1 Functional assisted migration to sustain ecosystem functions under climate change

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8 Abstract

- 9 1. Climate change is rapidly altering habitats, forcing many plant species to shift their
 distribution. However, slow dispersal rates and habitat fragmentation hinder their ability to
 track these changes, risking local extinctions and reduced ecosystem functioning. Current
 management strategies may not suffice to address these challenges.
- We propose functional assisted migration (FAM) as a novel strategy to sustain ecosystem
 functionality under climate change by translocating non-native plant species capable of filling
 functional gaps in vulnerable ecosystems. By aligning plant communities with future climate
 conditions, FAM further enhances ecosystem resilience to withstand additional stressors.
- 17 3. To operationalize FAM, we outline key criteria and a data-driven workflow for species 18 selection. Species selected for FAM should meet four key criteria: adaptation to the future 19 climate, adaptation to edaphic conditions, the ability to fill functional gaps, and a low risk of 20 invasiveness. The structured workflow, integrating climate analogue analyses, species 21 distribution models, and functional trait assessments, provides a data-driven backbone for 22 selecting non-native plant species suitable for FAM.
- Synthesis and applications: By prioritizing ecosystem functionality and resilience, FAM offers a
 forward-thinking solution to one of conservation science's most pressing challenges. FAM
 complements traditional conservation efforts by targeting regions where natural dispersal and
 conventional strategies fall short, but empirical research remains essential to validate its
 ecological impacts and contributions.

29 1. The need for functional assisted migration

30 Climate change significantly alters habitat suitability and the spatial distribution of species, with most 31 species expected to shift their ranges toward higher latitudes and altitudes (Chen et al., 2011). 32 However, rates of species redistributions are substantially lower than the velocity of climate change 33 (Corlett & Westcott, 2013; Lenoir et al., 2020). Factors such as slow dispersal speeds, habitat 34 fragmentation due to land-use changes, and reduced biotic connectivity following megafauna 35 extinctions (Fricke et al., 2022) have contributed to a seed dispersal crisis (Mendes et al., 2024). As a 36 result, many plant species are unable to keep pace with climate change, increasing the risk of (local) extinction (Pörtner et al., 2021). 37

38 Current adaptive management strategies, including enhancing species and genetic diversity, mitigating 39 local stressors and improving landscape connectivity (Hylander et al., 2022; Moore & Schindler, 2022), 40 may prove insufficient to address the rapid pace of climate change (Hällfors et al., 2017). Consequently, 41 there is a growing call for new, proactive interventionist strategies (Peterson St-Laurent et al., 2021; Prober et al., 2019). Unlike efforts to minimize migration barriers within landscapes, assisted migration 42 43 directly facilitates species' range shifts to keep pace with changing climates. Also referred to as assisted 44 colonization or managed relocation, this approach involves actively translocating species beyond their 45 native ranges to mimic natural range expansions that would occur under climate change if not for 46 anthropogenic barriers or time constraints (Hällfors et al., 2014). This strategy represents a paradigm 47 shift in conservation, challenging traditional principles that emphasize preserving local biodiversity and avoiding the introduction of alien species (Corlett & Westcott, 2013). While widely proposed as a 48 49 response to climate change, assisted migration remains highly debated and controversial due to its 50 potential ecological risks and the ethical implications of reshaping how ecosystems are valued and 51 managed (Prober et al., 2019). Logically, caution is required as newly introduced species may become 52 invasive and harm native biodiversity (Pyšek et al., 2020). Critics argue that the impacts of introductions on recipient communities are difficult to predict, advocating against assisted migration 53 54 based on the precautionary principle (Bucharova, 2017; Ricciardi & Simberloff, 2009). Nevertheless, 55 while the risk of biological invasions cannot be eliminated, careful selection of species for assisted 56 migration may help mitigate this concern.

Invasive alien species typically originate from regions that are spatially and often biogeographically distinct, encountering novel environmental conditions and biotic interactions in their introduced ranges (Urban, 2020). Contrarily, intracontinental, short-distance translocations of species tracking their bioclimatic envelopes are more likely to involve species with an evolutionary history shared with the recipient community. This significantly reduces the likelihood of enemy release and biological invasion (Brian & Catford, 2023). Additionally, species requiring translocation often possess traits such as poor dispersal ability, low competitiveness, or long life cycles, which stand in stark contrast to traits

associated with invasiveness (Palma et al., 2021; Zhao et al., 2023). In this paper, we focus on plant
communities as plants are less likely than animals to cause rapid extinctions in recipient communities,
as predation - an interaction absent in plant introductions - is the primary driver of such extinctions
(Sax & Gaines, 2008).

