Assisted colonisation for ecosystem function: a thought experiment for the British Isles

Charlie J. Gardner[1]*, James M. Bullock[2]

[1] Durrell Institute of Conservation and Ecology, University of Kent, Canterbury CT2 7NZ, UK

[2] UK Centre for Ecology and Hydrology, Wallingford OX10 8BB, UK

* Correspondence: cjamgardner@gmail.com

Words: 2673 (of which 250 in abstract)

No. of Figures: 0

Keywords: Adaptation, Assisted migration, Climate change, Ecosystem services, Forest, Range shift, Survival ecology, Translocation.

Abstract

Climate change is driving the rapid reorganisation of the world's biota as species shift their ranges to track suitable conditions, however habitat fragmentation and other barriers hinder this adaptive response for species with limited dispersal ability. The translocation of species into newly suitable areas to which they are unable to disperse naturally has been suggested to conserve species threatened by climate change, but has not been widely adopted because the deliberate introduction of non-native species poses invasion risks and runs counter to traditional conservation approaches and philosophies. Using the future of forest ecosystems in the British Isles as a thought experiment, we argue that mass-scale assisted colonisation will be required not to conserve threatened species, but for the maintenance of functional ecosystems themselves. As climate changes, existing forest plant and animal communities of northern Europe will increasingly die out. On the mainland they will be somewhat replaced by analogous species from further south, but in Great Britain this replacement will be limited to a subset of mobile species due to the ocean barrier. As a result, forests there will lack many important component species unless these are actively translocated, will have reduced resilience and adaptive capacity, and will eventually collapse. Given the need for functional ecosystems in a hotter and highly fragmented world, conservationists must shift from trying to prevent change to trying to shape the biotic changes that are now inevitable. We must shift from reactive to proactive approaches in order to facilitate the emergence of robust novel ecosystems.

Introduction

Climate change has increased global temperatures by an average of over 1.5°C (in the 12 months to June 2024) since the beginning of the industrial revolution, changing the local conditions to which all species are adapted. In response, many species have been shifting their ranges in order to track shifting niche space; typically, such movements are towards the poles and to higher altitude (Chen et al. 2011), though local climate variation, land use change and other factors result in great variation in the direction of movement (Rubenstein et al. 2023). For many species the pace of range expansion is insufficient to keep up with the pace of climate change (Ash et al. 2017, Román-Palacios & Wiens 2020), while others are prevented from shifting ranges by geographical barriers and, in particular, anthropogenic barriers caused by the clearance and fragmentation of habitats (Marjakangas et al. 2023, Platts et al. 2019). As a result, many populations and species face a high risk of extinction this century (Román-Palacios & Wiens 2020).

In response, conservationists have proposed a strategy of assisted colonisation (also known as assisted migration), whereby species are purposefully translocated to areas outside of their current ranges which are expected to become increasingly suitable for them as the climate changes, but to which they are unable to disperse of their own accord. First discussed in the literature in 2004 (Barlow & Martin 2004, McLachlan et al. 2007), the concept has attracted debate and criticism arising from a range of concerns, including ethics, feasibility, perceived sociopolitical barriers and, in particular, the risk of unintended biological invasions (e.g. Ricciardi & Simberloff 2009). This is perhaps unsurprising as conservationists are wary of species translocations due to a long history of negative biodiversity impacts arising from species introductions: indeed, alien invasive species were identified as one of the ‘four horsemen of the ecological apocalypse’ during the field’s early days as a discipline (Diamond 1984), and remain a major driver of biodiversity loss (Roy et al. 2023). As such, the approach was said to “[fly] in the face of conventional conservation approaches” (Hoegh-Guldberg et al. 2008), and little assisted colonisation has been carried out in practice (Butt et al. 2021, Twardek et al. 2022). Research on the approach has also declined since a peak in 2015 (Benomar et al. 2022), despite the growth of our understanding of climate change impacts on biodiversity in that time.

