

## RESEARCH ARTICLE

# Diversity for Restoration (D4R): Guiding the selection of tree species and seed sources for climate-resilient restoration of tropical forest landscapes

Tobias Fremout<sup>1,2</sup>  | Evert Thomas<sup>2</sup>  | Hermann Taedoumg<sup>3,4</sup>  | Siebe Briers<sup>1</sup> |  
 Claudia Elena Gutiérrez-Miranda<sup>5</sup> | Carolina Alcázar-Caicedo<sup>6</sup>  | Antonia Lindau<sup>7</sup> |  
 Hubert Mounmemi Kpoumie<sup>8</sup>  | Barbara Vinceti<sup>9</sup>  | Chris Kettle<sup>9,10</sup>  |  
 Marius Ekué<sup>4</sup>  | Rachel Atkinson<sup>2</sup>  | Riina Jalonen<sup>11</sup>  | Hannes Gaisberger<sup>9,12</sup>  |  
 Stephen Elliott<sup>13</sup>  | Esther Brechbühler<sup>10</sup> | Viviana Ceccarelli<sup>2</sup>  | Smitha Krishnan<sup>14</sup>  |  
 Harald Vacik<sup>7</sup>  | Gabriela Wiederkehr-Guerra<sup>9</sup>  | Beatriz Salgado-Negret<sup>15</sup>  |  
 Mailyn Adriana González<sup>6</sup> | Wilson Ramírez<sup>6</sup> | Luis Gonzalo Moscoso-Higuaita<sup>16</sup> |  
 Álvaro Vásquez<sup>17</sup> | Jessica Cerrón<sup>2</sup> | Colin Maycock<sup>18</sup>  | Bart Muys<sup>1</sup> 

<sup>1</sup>Division of Forest, Nature and Landscape, KU Leuven, Leuven, Belgium; <sup>2</sup>Alliance Bioversity International—CIAT, Lima, Peru; <sup>3</sup>Department of Plant Biology, Faculty of Science, University of Yaoundé, Yaoundé, Cameroon; <sup>4</sup>Alliance Bioversity International—CIAT, Yaoundé, Cameroon; <sup>5</sup>Facultad de Ciencias Forestales, Universidad Nacional Agraria La Molina, Lima, Peru; <sup>6</sup>Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia; <sup>7</sup>University of Natural Resources and Life Sciences (BOKU), Vienna, Austria; <sup>8</sup>University of Yaoundé, Yaoundé, Cameroon; <sup>9</sup>Alliance Bioversity International—CIAT, Maccaresse, Italy; <sup>10</sup>Department of Environmental System Science, ETH Zurich, Zurich, Switzerland; <sup>11</sup>Alliance Bioversity International—CIAT, Serdang, Malaysia; <sup>12</sup>Department of Geoinformatics, Paris Lodron University of Salzburg, Salzburg, Austria; <sup>13</sup>Environmental Science Research Centre and Forest Restoration Research Unit, Biology Department, Science Faculty, Chiang Mai University, Chiang Mai, Thailand; <sup>14</sup>Alliance Bioversity International—CIAT, Bengaluru, India; <sup>15</sup>Departamento de Biología, Facultad de Ciencias, Universidad Nacional de Colombia, Bogotá, Colombia; <sup>16</sup>Forestpa SAS, Medellín, Colombia; <sup>17</sup>Facultad de Ciencias Agrarias, Universidad Nacional de Colombia, Medellín, Colombia and <sup>18</sup>Faculty of Science and Natural Resources, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia

**Correspondence**

Tobias Fremout

Email: tobias.fremout@gmail.com

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**Abstract**

1. At the start of the UN Decade of Ecosystem Restoration (2021–2030), the restoration of degraded ecosystems is more than ever a global priority. Tree planting will make up a large share of the ambitious restoration commitments made by countries around the world, but careful planning is needed to select species and seed sources that are suitably adapted to present and future restoration site conditions and that meet the restoration objectives.
2. Here we present a scalable and freely available online tool, Diversity for Restoration (D4R), to identify suitable tree species and seed sources for climate-resilient tropical forest landscape restoration.
3. The D4R tool integrates (a) species habitat suitability maps under current and future climatic conditions; (b) analysis of functional trait data, local ecological

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knowledge and other species characteristics to score how well species match the restoration site conditions and restoration objectives; (c) optimization of species combinations and abundances considering functional trait diversity or phylogenetic diversity, to foster complementarity between species and to ensure ecosystem multifunctionality and stability; and (d) development of seed zone maps to guide sourcing of planting material adapted to present and predicted future environmental conditions. We outline the various elements behind the tool and discuss how it fits within the broader restoration planning process, including a review of other existing tools.

