Functional assisted migration to sustain ecosystem functions under climate change

Koenraad Van Meerbeek*[1,2], Senne Spreij[1], Marijke Geuskens[1], Chang Liu[1], Willem Goossens[1] & Stef Haesen[1,2]

[1]Department of Earth and Environmental Sciences, Celestijnenlaan 200E, 3001 Leuven, Belgium

[2]KU Leuven Plant Institute, KU Leuven, Leuven, Belgium

* Corresponding author: koenraad.vanmeerbeek@kuleuven.be

Abstract

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.
2. We propose functional assisted migration 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, functional assisted migration further enhances ecosystem resilience to withstand additional stressors.
3. To operationalize functional assisted migration, we outline key criteria and a data-driven workflow for species selection. Species selected for functional assisted migration should meet four key criteria: adaptation to the future climate, adaptation to edaphic conditions, the ability to fill functional gaps, and a low risk of invasiveness. The structured workflow, integrating climate analogue analyses, species distribution models, and functional trait assessments, provides a data-driven backbone for selecting non-native plant species suitable for functional assisted migration.
4. By prioritizing ecosystem functionality and resilience, functional assisted migration offers a forward-thinking solution to one of conservation science's most pressing challenges. Functional assisted migration 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.

1. Introduction

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

Current adaptive management strategies, including enhancing species and genetic diversity, mitigating local stressors and improving landscape connectivity (Hylander et al., 2022; Moore & Schindler, 2022), may prove insufficient to address the rapid pace of climate change (Hällfors et al., 2017). Consequently, 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 directly facilitates species' range shifts to keep pace with changing climates. Also referred to as assisted colonization or managed relocation, this approach involves actively translocating species beyond their native ranges to mimic natural range expansions that would occur under climate change if not for anthropogenic barriers or time constraints (Hällfors et al., 2014). This strategy represents a paradigm 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 response to climate change, assisted migration remains highly debated and controversial due to its potential ecological risks and the ethical implications of reshaping how ecosystems are valued and managed (Prober et al., 2019). Logically, caution is required as newly introduced species may become 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 based on the precautionary principle (Bucharova, 2017; Ricciardi & Simberloff, 2009). Nevertheless, while the risk of biological invasions cannot be eliminated, careful selection of species for assisted 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).

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

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

Besides driving species loss, climate change and other disturbances are expected to significantly impact ecosystem functioning. Beyond safeguarding species through translocation, assisted migration offers a promising strategy for restoring or maintaining ecosystem functions in communities threatened by climate-induced extinctions (Lundgren et al., 2024). Here, we introduce the concept of *functional assisted migration* (FAM), which focuses on maintaining ecosystem functionality through the deliberate introduction of species. This approach is similar to the concept of pull-assisted migration 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 overarching goal of sustaining ecosystem functions rather than simply describing the act of translocating species. By prioritizing benefits to the recipient community, functional assisted migration may help shift the risk-benefit balance, as species are introduced to enhance ecosystem functionality rather than merely posing a risk of invasion. This approach aligns with a broader trend in conservation that emphasizes the importance of ecosystem functionality and resilience to sustain ecosystem services under climate change (Moore & Schindler, 2022; Siegel et al., 2024). In this paper, we adopt a functional lens on assisted migration of plant species. We first elaborate on the concept, then present a six-step framework for its practical implementation. Finally, we apply the framework in a case study on Old Acidophilous Oak Woods in Northern Belgium.

2. Filling functional gaps to sustain ecosystem functioning

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

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 and translocated to fill actual or predicted functional gaps, helping to sustain ecosystem functioning under changing climate conditions (Fig. 1a). For example, the functional assisted migration of plants can alleviate constraints on the range expansion of specialist pollinators, supporting their ecological interactions (Stephan et al., 2021), whereas translocating warm-adapted tree species could help 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). 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 (Fig. 1b).

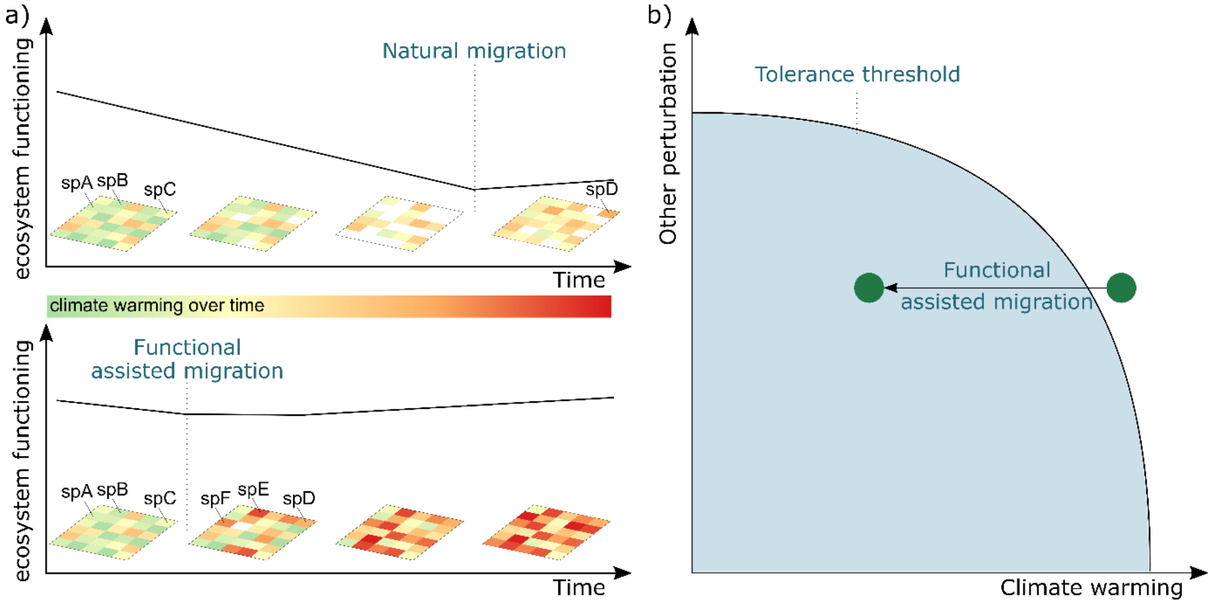

Fig. 1. (a) Ecosystem functioning is expected to decline under increasing climate warming as local species A, B, and C are unable to track shifting climate zones and are negatively impacted by climate change (top). Functional assisted migration of species D, E, and F can sustain ecosystem functioning by introducing species better adapted to the new climate conditions (bottom). Tiles represent species with 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 altitudes or latitudes. The blue zone illustrates the survival range of a species under specific environmental conditions.