Assisted colonisation has typically been framed by conservationists as an approach for conserving threatened species as climate change contracts their existing range (Butt et al. 2021), indeed the introduction to Britain of threatened southern European species, such as the Pyrenean desman, Iberian lynx and a butterfly, Provence chalkhill blue, was suggested over a decade ago (Thomas 2011). However, assisted colonisation could also be carried out in order to maintain or restore ecological function: in other words, the objective of a translocation could be to benefit the recipient ecosystem, not just to benefit the translocated species. This idea was also first discussed over a decade ago (Lunt et al. 2013), however it has been largely ignored in the conservation literature since (Benomar et al. 2022, Twardek et al. 2022): for example, Benomar et al. (2022) identified 71 prominent keywords frequently used in assisted colonisation-focused publications, but these did not include the terms ‘ecosystem’ or ‘function’ (though they did include ‘ecological restoration’ in the conservation literature, and ‘functional traits’ in the forestry-related literature). Here, we use a thought experiment considering the future forest ecosystems of the British Isles to restate the case made by Lunt and colleagues (2013), and argue that mass-scale assisted colonisation is likely to be required to maintain ecosystem function into the future. Rather than preventing species extinctions, the maintenance of the functioning ecosystems on which all biodiversity depends provides the strongest rationale for assisted colonisation in a rapidly heating world.

Europe’s shifting biota

At the peak of the Last Glacial Period (or ice age), 18,000 years ago, Scandinavia and the northern parts of what would become the British Isles were covered in ice; what is now southern England and the rest of northern and central Europe were tundra; and permafrost extended almost as far as the Mediterranean (Hewitt 1999). As the climate warmed and the ice retreated, whole communities of plants and animals shifted their ranges northwards in response (Giesecke et al. 2017, Hewitt 1999), expanding at the leading edge of their ranges through colonisation, and retreating at the trailing edge as populations became extinct. Great Britain (the largest island of the British Isles) was at the time the northwestern peninsula of Europe, connected to the mainland via the Doggerland land bridge, which permitted its colonisation by species unable to fly. However, rising sea levels submerged the land bridge by about 9000 years ago (Walker et al. 2020), severing the ecological connection with the mainland and preventing further colonisation by species with low-dispersal ability (such as non-flying animals, plants with short-distance seed dispersal, soil communities and freshwater communities). All wild species in the British Isles therefore either i) colonised by expanding from areas further south in the brief window between the retreat of the tundra and the rising of the seas, ii) were subsequently introduced by humans, or iii) subsequently colonised independently of humans.

The Holocene that succeeded the ice age has been a time of remarkable climatic stability, but European species are now shifting their ranges again in response to contemporary climate change (Hällfors et al. 2024, Howard et al. 2023). Europe’s forests are “undergoing a profound reorganisation” (Wessely et al. 2023), and with global temperatures expected to reach 3.2°C above the pre-industrial baseline by the end of the century (IPCC 2023), this trend is likely to accelerate and bring about wholesale changes to the European biota. By 2050 London is expected to experience a climate similar to that currently experienced in Barcelona (Bastin et al. 2019), and the north-west of Europe will become increasingly unsuitable for the tree (and other) species which currently dominate its forests (Mauri et al. 2022, 2023, Wessely et al. 2023). However, while forests on the mainland may be somewhat replenished by the colonisation of plant and animal species from further south, those of Great Britain will not be to the same extent, because it is an island.

As communities of plants and animals shift northwards through Europe, they will reach the English Channel. To highly-vagile species, such as birds and flying invertebrates, and plants with wind- or bird-dispersed seeds, this will pose little barrier: they will successfully expand into Britain, and they will be accepted as natural colonisers. This is already occurring; for example, several bird and invertebrate species have recently colonised the British Isles, and they are generally considered welcome additions to the British fauna (Cranston et al. 2022). However, for the majority non-flying species, including terrestrial mammals, reptiles, amphibians, non-volant arthropods, the invertebrate and fungal communities of leaf litter and soil, and all plants that are dispersed by neither birds nor the wind, the Channel will present a near-insurmountable barrier, and they will be unable to colonise (transoceanic dispersal by rafting does rarely occur (De Queiroz 2014) but is not a significant force over decadal timescales). As a result, the future forest communities of southern Great Britain will be highly impoverished compared to equivalent mainland areas at the same latitude, because many *natural components* of these ecosystems will be missing.