68 Emphasizing the risks while overlooking the potential benefits of assisted migration has hindered 69 essential conservation innovation (Brodie et al., 2021; Marvier & Kareiva, 2020). As a result, the 70 existing literature is dominated by theoretical frameworks (McLachlan et al., 2007; Prober et al., 2019), 71 opinion pieces (Bucharova, 2017; Ricciardi & Simberloff, 2009) and studies modelling the need for 72 species translocations (e.g. Bellis et al., 2020; Casazza et al., 2021), with only very few empirical 73 investigations (Twardek et al., 2023). For example, a recent review of species translocations within 74 protected areas identified only 148 (out of 956) studies focusing on plants, of which only four explicitly 75 addressed assisted migration (Langridge et al., 2021). The perceived risks associated with relocating 76 species beyond their current ranges, combined with the lack of standardized procedures and restrictive 77 environmental policies, have severely constrained empirical research on assisted migration, resulting 78 in a critical knowledge gap (Park & Talbot, 2018).

79 Urgent empirical studies are thus needed to assess the effectiveness and underlying mechanisms of 80 translocations, evaluate how novel interactions affect the persistence of translocated populations and 81 determine how these species influence the functioning of recipient ecosystems (Prober et al., 2019). 82 However, most existing studies and projects on assisted migration adhere to the traditional 83 conservation paradigm, focused on species threatened by climate change (Benomar et al., 2022; Butt 84 et al., 2021). Efforts to translocate species solely to prevent species extinction are likely to face 85 significant resistance and policy conflicts in recipient regions, where the perceived risks are seen to 86 outweigh the potential benefits (Davidson & Simkanin, 2008). Expanding the scope of research to 87 prioritize ecosystem functionality could help address these challenges while unlocking the potential of 88 assisted migration as a conservation tool.

89 Besides driving species loss, climate change and other disturbances are expected to significantly 90 impact ecosystem functioning. Beyond safeguarding species through translocation, assisted migration 91 offers a promising strategy for restoring or maintaining ecosystem functions in communities 92 threatened by climate-induced extinctions (Lundgren et al., 2024). Here, we introduce the concept of 93 functional assisted migration (FAM), which focuses on maintaining ecosystem functionality through 94 the deliberate introduction of species. This approach is similar to the concept of pull-assisted migration 95 proposed by Lunt et al. (Lunt et al., 2013), which also emphasized the introduction of species to support ecosystems. We use the term functional assisted migration because it highlights the 96 97 overarching goal of sustaining ecosystem functions rather than simply describing the act of 98 translocating species. By prioritizing benefits to the recipient community, functional assisted migration

99 may help shift the risk-benefit balance, as species are introduced to enhance ecosystem functionality 100 rather than merely posing a risk of invasion. This approach aligns with a broader trend in conservation 101 that emphasizes the importance of ecosystem functionality and resilience to sustain ecosystem 102 services under climate change (Moore & Schindler, 2022; Siegel et al., 2024). In this paper, we adopt 103 this functional perspective on assisted migration of plant species and propose a framework for its 104 practical implementation.

105 2. Filling functional gaps to sustain ecosystem functioning

106 Biodiversity and ecosystem functioning are linked in complex, non-linear ways. Higher levels of 107 biodiversity enhance a community's ability to capture resources, produce biomass, and cycle nutrients 108 efficiently (Cardinale et al., 2012). Furthermore, biodiversity contributes to greater ecosystem stability 109 in the face of disturbances (Loreau et al., 2021). However, traditional biodiversity metrics, such as 110 species richness, often fail to fully capture the relationship between biodiversity and ecosystem 111 functioning. Functional differences among plant species rather than species identity seem to play a 112 pivotal role in driving ecosystem processes and shaping ecological communities (Cadotte, 2017). 113 Representing biodiversity as a continuum of species' functional traits has therefore significantly 114 advanced our understanding of community assembly, ecosystem functioning and responses to 115 disturbances (e.g. Bektas et al., 2023). Theoretically, communities with greater functional diversity -116 characterized by a wide range of trait values - are expected to maintain higher levels of ecosystem 117 functioning. Complementing this, functional redundancy, where multiple species share similar 118 functional traits, enhances ecosystem stability under changing conditions. By providing an insurance 119 effect, functional redundancy ensures that the loss of a species is less likely to result in the complete 120 loss of critical ecosystem functions (de Bello et al., 2021). However, many natural ecosystems have 121 faced a history of degradation and species extinctions (Bardgett et al., 2021; Díaz & Malhi, 2022). As a 122 result, further species loss driven by climate change is likely to create functional gaps within local 123 communities, reducing overall ecosystem functioning. The ongoing loss of biodiversity among native 124 species is already negatively affecting ecosystem functioning, stability and ecosystem service provision 125 worldwide (Gammal et al., 2023; Wang et al., 2021).