3. Functional assisted migration in practice

To guide the selection of non-native plant species for functional assisted migration, we developed a structured six-step workflow (Fig. 2). This process integrates four key criteria that candidate species must meet to effectively sustain ecosystem functionality under changing climate conditions: (1) The 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 be capable of filling functional gaps induced by climate change. Non-native species should therefore 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 community data from climate analogues, i.e. areas where the current climate closely resembles the projected future climate of the target region (Dobrowski et al., 2021). In the subsequent steps, species that do not meet one or more of the criteria are progressively filtered out. Expert input from ecologists familiar with both the target and analogue regions is essential throughout, to validate species relevance and refine the selection. The final step involves experimental testing of selected species combinations to assess their performance and verify FAM outcomes under realistic conditions.

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 quantified as the Euclidean distance between the locations within a multidimensional climate space, which is defined by various climate variables. Ideally, this analysis should account for climate extremes, not just mean conditions, as extremes are expected to become more frequent in the future and may critically influence species distributions (Fonteyn et al., 2024). However, future climate datasets that include detailed information on extremes are not yet readily accessible. For regions with high climate similarity, plot data can be retrieved from plot databases such as sPlotOpen (Sabatini et al., 2021) and the European Vegetation Archive (Chytrý et al., 2016). Since climate similarity is a continuous metric, no universal threshold exists for identifying climate analogues. Therefore, we recommend performing the climate similarity analyses and subsequent steps using varying distance thresholds. The aim is to generate a broad list of candidate tree species for further analysis. Excluding too many species at this stage risks overlooking relevant ones, whereas casting a wide net is less problematic, as unsuitable species will be filtered out in the next steps. Additionally, given the uncertainty surrounding future greenhouse gas emission trajectories (IPCC, 2023), the climate similarity assessment can be repeated across different climate scenarios and time horizons, depending on the specific research questions and objectives. Each combination yields distinct climate projections and, consequently, different sets of suitable species.

Step 2: Co-occurrence analysis. Non-native species that often co-occur with the native species from the target community are likely to be adapted to similar biotic and abiotic conditions, and due to co-evolution with native species in similar environments, they are less likely to exhibit invasive behaviour within the target area. To begin, the composition of the target plant community must be characterized by identifying its characteristic species. This selection can be guided by expert knowledge or existing species lists. To identify non-native species that co-occur with the characteristic native species, several co-occurrence analysis methods are available (Arita, 2016). Among these, ordination analysis is widely used by ecologists, as it visualizes species in a low-dimensional space based on their co-occurrence patterns. 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-metric multidimensional scaling (NMDS). Recently, however, model-based ordination methods have emerged (van der Veen et al., 2021). These methods, grounded in the generalized linear regression framework, provide advanced tools for diagnosing model fit and conducting model selection. Another option is to calculate a dissimilarity index between each pair of species based on their co-occurrence (e.g. Bray-Curtis distance). From the ordination or dissimilarity results, non-native species positioned close to the characteristic species of the target community are selected for further analysis. The definition of "close", however, is not absolute. Both the distance and the number of close key native species are variables without clear thresholds. However, the patterns observed for native species in this analysis can help inform reasonable cut-off values. Specifically, the number of other native species within a distance of increasing radius could be calculated for each species. By analysing how native species cluster (and are thus close to other native species), one or more cut-off values can be determined to select non-native species for subsequent steps.