From reactive to proactive conservation

This thought experiment highlights an emerging yet urgent conundrum for conservationists and land managers in Britain. Prevailing conservation philosophies, approaches and legal frameworks counsel against the deliberate introduction of non-native species from mainland Europe, because to do so would be to meddle with nature and risk unintended consequences – specifically, the risk that a translocated species would become invasive and have negative ecological or economic impacts. However, the concept of ecological nativeness is not binary and not all non-natives are equally ‘alien’ (Lemoine & Svenning 2022): assisted colonisation would not involve the translocation of species from unrelated biotas on distant landmasses, which pose a high invasion risk (Mueller & Hellmann 2008), but only natural (and important) components of the ecosystems whose adaptation we are trying to facilitate.

According to the only existing decision framework for assisted colonisation in conservation, it should only be carried out if the candidate species for translocation is threatened with declines or extinction from climate change (Hoegh-Guldberg et al. 2008). This approach would suggest that the introduction of common forest trees and invertebrates to Britain from southern Europe is not required if these species are able to maintain populations on the mainland. However, in the absence of assisted colonisation the forests of southern Britain can be expected to suffer rapid impoverishment as the species which currently live there die out: if they are not replaced by analogous species better suited to the novel conditions, the ecosystem will collapse, and the region will be left without forests.

Forests are more than just populations of tree species and valuable habitats for biodiversity – they are complex ecosystems whose function depends on the interactions between their constituent species, and they provide irreplaceable ecosystem services. Regardless of whether British forests can contribute to the rescue of threatened European species, conservationists, land managers and the general public will want southern Britain to retain forests in future because they provide habitat for myriad species, store carbon, help prevent flooding, and carry significant amenity value for the people who use and love them (Mauri et al. 2023). If our objective were purely to conserve species then the translocation of mainland species to Britain may be seen as unnecessary, yet this thought experiment suggests that this may no longer be such an appropriate goal. What we should be striving for in a time of rapid climate change is the maintenance of functional, resilient, adaptable ecosystems that generate the ecosystems services we need to help avoid the worst of climate change and cope with its impacts (Gardner & Bullock, 2021). This requires us to shift from trying to conserve biodiversity per se, to instead trying to conserve ecosystem function because this is what will allow us to maintain the planetary conditions that allow biodiversity to thrive.

This, in turn, requires us to shift from a reactive to a proactive approach to maintaining biodiversity in a time of rapid change. Rather than looking to the past and trying to maintain historic patterns of biodiversity, which is an impossible goal in a changing climate, we should instead look to the future, ask ourselves what biodiversity we will need and want in a hotter world, and take whatever active steps are necessary to facilitate the dispersal of species and adaptation of ecosystems to emerging conditions. In the case of forest ecosystems in southern Britain, this will mean not only translocating the tree species that provide its physical structure, but also the fungal and invertebrate communities that allow trees to flourish, and the other plant and animal species that make up a forest ecosystem. In addition to translocating species beyond their current ranges, we will likely also need to carry out within-range ‘assisted gene flow’ for species whose current ranges span both Britain and southern Europe, such as the English oak *Quercus robur*, because the genetic material required for survival in Mediterranean climates is unlikely to be found within British populations. However, there appears to be little recognition of the need for active translocations to maintain forests or other ecosystems in areas where natural colonisation is inhibited by barriers. For example, the British Ecological Society’s major 2021 review of nature-based solutions in the UK makes no mention of assisted colonisation (Stafford et al., 2021).

The British Isles provides an illustrative example because the ocean barrier is easy to envisage, but in reality natural habitats are so fragmented across most of the world that most continental areas are effectively archipelagos of habitat islands within a matrix of agricultural land, roads, urban and other open areas of varying impenetrability for many species (Riitters et al. 2016). If, therefore, we conclude that broad-scale assisted colonisation will be required to maintain forests in southern England, then it may equally be so for other ecosystems across continental areas too.