4. *Synthesis and applications.* The Diversity for Restoration tool enables non-expert users to combine species traits, environmental data and climate change models to select tree species and seed sources that best match restoration site conditions and restoration objectives. Originally developed for the tropical dry forests of Colombia, the tool has now been expanded to the tropical dry forests of northwestern Peru–southern Ecuador and the countries of Burkina Faso and Cameroon, and further expansion is underway. Acknowledging that restoration has a wide range of meanings and goals, our tool is intended to support decision making of anyone interested in tree planting and seed sourcing in tropical forest landscapes, regardless of the purpose or restoration approach.

#### KEYWORDS

climate change, forest landscape restoration, functional and phylogenetic diversity, functional traits, habitat suitability models, seed sourcing, seed zones, species selection

## 1 | INTRODUCTION

In times of unprecedented human pressure on the Earth's planetary boundaries, ecosystem restoration is seen as a fundamental strategy to overcoming global environmental and socio-economic challenges (Aronson & Alexander, 2013; Suding et al., 2015). More recently, an increased emphasis on the interconnectedness of ecosystem health and human health, underlined brutally by the COVID-19 pandemic, is adding yet another impetus to restoration (Breed et al., 2020; Keesing & Ostfeld, 2021). Many ambitious restoration pledges have been made, such as Initiative 20 × 20 in Latin-America and AFR100 in Africa, both contributing to the Bonn Challenge which aims at initiating the restoration of 350 million hectares of degraded lands by 2030. Initiatives like the UN Decade of Ecosystem Restoration (2021–2030) and The One Trillion Tree initiative of the World Economic Forum build further on these global commitments (FAO, 2020). However, turning political commitments into successfully restored landscapes will require careful planning (Brancalion et al., 2020; Holl & Brancalion, 2020).

A considerable part of global restoration commitments will be achieved through tree planting (Brancalion et al., 2020). An important aspect of planning restoration efforts involving tree planting (or direct seeding, we refer to both as 'tree planting') is the selection of tree species and seed sources that match both restoration objectives and local site requirements (Atkinson et al., 2021;

Thomas et al., 2017). Given that trees are long-lived and play a central role in the functioning of forest landscapes, this selection has important long-lasting ecological and economic consequences. Species selection needs to be tailored to project-specific restoration objectives while maximizing persistence under current and future conditions at the restoration site, also considering local stress factors such as eroded soils or the risk of fire (Brancalion et al., 2020; Reubens et al., 2011; Thomas et al., 2017). In addition, unless every generation is to be planted anew as in some commercial plantations, the planting material of any given species should be genetically diverse enough to form viable, productive populations capable of regenerating and adapting to climate change (Lowe et al., 2011; Thomas et al., 2014). Hence, the selection of the most appropriate tree species and seed sources requires integration of different knowledge domains and techniques, such as habitat suitability modelling, functional trait analysis, traditional and expert knowledge and assessments of adaptive genetic variation (e.g. through provenance trials or genetic marker studies). As it is often difficult for restoration practitioners to integrate such knowledge in their decision making, especially in the tropics where local species richness is high and resources are limited, the knowledge-practice gap remains an important constraint to the implementation of diverse and climate-resilient restoration plantings (Jalonen et al., 2018; Reubens et al., 2011). Consequently, species selection and seed sourcing decisions are commonly driven

by availability of planting material, often resulting in the selection of a few well-known, often exotic tree species, rather than those species that best match the restoration site conditions and objectives, whereby climate change is typically not taken into account (Atkinson et al., 2021; Jalonen et al., 2018; Valette et al., 2020). This situation constrains the wider use of native tree species diversity in restoration, which would enhance biodiversity and climate change mitigation benefits from restoration efforts. Several decision support tools have been developed to guide tree species selection (e.g. Reubens et al., 2011; Van Der Wolf et al., 2017) and seed sourcing (e.g. Rossetto et al., 2019; Shryock et al., 2018) or both (plantevalg.dk), but no tools currently exist that combine both while also taking into account climate change.