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

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

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

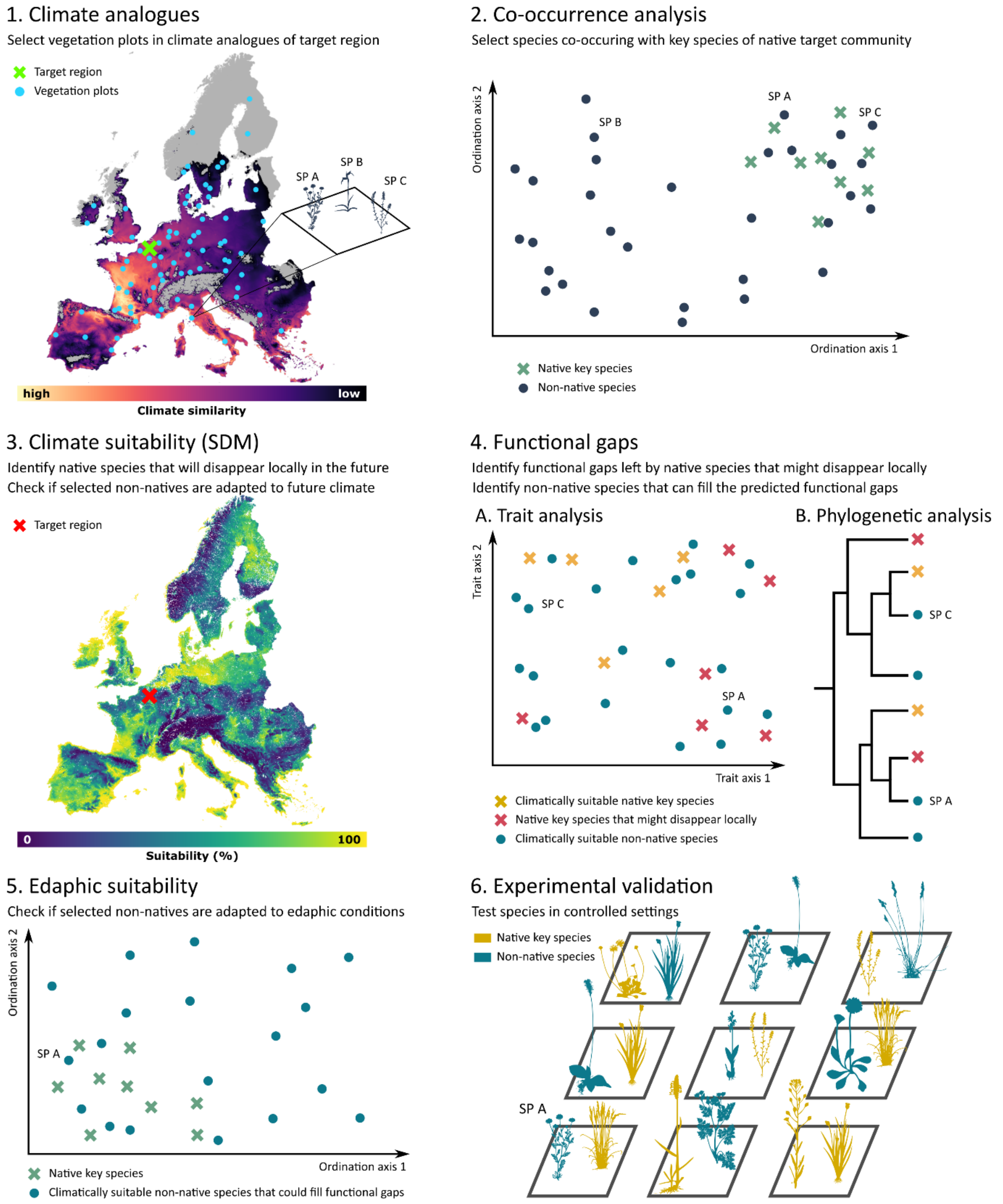

Fig. 2. A six-step process for selecting non-native plant species as candidates for functional assisted migration. The process starts by collecting plant community data from climate analogue regions, potentially identifying a broad pool of non-native species. At each subsequent step, species are progressively filtered out based on predefined selection criteria. Finally, the remaining candidate 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 neopolitanum) to construct the SDM in step 3 were extracted from GBIF.org.*

4. Case study

The case study focused on habitat type 9190 of the Natura 2000 framework, known as 'Old acidophilous oak woods with *Quercus robur* on sandy plains'. The habitat type is characterised not only by *Quercus robur*, but also by *Betula pendula* and *Betula pubescens*, often occurring alongside *Sorbus aucuparia* and *Populus tremula* (Fig. 3a). These habitats typically occur on oligotrophic, acidic sandy soils covering a narrow edaphic niche within the northern European plain (Fig. 3b; EC DG Env, 2013). The most urgent pressures on this forest type include eutrophication caused by air pollution, primarily from agriculture, as well as disturbances of the natural hydrological regimes (Paelinckx & Herr, 2019). Additionally, several of its key native tree species are threatened by climate change (Desie et al., 2024). Hence, there is an urgent need to protect these forests, especially given that Flanders - the northern part of Belgium - accommodates about 8% of the European share of this important habitat type. In this case study, we assess the potential of FAM to safeguard this forest type and its associated ecosystem functions in Flanders under climate change. All further analyses have been conducted with R v4.4.2 (R Core Team, 2025), with spatial data handled using the terra package (Hijmans, 2020).

Step 1: Climate analogues. To establish a reference point for the climate similarity analysis, we calculated the future climate in Flanders, over the period 2071-2100, by averaging all available global circulation models (GCMs) from CHELSA (Karger et al., 2017), and subsequently averaging all pixels across Flanders in order to come to an average future climate for Flanders. This was repeated for each of the 19 bioclimatic variables (BIO1-BIO19), both for the SSP3-7.0 and SSP5-8.5 scenarios. To identify areas in Europe where current climate conditions resemble the projected future climate of Flanders, we applied the same method to current climate data (1981–2010) from CHELSA for every 1 × 1 km^2 grid cell across Europe. A Principal Component Analysis (PCA) using the prcomp() function was then conducted to project these climatic conditions into a multidimensional climate space. Within this space, climate similarity was then measured as the Euclidean distance between the future climate of Flanders and current climates across Europe — with smaller distances indicating higher similarity.

Vegetation data were obtained from the EU-Forest database (Mauri et al., 2017), which compiles geo-referenced information on 242 commonly occurring tree species across Europe, drawing from sources such as the National Forest Inventories (NFI; Tomppo et al., 2010). As the most extensive dataset of tree species occurrences in natural environments across Europe, it provides a representative overview of the current distributions of these species. Since these data consist of individual presence points, we aggregated all species co-occurring within each 1 × 1 km^2 grid cell to construct artificial plots, treating each cell as a single vegetation assemblage. Finally, we selected plots located in regions with climates highly similar to the projected future climate of Flanders, defined by a Euclidean distance ≤ 1. Multiple thresholds were tested to generate a broad set of candidate tree species for the subsequent steps of the analysis. Additionally, we only included plots that included at least one of the key native species

(*Betula pendula*, *Betula pubescens*, *Pinus sylvestris*, *Populus tremula*, *Quercus petraea*, *Quercus robur*, *Tilia cordata* and *Sorbus aucuparia*) associated with habitat type 9190 as another preliminary filter to ensure only relevant plots were retained. In this way, we retained 3178 plots and 86 species under the SSP3-7.0 scenario and 2336 plots and 85 species under the SSP5-8.5 scenario, yielding a set of 90 non-native tree species (Supplementary Table S1).

Step 2: Co-occurrence analysis. We computed Bray-Curtis dissimilarity values between all tree species based on their co-occurrence in the EU-Forest database using the vegan package (Oksanen et al., 2024) under both future climate scenarios. For each species, we then counted the number of native key species falling within dissimilarity thresholds of 0.75, 0.80, 0.85, 0.90, and 0.95. Based on the results for the native key species, we selected 13 species in scenario SSP3-7.0 and 14 in SSP5-8.5. The resulting species lists showed substantial overlap, yielding a final set of 16 distinct non-native tree species (Supplementary Table S1).