Assisted colonisation is a growing area of research in forestry (Benomar et al. 2022), and its potential to help maintain forest timber productivity and other ecosystem services has been well modelled (Benito-Garzón & Fernández-Manjarrés 2015, Duveneck & Scheller 2015, Maury et al. 2023). But while sylviculturists, horticulturalists and agriculturalists routinely introduce species and varieties suited to emerging conditions with little hesitation, interest in assisted colonisation by conservationists appears to have stagnated and waned (Benomar et al. 2022) even as climate impacts on forests and biodiversity become ever more apparent.

Half the planet is expected to be covered by novel ecosystems by the end of this century (Ordonez et al. 2024) but, given the lack of ecological connectivity and the time lags involved in dispersal, they will be composed of only a high-mobility subset of the biota if they are left to reassemble without a helping hand. To maximise the diversity, resilience and adaptability of these ecosystems, we will need to actively translocate species and communities unable to disperse on their own. We will require mass-scale assisted colonisation.

Conclusions

Although conservation has, through its short history, principally been focused on maintaining biodiversity by preventing the extinctions of threatened species, climate change threatens not just species by ecosystems themselves. Since human societies, economies and all other species depend on the maintenance of functional ecosystems, this calls for a shift in conservation priorities. We must focus on the game not the players, maintaining ecological and evolutionary processes rather than particular species, and that requires us to cease trying to maintain the world as it was, and instead try to shape the world that will be (Gardner & Bullock 2021). Through climate change we are forcing species to shift their ranges, but we are simultaneously preventing many from doing so by fragmenting habitats and preventing dispersal. To have any hope of having functional ecosystems in future, we must facilitate biodiversity responses to climate change by helping species and communities overcome these novel anthropogenic barriers. This will require the urgent development of conservation policy, legislative frameworks and regulating bodies at the appropriate scales, as well as the research required to ensure these operate from a solid evidence base.

To paraphrase the proverb, the best time to plan and facilitate the establishment of the climate-resilient ecosystems of tomorrow was thirty years ago, but the next best time is now.

References

Ash, J. D., Givnish, T. J. & Waller, D. M. (2017) Tracking lags in historical plant species' shifts in relation to regional climate change. *Global Change Biology* 23: 1305–1315. https://doi.org/10.1111/gcb.13429.

Barlow, C., & Martin, P. S. (2004). Bring *Torreya taxifolia* north—now. *Wild Earth, Winter/Spring*, 52–56.

Bastin, J. -F., Clark, E., Elliott, T., Hart, S., van den Hoogen, J., Hordijk, I., Ma, H., Majumder, S., Manoli, G., Maschler, J., Mo, L., Routh, D., Yu, K., Zohner, C. M., & Crowther, T. W. (2019). Understanding climate change from a global analysis of city analogues. *PLoS ONE*, 4, e0217592. https://doi.org/10.1371/journal.pone.0217592.

Benito-Garzón, M. & Fernández-Manjarrés, J. F. (2015) Testing scenarios for assisted migration of forest trees in Europe. *New Forests* 46: 979–994. https://doi.org/10.1007/s11056-015-9481-9

Benomar, L., Elferjani, R., Hamilton, J., O'Neill, G., Echchakoui, S., Bergeron, Y. & Lamara, M. (2022) Bibliometric analysis of the structure and evolution of research on assisted migration. *Current Forestry Reports* 8: 199–213. https://doi.org/10.1007/s40725-022-00165-y

Butt, N., Chauvenet, A. L. M., Adams, V. M., Beger, M., Gallagher, R. V., Shanahan, D. F., Ward, M., Watson, J. E. M., & Possingham, H. P. (2020). Importance of species translocations under rapid climate change. *Conservation Biology, 35,* 775 – 783. https://doi.org/10.1111/cobi.13643

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science, 333(6405),* 1024–1026. https://doi.org/10.1126/science.1206432.

Cranston, J., Crowley, S.L. & Early, R. (2022) UK wildlife recorders cautiously welcome range-shifting species but incline against intervention to promote or control their establishment. *People and Nature* 4: 879–892. https://doi.org/10.1002/pan3.10325

De Queiroz, A. (2014) *The Monkey's Voyage: How Improbable Journeys Shaped the History of Life*. Basic Books, New York.