Here we present a scalable online decision support tool: 'Diversity for Restoration' (D4R; [www.diversityforrestoration.org](http://www.diversityforrestoration.org)) that enables restoration practitioners to make case-specific decisions on the most appropriate tree species and seed sources. Depending on user-defined inputs including restoration site location, local site conditions (e.g. steep slopes, compacted soils), restoration objectives (e.g. bird conservation, timber production) and climate change scenarios, the tool recommends tree species combinations and seed sourcing areas best aligned with these inputs. Recommended species combinations are accompanied by species-specific propagation information and basic monitoring suggestions (e.g. which variables to measure and how frequent, depending on the restoration objectives). As forest landscape restoration is interpreted variously by different stakeholders and scientists (Mansourian, 2018), our tool supports decision making of anyone interested in tree planting in tropical forest landscapes for any purpose regardless of the restoration approach. Use of the word 'restoration' in the following should be interpreted as such. The tool can be readily used by non-expert users, as long as they have some understanding about the restoration site conditions and restoration objectives. Typical users may include restoration project managers, NGOs, local governments, cooperatives or other institutions carrying out tree planting initiatives, scientists supporting restoration planning, among others.

Starting from a prototype version developed for the tropical dry forests (TDFs) of Colombia (Thomas et al., 2017), the tool has now been improved and expanded to the TDFs of northwestern Peru and southern Ecuador and the countries of Burkina Faso and Cameroon, and further scaling to other regions is underway. Figure 1 summarizes the tool mechanics, integrating four main elements: (a) habitat suitability modelling to assess the suitability of species to be grown at the restoration site under current and future climatic conditions; (b) analysis of functional trait data, local ecological knowledge and other relevant species characteristics to score how well species match the restoration site conditions and restoration objectives; (c) optimization of functional diversity or phylogenetic diversity to foster complementarity between species; and (d) development of seed zone maps to guide the sourcing of planting material adapted to present and expected future environmental conditions. In the following, we present the various elements behind the tool, illustrate how the tool fits within the broader restoration planning process,

including a review of currently available tools, and conclude with some practical considerations and the way forward.