Step 3: Climate suitability. We relied on SDM projections from Desie et al. (2024), who modelled future climate suitability for 270 native and non-native tree species in Flanders under three SSP scenarios (SSP1-2.6, SSP3-7.0, and SSP5-8.5). Their models used bioclimatic variables from the CHELSA dataset (Karger et al., 2017) for five global circulation models (GCMs) at 1 km resolution. Climate suitability for Flanders was calculated for both current and future conditions as the median suitability across all 1 km grid cells within the region. The change in median suitability was then used to derive a climate trend, defined as the average change in median suitability for 2071–2100 across the three scenarios, relative to historical conditions (1980–2010), and expressed as a percentage likelihood of occurrence. According to the SDM analysis, all native species except *Quercus robur* and *Populus tremula* exhibited a negative climate trend. These two species showed a neutral trend. Only 13 non-native species with a positive projected trend were retained as suitable species for the next step (Supplementary Table S1).

Step 4: Functional similarity. We assessed functional similarity between key native species and remaining non-native candidate species through a Principal Component Analysis (PCA) on the standardized values of seven plant traits. The selected traits represent key axes of plant form and function: leaf dry matter content, leaf carbon content, leaf C:N ratio, leaf nitrogen content, rooting depth, leaf area, and plant height. Trait data were extracted from the Global Spectrum of Plant Form and Function Database (plant height and leaf area; Díaz et al., 2022) and sPlotOpen (Sabatini et al., 2021). For most native species, potential suitable functional analogues could be found based on the proximity on the PCA plot (Fig. 3c), except for *Sorbus aucuparia* and the two native *Betula* species. *Quercus ilex* and *Q. suber* occupied an intermediate trait space between *P. sylvestris* and *Q. petraea*. Including these, a total of ten non-native species were retained after this step (Supplementary Table S1).

Step 5: Edaphic suitability. We evaluated the edaphic suitability of the ten non-native candidates by performing a PCA on their Ecological Indicator Values for Europe EIVE (EIVE; Dengler et al., 2023) for soil moisture (EIVE-M), soil nitrogen (EIVE-N), and soil reaction (EIVE-R), together with those of the key native species. A visual inspection of the analysis results identified *Quercus cerris, Q. suber, Q. pyrenaica*, and *Pinus pinaster* as potential climate-resilient candidates that share a suitable edaphic niche and could functionally replace *Q. petraea* and *P. sylvestris* (Figs. 3c and 4). *Fraxinus ornus* and *Acer monspessulanum* share similar trait profiles with *Tilia cordata* (Fig. 3c), but their preference for more alkaline soils than those typical of acidophilous oak forests may limit their suitability as replacements. *Robinia pseudoacacia* also emerged as a potential alternative. Despite its clear association with soils high in nitrogen, it was retained because it is a member of the *Fabaceae* family. Five species were retained for the final step (Supplementary Table S1).

Step 6: Final selection. A final screening was conducted to assess the invasiveness potential of candidate species. *Robinia pseudoacacia*, a non-European species known for its invasive behavior, is included on Belgium's watch list for invasive alien species (Branquart et al., 2015) and was therefore excluded. The resulting shortlist includes *Quercus cerris*, *Q. suber*, *Q. pyrenaica*, and *Pinus pinaster* as potential replacements for *Q. petraea* and *P. sylvestris*. No suitable alternatives were identified for the native *Betula* species, *Sorbus aucuparia*, or *Tilia cordata*. However, *Populus tremula*—which shares similarly high litter quality (low leaf C:N ratio)—could take on a more prominent role in future forest assemblages. Given that this selection is based on uncertain climate projections and statistical analyses, the final list of candidate species should be validated through field trials. These trials should ideally include the climate-resilient native species *Q. robur* and *P. tremula* to assess the candidates' potential to contribute to functionally resilient acidophilous oak forests under future environmental conditions.