Diamond, J. M. (1984). "Normal" extinctions of isolated populations. In M. H. Nitecki (Ed.) *Extinctions* (pp. 191–246). University of Chicago Press.

Duveneck, M. J. & Scheller, R. M. (2015) Climate-suitable planting as a strategy for maintaining forest productivity and functional diversity. *Ecological Applications* 25: 1653 – 1668. https://doi.org/10.1890/14-0738.1

Gardner, C. J., & Bullock, J. M. (2021). In the climate emergency, conservation must become survival ecology. *Frontiers in Conservation Science, 2,* 659912. https://doi.org/10.3389/fcosc.2021.659912.

Giesecke, T., Brewer, S., Finsinger, W., Leydet, M. & Bradshaw, R. H. (2017) Patterns and dynamics of European vegetation change over the last 15,000 years. *Journal of Biogeography* 44: 1441–1456. https://doi.org/10.1111/jbi.12974

Hällfors, M. H., Heikkinen, R. K., Kuussaari, M., Lehikoinen, A., Luoto, M., Pöyry, J., Virkkala, R., Saastamoinen, M., & Kujala, H. (2024) Recent range shifts of moths, butterflies, and birds are driven by the breadth of their climatic niche. *Evolution Letters* 8: 89–100. https://doi.org/10.1093/evlett/qrad004.

Hewitt, G. M. (1999) Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society* 68: 87–112.

Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D. B., Parmesan, C., Possingham, H. P. & Thomas, C. D. (2008). Assisted colonization and rapid climate change. *Science* 321: 345–346. https://doi.org/10.1126/science.1157897.

Howard, C., Marjakangas, E.-L., Morán-Ordóñez, A., Milanesi, P., Abuladze, A., Aghababyan, K., Ajder, V., Arkumarev, V., Balmer, D. E. Bauer, H. -G., Beale, C. M., Bino, T., Boyla, K. A., Burfield, I. J., Burke, B., Caffrey, B., Chodkiewicz, T., Del Moral, J. C., Dumbovic Mazal, V… Willis, S. G. (2023) Local colonisatios and extinctions of European birds are poorly explained by changes in climate suitability. *Nature Communications* 14: 4304. https://doi.org/10.1038/s41467-023-39093-1.

IPCC (2023) *Climate Change 2023 Synthesis Report: Summary for Policymakers*. Intergovernmental Panel on Climate Change, Geneva.

Lemoine, R. T. & Svenning, J. -C. (2022) Nativeness is not binary – a graduated terminology for native and non-native species in the Anthropocene. *Restoration Ecology* 30: e13636. https://doi.org/10.1111/rec.13636

Lunt, I. D., Byrne, M., Hellmann, J. J., Mitchell, N. J., Garnett, S. T., Hayward, M. W., Martin, T. G., MacDonald-Madden, E., Williams, S. E. & Kerstin K. Zander (2013) Using assisted colonisation to conserve biodiversity and restore ecosystem function under climate change. *Biological Conservation* 157: 172–177. https://doi.org/10.1016/j.biocon.2012.08.034

Marjakangas, E.-L., Bosco, L., Versluijs, M., Xu, Y., Santangeli, A., Holopainen, S., Mäkeläinen, S., Herrando, S., Keller, V., Voříšek, P., Brotons, L., Johnston, A., Princé, K., Willis, S. G., Aghababyan, K., Ajder, V., Balmer, D. E., Bino, T., Boyla, K. A., … Lehikoinen, A. (2023) Ecological barriers mediate spatiotemporal shifts of bird communities at a continental scale. *Proceedings of the National Academy of Sciences, USA,* 120: e2213330120. https://doi.org/10.1073/pnas.2213330120.