## 2 | METHODS INTEGRATED IN THE DECISION SUPPORT TOOL

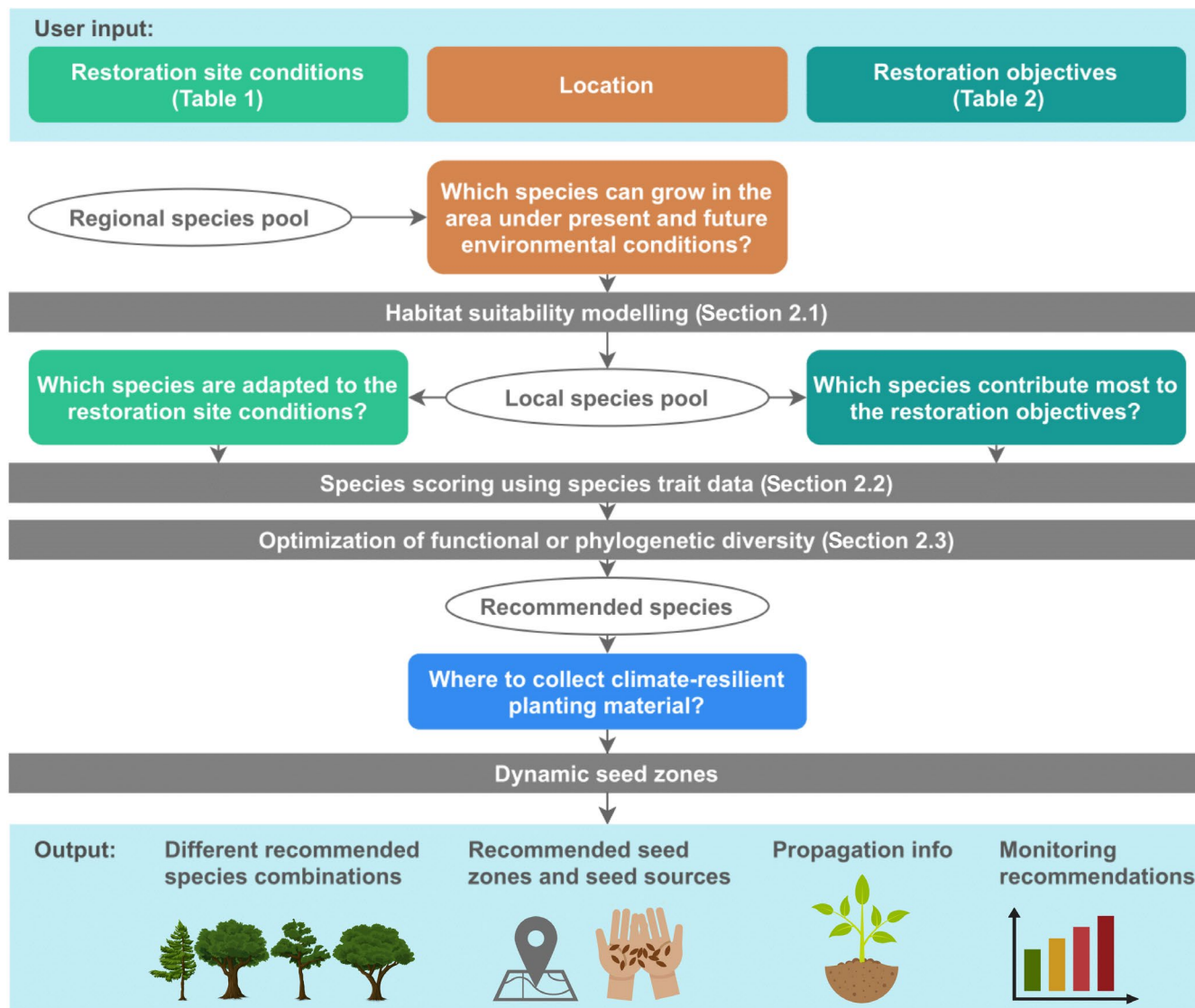
### 2.1 | Habitat suitability modelling

The tool starts from a regional species pool (with the number of species currently varying between 74 for Burkina Faso and 224 for Cameroon), consisting of mainly native species but also including a limited number of socio-economically important exotic species. To filter out those species not suited to the present or predicted future environmental conditions at a restoration site, the tool uses habitat suitability models, also called species distribution models. These models correlate species presence locations with the environmental conditions at these locations to estimate the spatial distribution of suitable habitat of species. While such correlative habitat suitability models have certain limitations, many of them can be overcome by applying appropriate modelling techniques and interpretation (Araújo & Peterson, 2012). The alternative—use of mechanistic models based on species physiology—to estimate the impact of climate change on species distributions, is impractical when dealing with tropical forests, which typically have very high species richness. Modelling was carried out using an ensemble approach, that is, combining the predictions of different algorithms, implemented in the 'BIODIVERSITYR' package for R (Kindt, 2018), which were combined in single consensus distribution maps for each of the species. Inputs and outputs of the modelling are illustrated in Figure 2, further methodological details are given in Fremout et al. (2020).

Calibrated habitat suitability models were projected to future climatic conditions for the 2050s and 2070s, as predicted by different general circulation models (GCMs, also called global climate models) under the representative concentration pathways RCP4.5 and RCP8.5, the latter being the worst-case scenario and the former a more optimistic scenario. The time horizon and RCP considered by the tool are determined by the user. Selected GCMs differ between regions, ranging from the AfriClim ensemble (Platts et al., 2014) for Burkina Faso to six GCMs in Cameroon.

### 2.2 | Species scoring using species trait data

After indicating the location of a restoration plot on a map, users of the tool are asked to indicate the prevalent local site conditions (Table 1), consisting mostly of anthropogenic and water- and soil-related stress conditions, and to select the priority restoration objectives (Table 2), the latter of which are grouped in four categories: (a) biodiversity conservation, (b) regulating ecosystem services, (c) agroforestry and commercial uses and (d) traditional uses (Table 2). Users have the option to weigh different restoration objective categories.