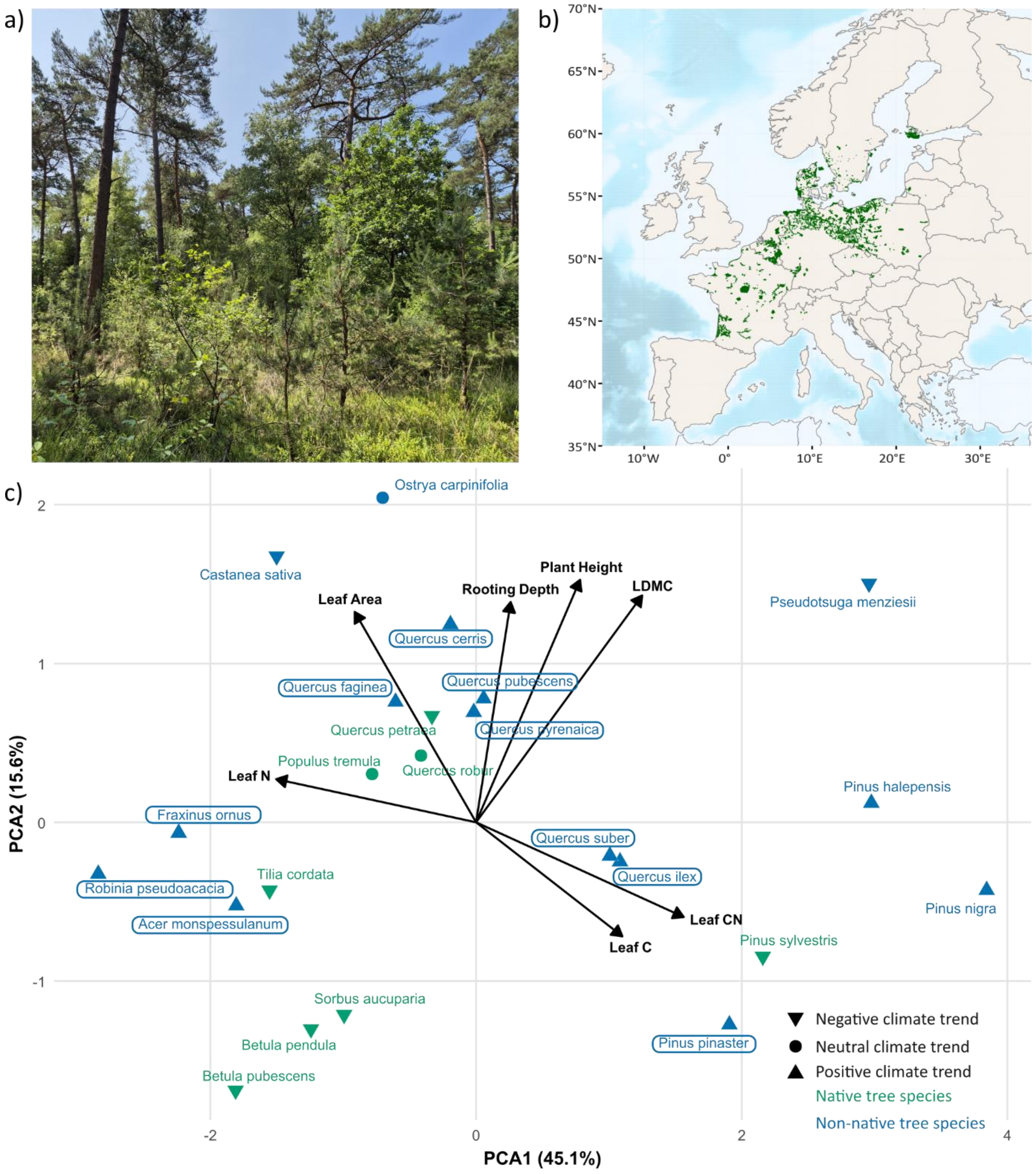

Fig. 3. a) Acidophilous oak woods in Hamont-Achel (Belgium). Picture: xxx; b) Natura 2000 sites with the habitat type 9190 in Europe (EEA, 2022); c) Ordination plot (PCA) with the results of the SDM (step 3) and functional similarity analysis (step 4). The outlined species are retained as input for step 5.

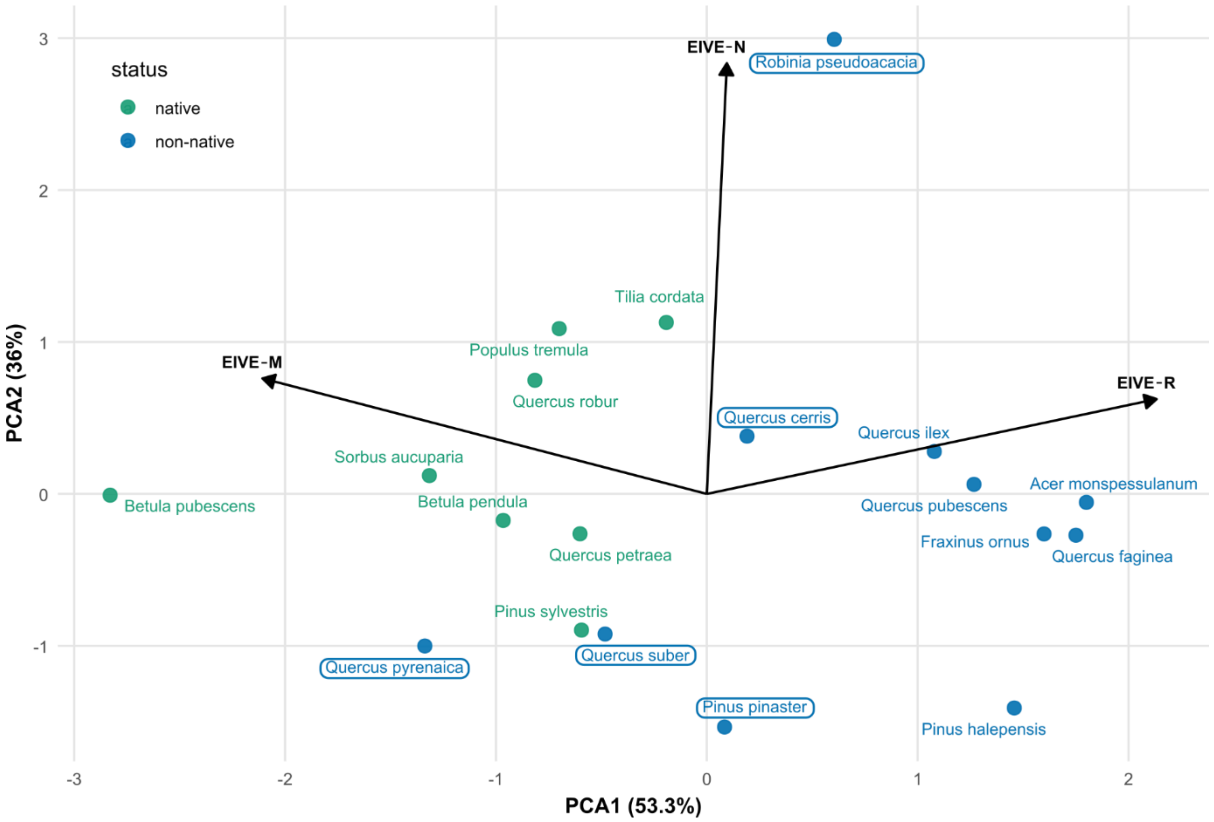

Fig. 4. Results of edaphic suitability analysis (step 5) in the case study. Ordination biplot on the EIVE *(Ecological Indicator Values for Europe)* values for soil moisture (EIVE-M), soil nitrogen (EIVE-N) and soil reaction (EIVE-R) with native and non-native species. The outlined species are retained as input for step 6.

5. Conclusion

Current management strategies are unlikely to suffice in addressing the unprecedented rates of 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 ecosystem functionality by introducing species capable of filling functional gaps created by climate 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 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 under future climate scenarios in the target area. The novel communities are expected to better withstand future challenges, such as increased drought and elevated temperatures, while maintaining ecosystem functionality. However, empirical data are crucial to validate this hypothesis, optimise the implementation and address potential risks. Note that FAM does not aim to replace traditional conservation methods but to complement them. Natural dispersal mechanisms should still be supported by enhancing biotic connectivity and reducing landscape fragmentation to facilitate species' 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 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 the most pressing challenges in conservation science.

