptation. 224 (2009).
17. Lal, R. et al. Management to mitigate and adapt to climate change. Journal of Soil and Water Conservation 66, 276–285 (2011).
18. Kotwal, P. C., Omprakash, M. D., Gairola, S. & Dugaya, D. Ecological indicators: Imperative to sustainable forest management. Ecological Indicators 8, 104–107 (2008).
19. Chapin, F. S., Danell, K., Elmqvist, T., Folke, C. & Fresco, N. Managing Climate Change Impacts to Enhance the Resilience and Sustainability of Fennoscandian Forests. AMBIO: A Journal of the Human Environment 36, 528–533 (2007).
20. Richardson, D. M. et al. Multidimensional evaluation of managed relocation. Proceedings of the National Academy of Sciences of the United States of America 106, 9721–4 (2009).

21. Benito Garzón, M., Alía, R., Robson, T. M. & Zavala, M. A. Intra-specific variability and plasticity influence potential tree species distributions under climate change. Global Ecology and Biogeography 20, 766–778 (2011).
22. Savolainen, O., Pyhäjärvi, T. & Knürr, T. Gene Flow and Local Adaptation in Trees. Annual Review of Ecology, Evolution, and Systematics 38, 595–619 (2007).
23. Carnicer, J. et al. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. Proceedings of the National Academy of Sciences of the United States of America 108, 1474–8 (2011).
24. Sánchez-Salguero, R., Navarro-Cerrillo, R. M., Swetnam, T. W. & Zavala, M. A. Is drought the main decline factor at the rear edge of Europe? The case of southern Iberian pine plantations. Forest Ecology and Management 271, 158–169 (2012).
25. Zhu, K., Woodall, C. W. & Clark, J. S. Failure to migrate: lack of tree range expansion in response to climate change. Global Change Biology 18, 1042–1052 (2012).
26. Marris, E. Moving on assisted migration. Nature Reports Climate Change 112–113 (2008).doi:10.1038/climate.2008.86
27. Fernández-Manjarrés, J. F. & Tschanz, L. Assisted colonization: protect managed forests. Science 330, 1319 (2010).
28. Kreyling, J. et al. Assisted Colonization: A Question of Focal Units and Recipient Localities. Restoration Ecology 19, 433–440 (2011).
29. Rull, V. Sustainability, capitalism and evolution. Nature conservation is not a matter of maintaining human development and welfare in a healthy environment. EMBO reports 12, 103–6 (2011).
30. Frascaria-Lacoste, N. & Fernández-Manjarrés, J. Assisted Colonization of Foundation Species: Lack of Consideration of the Extended Phenotype Concept-Response to Kreyling et al. (2011). Restoration Ecology 20, 296–298 (2012).
31. Ukrainetz, N. K., O'Neill, G. A. & Jaquish, B. Comparison of fixed and focal point seed transfer systems for reforestation and assisted migration: a case study for interior spruce in British Columbia. Canadian Journal of Forest Research 41, 1452–1464 (2011).
32. Gray, L. K. & Hamann, A. Strategies for reforestation under uncertain future climates: guidelines for Alberta, Canada. PloS one 6, e22977 (2011).
33. Matziris, D. I. Variation in growth and quality characteres in Pinus pinaster provenances grown at seven sites in Greece. Genetica 168-173, (1982).
34. Alia, R., Gil, L. & Pardos, J. A. Performance of 43 Pinus pinaster provenances on 5 locations in central Spain. Silvae Genetica 44, 75–81 (1995).
35. Alia, R., Moro, J. & Denis, J. Performance of Pinus pinaster provenances in Spain: interpretation of the genotype by environment interaction. Canadian Journal of Forest Research 27, 1548–1559 (1997).
36. Gonzalez-Martinez, S. ., Alia, R. & Gil, L. Population genetic structure in a Mediterranean pine (Pinus pinaster Ait.): a comparison of allozyme markers and quantitative traits. Heredity 89, 199–206 (2002).
37. Roussel, G. Une bréve histoire de la recherche forestiére en Aquitaine. 3 (2007).
38. Boisseaux, T. Influence de l'origine genetique (landaise ou iberique) des peuplements de pin maritime sur les degats causes par le froid de janvier 1985 au massif forestier aquitain. 67 (1986).
39. Harfouche, A. & Kremer, A. Provenance hybridization in a diallel mating scheme of maritime pine (Pinus pinaster). I. Means and variance components. Canadian Journal of Forest Research 30, 1–9 (2000).
40. Guinedeau, J. Effets des grands froids de février 1956 sur les espéces forestiéres des Landes de Gascone. Revue Forestiére Française 1, 28–33 (1957).
41. Bonneau, M., Gelpe, J. & Le Tacon, F. A propos du dépérissement du pin portugais dans le Landes. Revue Forestiére Française 343–350 (1969).
42. Doré, C. & Varoquaux, F. Histoire et amélioration de cinquante plantes cultivées. 840 (Paris, 2006).
43. Pilcher, J. R. Wood Trees and Forests in Ireland. (Royal Irish Academy: Dublin, 1995).