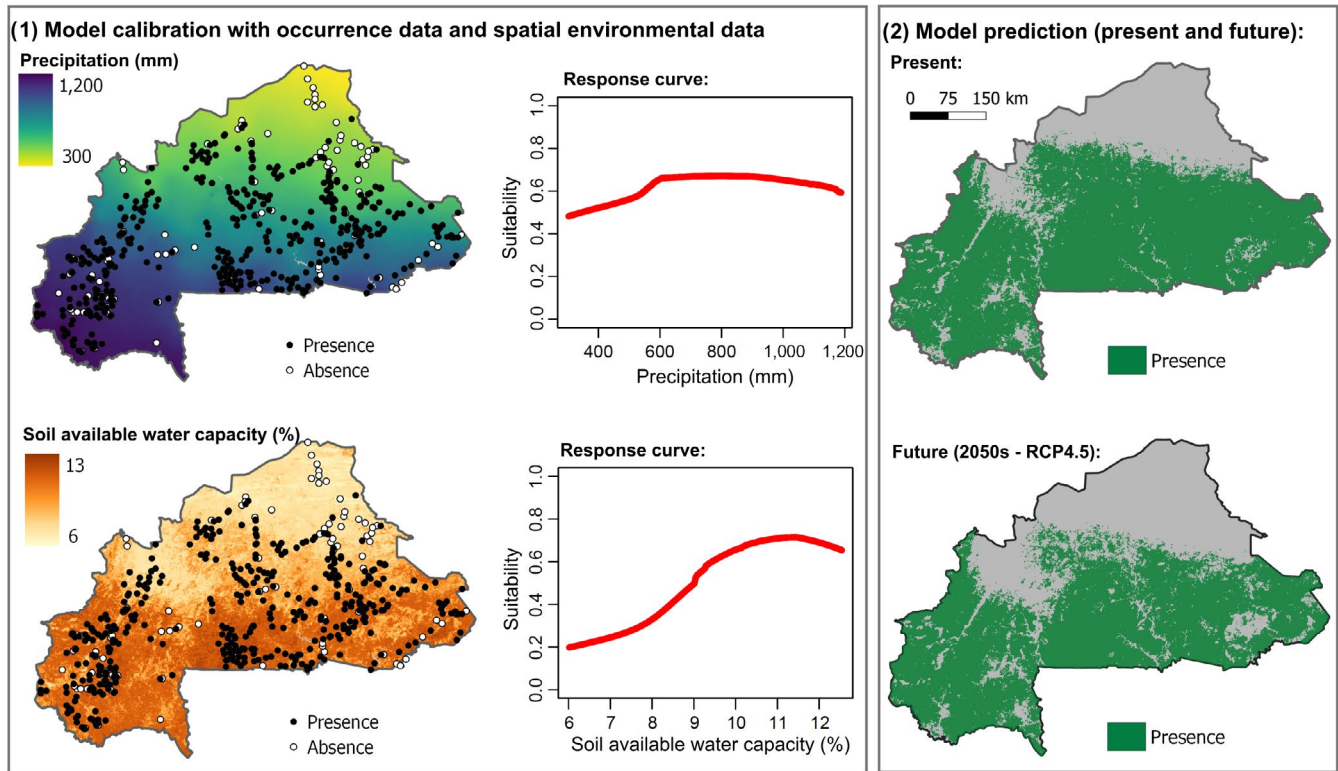


**FIGURE 1** Schematic overview of the different components of the Diversity for Restoration tool. Tables 1 and 2 and Sections 2.1–2.4 refer to the corresponding tables and sections of the present paper

To score how well candidate species match restoration site conditions and restoration objectives, the tool uses various species characteristics data, including functional traits, local ecological knowledge and expert knowledge, among others, to which we will refer as 'traits' for simplicity. They include mostly functional traits in the classical sense, that is, morpho-physiological-phenological characteristics that indirectly affect the fitness of individuals (Violle et al., 2007), but also include (a) local uses (e.g. firewood), (b) conservation priorities (e.g. IUCN Red List status) and (c) information about species' adaptation to site conditions or ability to contribute to restoration objectives without mention of specific functional traits (e.g. 'recommended for riverine protection'). Traits include both categorical (e.g. pollination mode) and continuous variables (e.g. wood density), but given the considerable intraspecific variation for most of these continuous traits, the latter were also converted into categorical variables (e.g. wood densities lower than  $0.4 \text{ g/cm}^3$  were classified as 'low', those

between 0.4 and 0.6 as 'intermediate', and those higher than 0.6 as 'high').

To estimate how well species match the site conditions and restoration objectives in a quantitative way, the tool scores species using a trait-based scoring approach (Figure 3). Based on literature review and expert judgement, we assigned weights to traits according to the expected magnitude of their influence on species' adaptation to site conditions or contribution to restoration objectives, ranging from 1 to 5. For example, the trait 'fodder and forage' was given a higher weight than 'rooting depth' for the restoration objective 'silvopastoral systems' (Figure 3). In addition, we assigned each trait level with an aptness score, ranging from 0 to 1, with 0.5 corresponding to a 'neutral' score. For example, evergreen species were given a score of 1 for the objective 'silvopastoral systems', because they provide shade (and possibly fodder) year-round, while semi-deciduous and deciduous species were given scores of 0.5 and 0 respectively. To avoid overestimating species aptness in the case