References

Arita, H. T. (2016). Species co-occurrence analysis: pairwise versus matrix-level approaches. *Global Ecology and Biogeography*, *25*(11), 1397–1400.

Bardgett, R. D., Bullock, J. M., Lavorel, S., Manning, P., Schaffner, U., Ostle, N., Chomel, M., Durigan, G., L Fry, E., & Johnson, D. (2021). Combatting global grassland degradation. *Nature Reviews Earth & Environment*, *2*(10), 720–735.

Bektaş, B., Thuiller, W., Renaud, J., Guéguen, M., Calderón-Sanou, I., Valay, J. G., Colace, M. P., & Münkemüller, T. (2023). A spatially explicit trait-based approach uncovers changes in assembly processes under warming. *Ecology Letters*, *26*(7), 1119–1131. https://doi.org/10.1111/ELE.14225

Bellis, J., Bourke, D., Maschinski, J., Heineman, K., & Dalrymple, S. (2020). Climate suitability as a predictor of conservation translocation failure. *Conservation Biology*, *34*(6), 1473–1481.

Benomar, L., Elferjani, R., Hamilton, J., O'Neill, G. A., Echchakoui, S., Bergeron, Y., & Lamara, M. (2022). Bibliometric analysis of the structure and evolution of research on assisted migration. *Current Forestry Reports*, *8*(2), 199–213.

Branquart, E., Vanderhoeven, S., Van Landuyt, W., Van Rossum, F., & Verloove Filip. (2015, August 14). *Harmonia database: Robinia pseudoacacia*. Harmonia Version 1.2, Belgian Forum on Invasive Species.

Brian, J. I., & Catford, J. A. (2023). A mechanistic framework of enemy release. *Ecology Letters*, *26*(12), 2147–2166.

Brodie, J. F., Lieberman, S., Moehrenschlager, A., Redford, K. H., Rodríguez, J. P., Schwartz, M., Seddon, P. J., & Watson, J. E. M. (2021). Global policy for assisted colonization of species. *Science*, *372*(6541), 456–458.

Brun, P., Zimmermann, N. E., Hari, C., Pellissier, L., & Karger, D. N. (2022). Global climate-related predictors at kilometer resolution for the past and future. *Earth System Science Data*, *14*(12), 5573–5603.

Bucharova, A. (2017). Assisted migration within species range ignores biotic interactions and lacks evidence. *Restoration Ecology*, *25*(1), 14–18. https://doi.org/10.1111/rec.12457

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. (2021). Importance of species translocations under rapid climate change. *Conservation Biology*, *35*(3), 775–783.

Cadotte, M. W. (2017). Functional traits explain ecosystem function through opposing mechanisms. *Ecology Letters*, *20*(8), 989–996.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., MacE, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. In *Nature* (Vol. 486, Issue 7401, pp. 59–67). Nature Publishing Group. https://doi.org/10.1038/nature11148

Casazza, G., Abeli, T., Bacchetta, G., Dagnino, D., Fenu, G., Gargano, D., Minuto, L., Montagnani, C., Orsenigo, S., & Peruzzi, L. (2021). Combining conservation status and species distribution models for planning assisted colonisation under climate change. *Journal of Ecology*, *109*(6), 2284–2295.

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*(6045), 1024–1026. https://doi.org/10.1126/science.1206432

Chytrý, M., Hennekens, S. M., Jiménez-Alfaro, B., Knollová, I., Dengler, J., Jansen, F., Landucci, F., Schaminée, J. H. J., Aćić, S., & Agrillo, E. (2016). European Vegetation Archive (EVA): an integrated database of European vegetation plots. *Applied Vegetation Science*, *19*(1), 173–180.

Corlett, R. T., & Westcott, D. A. (2013). Will plant movements keep up with climate change? In *Trends in Ecology and Evolution* (Vol. 28, Issue 8, pp. 482–488). https://doi.org/10.1016/j.tree.2013.04.003

Crall, J. D., Switzer, C. M., Oppenheimer, R. L., Versypt, A. N. F., Dey, B., Brown, A., Eyster, M., Guérin, C., Pierce, N. E., & Combes, S. A. (2018). Neonicotinoid exposure disrupts bumblebee nest behavior, social networks, and thermoregulation. *Science*, *362*(6415), 683–686.

Davidson, I., & Simkanin, C. (2008). Skeptical of assisted colonization. *Science*, *322*(5904), 1048–1049.

de Bello, F., Lavorel, S., Hallett, L. M., Valencia, E., Garnier, E., Roscher, C., Conti, L., Galland, T., Goberna, M., & Májeková, M. (2021). Functional trait effects on ecosystem stability: assembling the jigsaw puzzle. *Trends in Ecology & Evolution*, *36*(9), 822–836.

De Frenne, P., Graae, B. J., Rodríguez-Sánchez, F., Kolb, A., Chabrerie, O., Decocq, G., De Kort, H., De Schrijver, A., Diekmann, M., & Eriksson, O. (2013). Latitudinal gradients as natural laboratories to infer species' responses to temperature. *Journal of Ecology*, *101*(3), 784–795.

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D. M., Decocq, G., & De Pauw, K. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, *27*(11), 2279–2297.

Dee, L. E., Cowles, J., Isbell, F., Pau, S., Gaines, S. D., & Reich, P. B. (2019). When do ecosystem services depend on rare species? *Trends in Ecology & Evolution*, *34*(8), 746–758.

Dengler, J., Jansen, F., Chusova, O., Hüllbusch, E., Nobis, M. P., Van Meerbeek, K., Axmanová, I., Bruun, H. H., Chytrý, M., Guarino, R., Karrer, G., Moeys, K., Raus, T., Steinbauer, M. J., Tichý, L., Tyler, T., Batsatsashvili, K., Bita-Nicolae, C., Didukh, Y., … Gillet, F. (2023). Ecological Indicator Values for Europe (EIVE) 1.0. *Vegetation Classification and Survey*, *4*, 7–29. https://doi.org/10.3897/VCS.98324

Desie, E., Muys, B., Casier, M., Fonteyn, W., Van Meerbeek, K., Haesen, S., Van Beek, E., Chevalier, R., Nyssen, B., Thomassen, E., Jense, W., Dassonville, N., Losseau, J., & Badalementi, L. (2024). *Eindrapport Klimaatbomen - Opmaak van een lijst en begeleidend document met aangepaste boomsoorten en herkomsten voor Vlaanderen in functie van klimaatverandering*.