44. Dhubahain, A., Maguire, K. & Farrelly, N. The harvesting behavior of Irish private forest owners and the suitability of the private estate for thinning. IUFRO Conference: small scale in a changing world: opportunities and challenges and the role of extension and technology transfer 128–137 (2010).
45. NFI National Forest Inventory - Republic of Ireland. Results. (Johnstown Castle State, CO Wesford, Ireland, 2007).
46. Hemery, G. E. et al. Growing scattered broadleaved tree species in Europe in a changing climate: a review of risks and opportunities. Forestry 83, 65–81 (2009).
47. Fernandez-Manjarres, J. F., Gerard, P. R., Dufour, J., Raquin, C. & Frascaria-Lacoste, N. Differential patterns of morphological and molecular hybridization between Fraxinus excelsior L. and Fraxinus angustifolia Vahl (Oleaceae) in eastern and western France. Molecular ecology 15, 3245–57 (2006).
48. Thomasset, M. Hybrid alien ash: Fraxinus excelsior x F. angustifolia in Ireland and its potential for interbreeding with native ash. (2011).
49. Gérard, P. et al. Chilled but not frosty: understanding the role of climate in the hybridization between the Mediterranean Fraxinus angustifolia Vahl and the temperate F. excelsior L. ash trees (Oleaceae). Journal of Biogeography
50. Benito Garzón, M., Leadley, P. W. & Fernandez-Manjarrés, J. F. Understanding global biome exposure to climate change through the Holocene - Anthropocene transition. PloS One
51. Wang, T., O'Neill, G. A. & Aitken, S. N. Integrating environmental and genetic effects to predict responses of tree populations to climate. Ecological Applications 20, 153–163 (2010).
52. Cattiaux, J. et al. Winter 2010 in Europe: A cold extreme in a warming climate. Geophysical Research Letters 37, L20704 (2010).
53. Coumou, D. & Rahmstorf, S. A decade of weather extremes. Nature Climate Change 2, 491–496 (2012).
54. Williams, J. W., Jackson, S. T. & Kutzbach, J. E. Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences of the United States of America 104, 5738–42 (2007).
55. Easterling, D. R. Climate Extremes: Observations, Modeling, and Impacts. Science 289, 2068–2074 (2000).
56. Allan, R. P. & Soden, B. J. Atmospheric warming and the amplification of precipitation extremes. Science 321, 1481–4 (2008).
57. Kopf, S., Ha-Duong, M. & Hallegatte, S. Using maps of city analogues to display and interpret climate change scenarios and their uncertainty. Natural Hazards and Earth System Sciences 8, 905–918 (2008).