**FIGURE 2** Illustration of habitat suitability modelling for *Vitellaria paradoxa* (shea tree) in Burkina Faso. Annual precipitation and soil available water capacity are shown here as examples of predictor variables, but note that the models consider a wide range of climate and soil variables. Only presence and absence locations within Burkina Faso are shown, but note that both were selected from a wider geographic extent

of missing data, these were given a score of 0. While specific traits can be linked to multiple site conditions and/or restoration objectives, the weights assigned to the traits and the scores assigned to the trait levels are specific to particular site conditions or restoration objectives. For each of the site conditions and restoration objectives selected by the user, the tool calculates species aptness scores as the weighted average of the trait-specific scores described above. The overall match of species to the combination of site conditions and restoration objectives selected by the user is estimated by averaging the corresponding aptness scores, giving equal weights to the scores linked to the selected restoration site conditions and restoration objectives respectively.

We included around 85 traits in the scoring (exact number depending on the location) and established the relationships between these traits and species' contributions to restoration objectives and ability to persist under given site conditions through literature review and expert judgement (Tables S1.1 and S1.2, Supporting Information 1). Trait data were sourced from a variety of sources, including scientific articles, books and databases such as TRY (Kattge et al., 2020) and the Agroforestry database (Orwa et al., 2009). In the TDFs of northwestern Peru and southern Ecuador, this was complemented by local ecological knowledge on species' uses, conservation status and resistance to stress conditions sourced through interviews in local communities, which prove to be a more than valuable complement to scientific knowledge (Fremout, Gutiérrez-Miranda, et al., 2021).

### 2.3 | Optimization of functional or phylogenetic diversity

After filtering the regional species pool using habitat suitability models (Section 2.1) and scoring the retained species using the trait-based scoring approach (Section 2.2), the tool calculates the recommended relative species abundances (i.e. relative planting densities) by jointly optimizing species aptness scores and functional or phylogenetic diversity. The use of diverse species assemblages has several advantages. First, it has the potential to improve specific ecosystem functions through complementarity effects, that is, niche differentiation and facilitation, and selection effects, that is, high-performing species are more likely to occur in and dominate more diverse communities (Loreau & Hector, 2001). As a single species is unlikely to have high levels of all ecosystem functions, diverse species assemblages are essential to ensure ecosystem multifunctionality (van der Plas et al., 2016). Furthermore, when species fulfilling similar functions respond differently to environmental disturbances, the decline in function of one species may be compensated for by another species (Mori et al., 2013). In this way, diverse species assemblages can contribute to the recovery of more stable ecosystem functions. In addition, more functionally diverse communities are less likely to leave ecological niches unfilled, thus reducing opportunities for invasive species to establish. Both functional and phylogenetic diversity are good predictors of biodiversity—ecosystem function

Type of site condition	Site condition
Water related	Extreme drought Flooding risk Next to a perennial river or waterbody Irrigated or next to irrigated farmland
Soil related	Compacted soils Shallow or rocky soils Saline soils Sandy soils Heavy clay soils Ferralitic soils Eroded soils Degraded soils due to mining or pollution
Others	Fire Fragmentation Grazing pressure Steep slopes

**TABLE 1** Site conditions included in the tool. There is no minimum or maximum number of conditions that needs to be selected; users can skip this question if none of the listed conditions are prevalent. These conditions are based on the most important stress conditions in the regions where the tool is currently functional, but additional conditions can and will likely be included in other regions

relationships (e.g. Cadotte et al., 2009; Flynn et al., 2011), ecosystem multifunctionality (e.g. Gross et al., 2017; Huang et al., 2019), ecosystem stability (e.g. Cadotte et al., 2012; Hallett et al., 2017) and invasion resistance of the ecosystem being restored (e.g. Funk et al., 2008; Qin et al., 2020). The choice between optimizing functional or phylogenetic diversity is not trivial. Therefore, we opted to optimize functional diversity by default, while also giving expert users the option to maximize phylogenetic diversity as one of the biodiversity-related objectives.

The tool optimizes functional or phylogenetic diversity by choosing relative species abundances (the maximum number of species being user-defined) by maximizing functional or phylogenetic distance while making sure the average aptness score of the species assemblage converges on a specific value (Appendix S2.2), using the 'SELECT' package for R (Laughlin et al., 2018). Functional distance between species is calculated with the 'FD' package (Laliberté et al., 2014) as the Gower distance between a set of traits readily available for most species (leaf phenology, maximum height, rooting depth, seed mass, specific leaf area, wood density). Phylogenetic distance is calculated with the 'APE' package (Paradis & Schliep, 2018), using phylogenetic trees constructed with the 'V.PHYLOMAKER' package (Jin & Qian, 2019). Recognizing that there are no silver bullet solutions to species selection, the tool generates three different options of recommended species combinations, the first one striking a balance between species aptness scores and functional or phylogenetic diversity, and the two other options putting more focus on diversity and species aptness respectively. Methodological details are provided in Appendix S2.2.