126 Relying solely on natural migration is unlikely to prevent future declines in ecosystem functioning. Through functional assisted migration, plant species with suitable functional traits can be identified 127 128 and translocated to fill actual or predicted functional gaps, helping to sustain ecosystem functioning 129 under changing climate conditions (Figure 1a). For example, the functional assisted migration of plants 130 can alleviate constraints on the range expansion of specialist pollinators, supporting their ecological 131 interactions (Stephan et al., 2021), whereas translocating warm-adapted tree species could help 132 maintain a closed forest canopy, preserving critical buffer capacity and microclimate conditions during future drought-spells, essential for the survival of many forest-dwelling species (Xu & Prescott, 2024). 133

Additionally, climate warming often interacts with other anthropogenic stressors, creating multidirectional global changes that reduce species' tolerance (sensu Van Meerbeek et al., 2021) to individual perturbations (Crall et al., 2018; Williams et al., 2013). By aligning plant communities with future climate conditions, FAM enhances the resilience of ecosystems to withstand additional stressors, such as extreme droughts or nitrogen deposition (Figure 1b).





Figure 1. (a) Ecosystem functioning is expected to decline under increasing climate warming as local 141 species A, B, and C are unable to track shifting climate zones and are negatively impacted by climate 142 change (top). Functional assisted migration of species D, E, and F can sustain ecosystem functioning by 143 144 introducing species better adapted to the new climate conditions (bottom). Tiles represent species with 145 varying optimal temperature ranges, indicated by different colours. (b) Functional assisted migration can also enhance tolerance to additional stressors, such as drought, by relocating species to higher 146 147 altitudes or latitudes. The blue zone illustrates the survival range of a species under specific 148 environmental conditions.

149 3. Functional assisted migration in practice

150 To guide the selection of non-native plant species for functional assisted migration, we developed a 151 structured six-step workflow (Figure 2). This process integrates four key criteria that candidate species must meet to effectively sustain ecosystem functionality under changing climate conditions: (1) The 152 153 species should be adapted to future climate conditions of the target region; (2) The species should be adapted to edaphic conditions, including soil moisture, pH and nutrient levels; (3) The species should 154 155 be capable of filling functional gaps induced by climate change. Non-native species should therefore 156 have functional traits or phylogenies similar to those of the native species they are intended to replace; (4) The species should pose a low risk of invasiveness. The process begins with gathering plant 157 158 community data from climate analogues, i.e. areas where the current climate closely resembles the 159 projected future climate of the target region (Dobrowski et al., 2021). In subsequent steps, species 160 that fail to meet the criteria are progressively excluded. Finally, we recommend experimental research

161 to test species combinations and empirically evaluate the outcomes of FAM with the selected species.

162 Step 1: Climate analogues - The first step involves conducting a climate similarity assessment to identify non-native species growing in climate analogues for the target region. Climate similarity can be 163 164 quantified as the Euclidean distance between the locations within a multidimensional climate space, 165 which is defined by various climate variables. This analysis must account for climate extremes, not just 166 mean conditions, as extremes are expected to become more frequent in the future and could play a 167 critical role in shaping species distributions (Fonteyn et al., 2024). For regions with high climate similarity, plot data are retrieved from plot databases such as sPlotOpen (Sabatini et al., 2021) and the 168 169 European Vegetation Archive (Chytrý et al., 2016). Since climate similarity is a continuous metric, no 170 universal threshold exists for identifying climate analogues. Therefore, we recommend performing the 171 climate similarity analyses and subsequent steps using varying distance thresholds. Additionally, the 172 climate similarity assessment can be repeated for different climate scenarios and time horizons 173 according to the research questions and goals, each yielding distinct plots and, consequently, varying 174 species sets.