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., & Prentice, I. C. (2022). The global spectrum of plant form and function: enhanced species-level trait dataset. *Scientific Data*, *9*(1), 755.

Díaz, S., & Malhi, Y. (2022). Biodiversity: Concepts, patterns, trends, and perspectives. *Annual Review of Environment and Resources*, *47*(1), 31–63.

Dobrowski, S. Z., Littlefield, C. E., Lyons, D. S., Hollenberg, C., Carroll, C., Parks, S. A., Abatzoglou, J. T., Hegewisch, K., & Gage, J. (2021). Protected-area targets could be undermined by climate change-driven shifts in ecoregions and biomes. *Communications Earth & Environment*, *2*(1), 198.

EC DG Env. (2013). *Interpretation Manual of European Union Habitats, version EUR28*.

EEA. (2022). *Natura 2000 - Spatial data*. https://www.eea.europa.eu/data-and-maps/data/natura-14/natura-2000-spatial-data

Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, *77*(4), 802–813.

Fonteyn, W., Serra-Diaz, J. M., Muys, B., & Van Meerbeek, K. (2024). Incorporating climatic extremes using the GEV distribution improves SDM range edge performance. *Journal of Biogeography*.

Fricke, E. C., Ordonez, A., Rogers, H. S., & Svenning, J.-C. (2022). The effects of defaunation on plants' capacity to track climate change. *Science*, *375*(6577), 210–214.

Gammal, J., Hewitt, J., Gladstone-Gallagher, R., Thrush, S., Douglas, E., Lohrer, A., & Pilditch, C. (2023). Stressors increase the impacts of coastal macrofauna biodiversity loss on ecosystem multifunctionality. *Ecosystems*, *26*(3), 539–552.

Hällfors, M. H., Aikio, S., & Schulman, L. E. (2017). Quantifying the need and potential of assisted migration. In *Biological Conservation* (Vol. 205, pp. 34–41). Elsevier Ltd. https://doi.org/10.1016/j.biocon.2016.11.023

Hällfors, M. H., Vaara, E. M., Hyvärinen, M., Oksanen, M., Schulman, L. E., Siipi, H., & Lehvävirta, S. (2014). Coming to terms with the concept of moving species threatened by climate change–a systematic review of the terminology and definitions. *PloS One*, *9*(7), e102979.

Hijmans, R. J. (2020). terra: Spatial Data Analysis. In *CRAN: Contributed Packages*. https://doi.org/10.32614/CRAN.package.terra

Hylander, K., Greiser, C., Christiansen, D. M., & Koelemeijer, I. A. (2022). Climate adaptation of biodiversity conservation in managed forest landscapes. *Conservation Biology*, *36*(3), e13847.

IPCC. (2023). *Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]*. https://doi.org/10.59327/IPCC/AR6-9789291691647

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth’s land surface areas. *Scientific Data*, *4*(1), 170122. https://doi.org/10.1038/sdata.2017.122

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., & Abedi, M. (2020). TRY plant trait database–enhanced coverage and open access. *Global Change Biology*, *26*(1), 119–188.

Langridge, J., Sordello, R., & Reyjol, Y. (2021). Existing evidence on the outcomes of wildlife translocations in protected areas: a systematic map. *Environmental Evidence*, *10*(1), 1–31.

Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., & Grenouillet, G. (2020). Species better track climate warming in the oceans than on land. *Nature Ecology and Evolution*, *4*(8), 1044–1059. https://doi.org/10.1038/s41559-020-1198-2

Loreau, M., Barbier, M., Filotas, E., Gravel, D., Isbell, F., Miller, S. J., Montoya, J. M., Wang, S., Aussenac, R., & Germain, R. (2021). Biodiversity as insurance: from concept to measurement and application. *Biological Reviews*, *96*(5), 2333–2354.

Lundgren, E. J., Wallach, A. D., Svenning, J., Schlaepfer, M. A., Andersson, A. L. A., & Ramp, D. (2024). Preventing extinction in an age of species migration and planetary change. *Conservation Biology*, e14270.

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

Mammola, S., & Cardoso, P. (2020). Functional diversity metrics using kernel density n-dimensional hypervolumes. *Methods in Ecology and Evolution*, *11*(8), 986–995.

Marvier, M., & Kareiva, P. (2020). *It is time to rebalance the risk equation*. Wiley Online Library.

Mauri, A., Strona, G., & San-Miguel-Ayanz, J. (2017). EU-Forest, a high-resolution tree occurrence dataset for Europe. *Scientific Data*, *4*(1), 160123. https://doi.org/10.1038/sdata.2016.123

McLachlan, J. S., Hellmann, J. J., & Schwartz, M. W. (2007). A framework for debate of assisted migration in an era of climate change. In *Conservation Biology* (Vol. 21, Issue 2, pp. 297–302). https://doi.org/10.1111/j.1523-1739.2007.00676.x

Mendes, S. B., Olesen, J. M., Memmott, J., Costa, J. M., Timóteo, S., Dengucho, A. L., Craveiro, L., & Heleno, R. (2024). Evidence of a European seed dispersal crisis. *Science*, *386*(6718), 206–211. https://doi.org/10.1126/science.ado1464

Moore, J. W., & Schindler, D. E. (2022). Getting ahead of climate change for ecological adaptation and resilience. *Science*, *376*(6600), 1421–1426.

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., & Szoecs, E. (2024). vegan: Community ecology package (2.6-8). *CRAN*.

Paelinckx, D., & Herr, C. (2019). *Analyse van de gerapporteerde drukken en bedreigingen voor de Natura 2000 habitattypen (Adviezen van het Instituut voor Natuur- en Bosonderzoek; Nr. INBO.A.3832)*.