## 2.4 | Seed zone maps

Tree planting requires consideration of the provenance(s) of the planting material. A common recommendation is to source locally, to ensure adaptation to local environmental conditions and to avoid disruption of population genetic patterns (McKay et al., 2005;

Vander Mijnsbrugge et al., 2010). However, the scale of local adaptation in trees is likely much broader (Boshier et al., 2015) than prevailing seed sourcing practices, which tend to involve seed collection at very close distances to the planting site (Jalonen et al., 2018). Furthermore, remaining local seed sources are often fragmented, reducing their genetic diversity (Vranckx et al., 2012) and increasing the risks of inbreeding and concomitantly poor growth and mortality of seedlings (Broadhurst et al., 2006). In the light of ongoing and accelerating climate change, it may also be prudent to supplement local provenances with 'climate-matched' provenances, that is, where current climatic conditions are similar to those anticipated in the future at the planting site, also called 'predictive provenancing' (e.g. Crowe & Parker, 2008; Gray & Hamann, 2011).

Seed zones, also called seed transfer zones or seed provenance zones, are a useful tool to guide seed sourcing decisions. They are geographic areas in which planting material can be moved freely while minimizing the risk of reducing population fitness and disrupting population genetic patterns (Miller et al., 2011). To facilitate climate-resilient seed sourcing, the D4R tool uses dynamic seed zones (Kramer & Havens, 2009; Vitt et al., 2010), whose boundaries can change under climate change. Since genetic distance between trees within and across populations is explained by geographic distance, environmental distance or both (Fremout, Thomas, Bocanegra-González, et al., 2021; Jiang et al., 2019; Sexton et al., 2014), environmentally homogeneous seed zones were constructed, while also avoiding large geographic distances between locations within the same seed zone, by clustering climate and soil variables along with longitude and latitude. The optimal number of seed zones is ideally determined by the results of provenance trials (e.g. Crow et al., 2018; Kramer et al., 2015). In the absence of these, population genetic data (e.g. Durka et al., 2017; Fremout, Thomas, Taedoung, et al., 2021) or expert knowledge can be used, as we did for the TDFs of Colombia and the other regions where the tool is functional respectively. To facilitate pragmatic implementation of these seed zones, considering that the logistic capacity of restoration practitioners in tropical countries is often limited, we constructed a

**TABLE 2** Restoration objectives included in the tool. These objectives are based on the most common restoration objectives and local uses in the regions where the tool is currently functional, but additional restoration objectives can and will likely be included in other regions

Type of restoration objective	Objective
Biodiversity conservation	Bats Birds Endemic woody species Nurse plants Pollinating insects and ants Spectacled bear** Terrestrial mammals Threatened woody species White-tailed deer* White-winged guan**
Regulating ecosystem services	Carbon sequestration Erosion control Riverine protection: ephemeral streams Riverine protection: perennial streams Soil fertility improvement
Agroforestry and commercial uses	Alley cropping Biodiesel Charcoal Commercial timber Fibre for paper production Live fences and hedgerows Non-wood products with economic potential Shade tree agroforestry Silvopastoral systems and forage production Windbreaks
Traditional uses	Cosmetics Cultural uses Dye Fibre Firewood Food Handicrafts Honey Medicinal plants Ornamental species Poison and insect repellent Timber for local use Tools

\*Only included in Peru–Ecuador and Colombia.; \*\*Only included in Peru–Ecuador.