Mauri, A., Girardello, M., Strona, G., Beck, P. S. A., Forzieri, G., Caudullo, G., Manca, F. & Cescatti (2022) EU-Trees4F, a dataset on the future distribution of European tree species. *Scientific Data* 9: 37. https://doi.org/10.1038/s41597-022-01128-5

Mauri, A., Girardello, M., Forzieri, G., Manca, F., Beck, P. S. A., Cescatti, A. & Strona, G. (2023) Assisted tree migration can reduce but not avert the decline of forest ecosystem services in Europe. *Global Environmental Change* 80: 102676. https://doi.org/10.1016/j.gloenvcha.2023.102676

McLachlan, J. S., Hellmann, J. J., & Schwartz, M. W. (2007). A framework for debate of assisted migration in an era of climate change. *Conservation Biology, 21,* 297–302. https://doi.org/10.1111/j.1523-1739.2007.00676.x.

Mueller, J. M. & Hellmann, J. J. (2008) An assessment of invasion risk from assisted migration. *Conservation Biology* 22: 562–567. https://doi.org/10.1111/j.1523-1739.2008.00952.x

Ordonez, A., Riede, F., Normand, S. & Svenning, J. -C. (2024) Towards a novel biosphere by 2300: rapid and extensive global and biome-wide climatic novelty in the Anthropocene. *Philosophical Transactions of the Royal Society* B 379: 20230022 https://doi.org/10.1098/rstb.2023.0022.

Platts, P. J., Mason, S. C., Palmer, G., Hill, J. K., Oliver, T. H., Powney, G. D., Fox, R. & Thomas, C. D. (2019) Habitat availability explains variation in climate-driven range shifts across multiple taxonomic groups. *Scientific Reports* 9: 15039. https://doi.org/10.1038/s41598-019-51582-2.

Ricciardi, A., & Simberloff, D. S. (2009). Assisted colonisation is not a viable conservation strategy. *Trends in Ecology and Evolution, 24,* 248–253. https://doi.org/10.1016/j.tree.2008.12.006.

Riitters, K., Wickham, J., Costanza, J. K. & Vogt, P. (2016) A global evaluation of forest interior area dynamics using tree cover data from 2000 to 2012. *Landscape Ecology* 31: 137–148. https://doi.org/10.1007/s10980-015-0270-9

Román-Palacios, C., & Wiens, J.J. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences, USA, 117,* 4211–4217 https://doi.org/10.1073/pnas.1913007117.

Roy, H. E., Pauchard, A., Stoett, P. & Renard Truong, T. (2023) *Thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. IPBES Secretariat, Bonn.

Rubenstein, M. A., Weiskopf, S. R., Bertrand, R., Carter, S. L., Compte, L., Eaton, M. J., Johnson, C. G., Lenoir, J., Lynch, A. J., Miller, B. W., Morelli, T. L., Rodriguez, M. A., Terando, A. & Thompson, L. M. (2023) Climate change and the global redistribution of biodiversity: substantial variation in empirical support for expected range shifts. *Environmental Evidence* 12: 7. https://doi.org/10.1186/s13750-023-00296-0.

Stafford, R., Chamberlain, B., Claevey, L., Gillingham, P. K., McKain, S., Morecroft, M.D., Morrison-Bell, C., & Watts, O. (2021) *Nature-based Solutions for Climate Change in the UK: a Report by the British Ecological Society*. British Ecological Society, London.

Thomas, C. D. (2011) Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends in Ecology and Evolution, 26,* 216–221. https://doi.org/10.1016/j.tree.2011.02.006.

Twardek, W. M., Taylor, J. J., Rytwinski, T., Aitken, S. N., MacDonald, A., Van Bogaert, R. & Cooke, S. J. (2023) The application of assisted migration as a climate change adaptation tactic: An evidence map and synthesis. *Biological Conservation* 280: 109932. https://doi.org/10.1016/j.biocon.2023.109932

Walker, J., Gaffney, V., Fitch, S., Muru, M., Fraser, A., Bates, M., & Bates, R. (2020) A great wave: the Storegga tsunami and the end of Doggerland? *Antiquity* 94: 1409–1425.

Wessely, J., Esst, F., Fledler, K., Gattringer, A., Hülber, B., Ignateva, O., Moser, D., Rammer, W., Dullinger, S. & Seidl, R. (2024) A climate-induced tree species bottleneck for forest management in Europe. *Nature Ecology & Evolution* 8: 1109 – 1117. https://doi.org/10.1038/s41559-024-02406-8