Pagad, S., Bisset, S., Genovesi, P., Groom, Q., Hirsch, T., Jetz, W., Ranipeta, A., Schigel, D., Sica, Y. V, & McGeoch, M. A. (2022). Country compendium of the global register of introduced and invasive species. *Scientific Data*, *9*(1), 391.

Palma, E., Vesk, P. A., White, M., Baumgartner, J. B., & Catford, J. A. (2021). Plant functional traits reflect different dimensions of species invasiveness. *Ecology*, *102*(5), e03317.

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*(2), 289–290.

Park, A., & Talbot, C. (2018). Information underload: ecological complexity, incomplete knowledge, and data deficits create challenges for the assisted migration of forest trees. *BioScience*, *68*(4), 251–263.

Peterson St-Laurent, G., Oakes, L. E., Cross, M., & Hagerman, S. (2021). R–R–T (resistance–resilience–transformation) typology reveals differential conservation approaches across ecosystems and time. *Communications Biology*, *4*(1), 39.

Pörtner, H.-O., Scholes, R. J., Agard, J., Archer, E., Arneth, A., Bai, X., Barnes, D., Burrows, M., Chan, L., & Cheung, W. L. W. (2021). *Scientific outcome of the IPBES-IPCC co-sponsored workshop on biodiversity and climate change*.

Prober, S. M., Doerr, V. A. J., Broadhurst, L. M., Williams, K. J., & Dickson, F. (2019). Shifting the conservation paradigm: a synthesis of options for renovating nature under climate change. In *Ecological Monographs* (Vol. 89, Issue 1). Ecological Society of America. https://doi.org/10.1002/ecm.1333

Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., & Genovesi, P. (2020). Scientists' warning on invasive alien species. *Biological Reviews*, *95*(6), 1511–1534.

R Core Team. (2025). *R: A Language and Environment for Statistical Computing*. https://www.R-project.org/

Ricciardi, A., & Simberloff, D. (2009). Assisted colonization is not a viable conservation strategy. *Trends in Ecology and Evolution*, *24*(5), 248–253. https://doi.org/10.1016/j.tree.2008.12.006

Sabatini, F. M., Lenoir, J., Hattab, T., Arnst, E. A., Chytrý, M., Dengler, J., De Ruffray, P., Hennekens, S. M., Jandt, U., & Jansen, F. (2021). sPlotOpen–An environmentally balanced, open-access, global dataset of vegetation plots. *Global Ecology and Biogeography*, *30*(9), 1740–1764.

Sax, D. F., & Gaines, S. D. (2008). Species invasions and extinction: The future of native biodiversity on islands. *Proceedings of the National Academy of Sciences*, *105*(supplement_1), 11490–11497. https://doi.org/10.1073/pnas.0802290105

Siegel, K. J., Cavanaugh, K. C., & Dee, L. E. (2024). Balancing multiple management objectives as climate change transforms ecosystems. *Trends in Ecology & Evolution*, *39*(4), 381–395.

Stephan, P., Bramon Mora, B., & Alexander, J. M. (2021). Positive species interactions shape species' range limits. *Oikos*, *130*(10), 1611–1625.

Streit, R. P., & Bellwood, D. R. (2023). To harness traits for ecology, let's abandon 'functionality.' *Trends in Ecology & Evolution*, *38*(5), 402–411.

Swenson, N. G. (2019). *Phylogenetic ecology: A history, critique, and remodeling*. University of Chicago Press.

Tomppo, E., Gschwantner, T., Lawrence, M., & McRoberts, R. E. (2010). National Forest Inventories. In E. Tomppo, T. Gschwantner, M. Lawrence, & R. E. McRoberts (Eds.), *National Forest Inventories: Pathways for Common Reporting*. Springer Netherlands. https://doi.org/10.1007/978-90-481-3233-1

Twardek, W. M., Taylor, J. J., Rytwinski, T., Aitken, S. N., MacDonald, A. L., 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.

Urban, M. C. (2020). Climate-tracking species are not invasive. *Nature Climate Change*, *10*(5), 382–384. https://doi.org/10.1038/s41558-020-0770-8

Valavi, R., Guillera-Arroita, G., Lahoz-Monfort, J. J., & Elith, J. (2022). Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. *Ecological Monographs*, *92*(1), e01486.

van der Veen, B., Hui, F. K. C., Hovstad, K. A., Solbu, E. B., & O'Hara, R. B. (2021). Model-based ordination for species with unequal niche widths. *Methods in Ecology and Evolution*, *12*(7), 1288–1300.

Van Meerbeek, K., Jucker, T., & Svenning, J. (2021). Unifying the concepts of stability and resilience in ecology. *Journal of Ecology*.

Wang, S., Loreau, M., De Mazancourt, C., Isbell, F., Beierkuhnlein, C., Connolly, J., Deutschman, D. H., Doležal, J., Eisenhauer, N., & Hector, A. (2021). Biotic homogenization destabilizes ecosystem functioning by decreasing spatial asynchrony. *Ecology*, *102*(6), e03332.

Williams, A. P., Allen, C. D., Macalady, A. K., Griffin, D., Woodhouse, C. A., Meko, D. M., Swetnam, T. W., Rauscher, S. A., Seager, R., & Grissino-Mayer, H. D. (2013). Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, *3*(3), 292.

Xu, W., & Prescott, C. E. (2024). Can assisted migration mitigate climate-change impacts on forests? *Forest Ecology and Management*, *556*, 121738.

Yang, Y., Halbritter, A. H., Klanderud, K., Telford, R. J., Wang, G., & Vandvik, V. (2018). Transplants, open top chambers (OTCs) and gradient studies ask different questions in climate change effects studies. *Frontiers in Plant Science*, *9*, 1574.

Zhao, Z., Hui, C., Peng, S., Yi, S., Li, Z., Reddy, G. V. P., & van Kleunen, M. (2023). The world's 100 worst invasive alien insect species differ in their characteristics from related non-invasive species. *Journal of Applied Ecology*, *60*(9), 1929–1938.