Supplementary Material: Figure S1

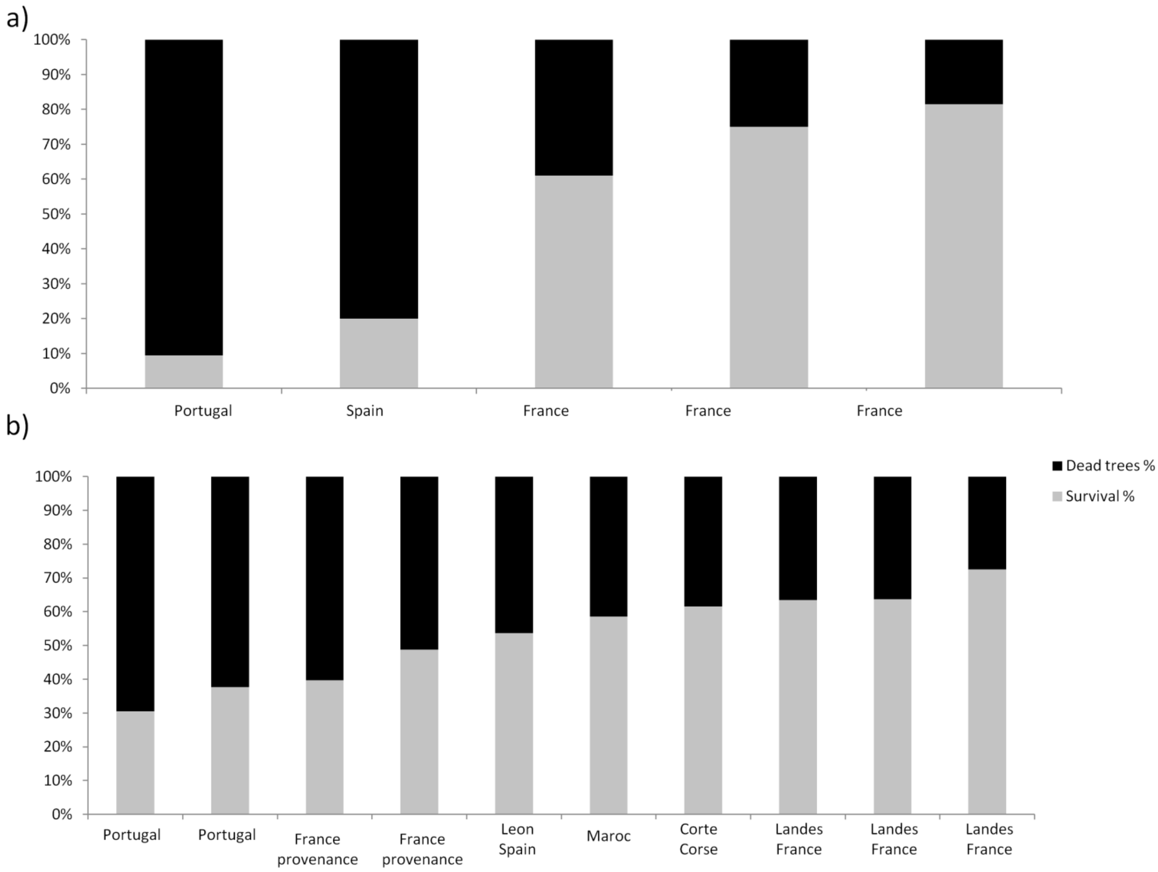

Figure S1. Early evidence of Iberian Pinus pinaster sensitivity to frost. a) Survival rates after the 1960 winter (adapted from Bouvarel[1], 1960). Based on 697 one-year-old seedlings planted in Nancy (northeast France). b) Survival rates of P. pinaster seedlings (2 to 4) planted in Aquitaine, France (Adapted from Illy[2], 1966).

Supplementary Material: Methods

Climate data

The CRU database was used to generate present analogous scenarios of climate. Eight climate variables were included in the PCA analysis: mean annual temperature, maximum summer temperatures, minimum winter temperatures, annual precipitation, coefficient of precipitation variation, summer precipitation and winter precipitation.

Estimation of Climate Analogues

To find climates analogous to those of the plantations, we calculated the climate anomalies of each pixel with respect to the plantation sites (Landes and Kildalkey). The climate anomalies were then analysed by Principal Component Analysis (PCA), where values close to zero indicate that the pixel is a climate analogue of the respective target plantation (Figure 2). The geographical display of the first principal component that gathers 50% of the variance explained by the PCA is shown in Figure 2. Significant correlations for the four principal components (C1 to C4) for both PCA analyses are summarised in Supplementary Table 1 and Table 2.

Components			
	C1	**C2**	**C3**
% of variance	0.49	0.32	0.11
Cumulative variance	0.49	0.81	0.92
Loadings			
Mean annual temperature	0.48	0.12	-0.04
Monthly temperature variance	-0.06	-0.55	0.37
Maximum temperature	0.45	-0.13	0.11
Minimum temperature	0.39	0.36	-0.22
Mean annual precipitation	-0.31	0.45	0.28
Coefficient of precipitation variation	0.30	-0.01	0.78
Summer precipitation	-0.47	0.01	0.12
Winter precipitation	-0.06	0.57	0.33

Table S1. Summary of the PCA analysis on the climatic anomalies in relation to the Landes (France).

Additional Material References

1. Bouvarel, P. Note sur la résistance au froid de quelques provenances de pin maritime. *Revue Forestiére Française* **7**, 495-508 (1960).
2. Illy, G. Recherches sur l'amélioration génétique du Pin maritime. *Annals of Forest Science* **23**, 756-948 (1966).