175 Step 2: Co-occurrence analysis - Non-native species that often co-occur with the native species from 176 the target community are likely to be adapted to similar biotic and abiotic conditions, and due to co-177 evolution with native species in similar environments, they are less likely to exhibit invasive behaviour 178 within the target area. To begin, the composition of the target plant community must be characterized 179 by identifying its characteristic species. This selection can be guided by expert knowledge or existing 180 species lists. To identify non-native species that co-occur with these characteristic species, several co-181 occurrence analysis methods are available (Arita, 2016). Among these, we recommend ordination 182 analysis, which positions species in a low-dimensional space based on their co-occurrence patterns. 183 Species that frequently co-occur in vegetation plots are placed closer together in the ordination diagram. Traditionally, ordination of vegetation data (plots × species) has been performed using non-184 185 metric multidimensional scaling (NMDS). Recently, however, model-based ordination methods have 186 emerged (van der Veen et al., 2021). These methods, grounded in the generalized linear regression 187 framework, provide advanced tools for diagnosing model fit and conducting model selection. From the 188 ordination results, non-native species positioned close to the characteristic species of the target 189 community are selected for further analysis. The definition of "close" in ordination space is, however, 190 not absolute. Both the distance and the number of close characteristic native species are variables 191 without clear thresholds. However, the information provided by the native species can be used to 192 establish reasonable cut-offs. Specifically, the number of other native species within a circle of 193 increasing radius could be calculated for each species in the ordination diagram. By analysing how 194 native species cluster in ordination space (and are thus close to other native species), one or more cut-195 off values can be determined to select non-native species for subsequent steps.

196 Step 3: Climate suitability - Even though non-native species are selected from plots in climate analogue 197 regions, these plots might still be at the edge of the species' distribution range. As a result, the future 198 climate conditions in the target region might only marginally support certain non-native species. To 199 refine the selection, species distribution modelling (SDM) can be used to evaluate the suitability of 200 future climate conditions for each non-native species and the trend in suitability from the present to 201 the future. Only non-native species with a positive trend and high future climate suitability should 202 proceed to further analyses. Simultaneously, SDMs should be conducted for the characteristic native 203 species of the target plant community. This will help identify native species likely to struggle under 204 future climate conditions, which is essential for recognizing potential future functional gaps in the 205 ecosystem (see Step 4). SDMs can be executed using the plot databases from Step 1 and presence-206 absence algorithms such as logistic regression or Boosted Regression Trees (Elith et al., 2008). 207 Alternatively, presence-only data from large databases, such as GBIF.org, can be utilized with 208 algorithms like MaxEnt, which is specifically designed for presence-only data (Valavi et al., 2022).

209 Step 4: Functional gaps - Predicted species loss driven by climate change and other disturbances can 210 be analysed in terms of changes in functional trait space, i.e. the multidimensional space defined by 211 functional traits as axes. To explore this, data for traits relevant to the target ecosystem functions (Streit 212 & Bellwood, 2023) of all species should first be extracted from trait databases such as TRY (Kattge et 213 al., 2020). For example, if the objective is to preserve the microclimate buffering capacity of a forest, 214 traits like maximum tree height, leaf area index, and deciduousness are particularly important (De 215 Frenne et al., 2021). By applying ordination analysis, native species assemblages can be visualized 216 within a low-dimensional trait space (Mammola & Cardoso, 2020). Overlaying these graphs with 217 information from the SDMs (Step 3) enables the identification of potential functional gaps. Adding 218 climate-resilient non-native species to these graphs helps pinpoint candidates that could fill these 219 functional gaps. As an alternative to functional traits, phylogenetic relatedness can be used as a proxy 220 for functional similarity, leveraging the concept of phylogenetic niche conservatism - the tendency of 221 closely related species to share similar traits (Swenson, 2019). Using tools like the Analysis of 222 Phylogenetics and Evolution (APE) package in R (Paradis et al., 2004), researchers can construct a 223 phylogenetic tree that includes both native and non-native species. By marking native species likely to 224 face local extinction, it becomes possible to identify non-native species that could serve as suitable 225 candidates for functional assisted migration.

Step 5: Edaphic suitability - In addition to climate suitability, it is essential to consider edaphic suitability when selecting non-native species. The chosen species should be well-adapted to the soil conditions of the target area. While edaphic variables can be integrated into species distribution models (SDMs), the coarse spatial resolution of available geodata often fails to capture fine-scale environmental variation. To address this limitation, edaphic suitability should be verified through an additional step. A practical approach involves using ecological indicator values, which are ordinal scales

that describe the optimal conditions of a species' realized ecological niche along specific environmental gradients (Dengler et al., 2023). Ecological indicator values for soil moisture, soil pH, and soil nitrogen content in non-native species can be compared to those of characteristic species within the native community, ensuring alignment with the local edaphic conditions.

236 Step 6: Experimental validation - To minimize the risk of introducing harmful invasive species, a 237 thorough final assessment of invasiveness is essential. This involves cross-referencing candidate 238 species with existing invasive species lists from other regions (e.g. Pagad et al., 2022) and consulting 239 experts to exclude any species with invasive potential. Additionally, experimental research plays a 240 critical role in evaluating the effects of functional assisted migration on recipient communities, species 241 interactions and overall ecosystem functioning. To achieve this, combinations of native and selected 242 non-native species should be tested under controlled environmental conditions. Ideally, these 243 experiments should be conducted in the target region but under conditions that simulate the 244 anticipated future climate. This can include climate warming experiments using open-top chambers or 245 active heating methods (Yang et al., 2018). Alternatively, experiments based on space-for-time 246 substitutions in climate-analogue regions offer a simpler approach (De Frenne et al., 2013). If the 247 workflow identifies multiple alternative non-native species to fill the same functional gap, additional 248 selection criteria can be applied. For example, prioritizing rare species may be beneficial, as they are 249 highly vulnerable and often contribute disproportionately to ecosystem functioning (Dee et al., 2019).

1. Climate analogues

Select vegetation plots in climate analogues of target region





Identify native species that will disappear locally in the future Check if selected non-natives are adapted to future climate



2. Co-occurrence analysis

Native key species Non-native species

4. Functional gaps

Ordination axis 2

Select species co-occuring with key species of native target community

Identify functional gaps left by native species that might disappear locally

SP A

Ordination axis 1

251

Figure 2. A six-step process for selecting non-native plant species as candidates for functional assisted 252 migration. The process starts by collecting plant community data from climate analogue regions, 253 potentially identifying a broad pool of non-native species. At each subsequent step, species are 254 progressively filtered out based on predefined selection criteria. Finally, the remaining candidate 255 256 species should be evaluated through controlled experiments. CHELSA bioclimatic variables were used to construct the SDM and climate similarity maps (Brun et al., 2022). Occurrence data (Allium 257 258 neopolitanum) were extracted from GBIF.org.

260 4. Concluding remarks

261 Current management strategies are unlikely to suffice in addressing the unprecedented rates of 262 climate change, which are expected to result in local species extinctions and diminished ecosystem functioning. Functional assisted migration (FAM) offers an innovative approach to maintaining 263 264 ecosystem functionality by introducing species capable of filling functional gaps created by climate 265 change. In this paper, we propose criteria and a step-by-step framework to guide species selection for FAM, aiming to establish novel plant communities that are resilient to climate change impacts. To 266 267 maximize success, FAM should prioritize short-range intracontinental translocations of plant species that already co-exist with native communities, are well-adapted to local soil conditions, and can thrive 268 269 under future climate scenarios in the target area. The novel communities are expected to better 270 withstand future challenges, such as increased drought and elevated temperatures, while maintaining 271 ecosystem functionality. However, empirical data are crucial to validate this hypothesis, optimise the 272 implementation and address potential risks. Note that FAM does not aim to replace traditional 273 conservation methods but to complement them. Natural dispersal mechanisms should still be 274 supported by enhancing biotic connectivity and reducing landscape fragmentation to facilitate species' 275 ability to track shifting climate zones. Nonetheless, FAM should be considered as a targeted strategy in regions where conventional conservation methods fall short. Further research is needed to identify 276 277 ecosystems and plant communities most at risk of losing functionality under future climate conditions. By prioritizing ecosystem functionality and resilience, FAM offers a forward-thinking solution to one of 278 279 the most pressing challenges in conservation science.

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