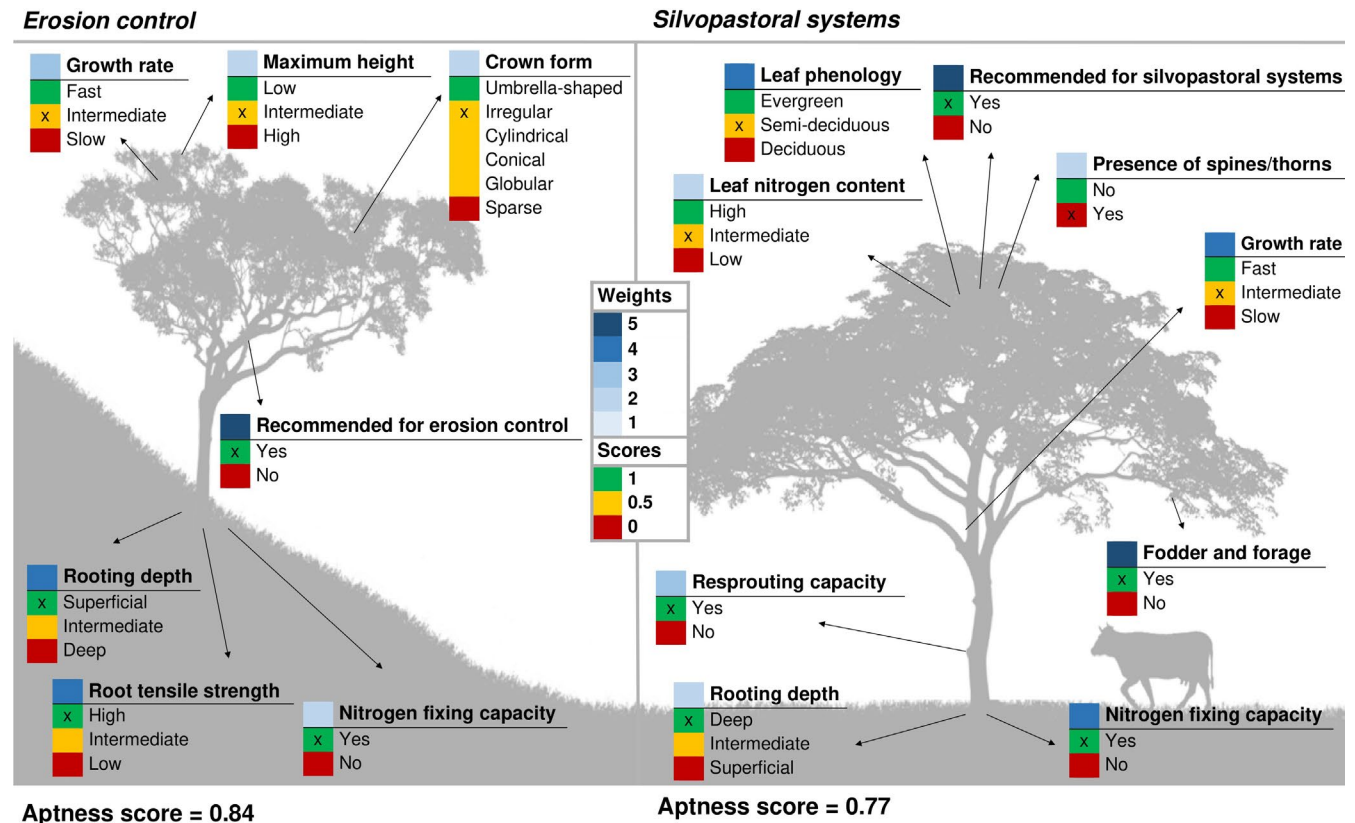
single set of seed zones for each target country or ecosystem, applicable across the tree species considered. Analogous to the habitat suitability maps, we projected the seed zone maps to future climatic conditions for each of the selected GCMs (see Section 2.1) under emission scenarios RCP4.5 and RCP8.5 for the 2050s and 2070s, as illustrated in Figure 4. Further methodological details can be found in Fremout, Thomas, Taedoumg, et al. (2021).

Using the seed zones outlined above, the tool recommends mixing planting material from the seed zone in which the planting site is currently located (i.e. local provenancing) with material from areas currently located in the seed zone anticipated at the planting site under future climatic conditions (i.e. predictive provenancing). While GCMs usually coincide in predicting temperature increases under climate change, the direction of predicted precipitation changes is not always consistent. As a result, GCMs do not always coincide with each other in future seed zone projections, in which case the tool

recommends sourcing part of the planting material in each of the future seed zones as predicted by different GCMs. This approach coincides with the risk-minimizing ‘portfolio approach’ of seed sourcing proposed by Crowe and Parker (2008), directly incorporating the uncertainty of future climate predictions (Figure 5).

### 3 | THE ROLE OF THE TOOL IN RESTORATION PLANNING AND DECISION MAKING

Past forest restoration initiatives have often failed due to various reasons, such as species-site mismatches, inappropriate silvicultural techniques, planting material with a low inter- and intraspecific diversity, lack of post-planting maintenance and monitoring, lack of benefits for local communities, land tenure security issues,



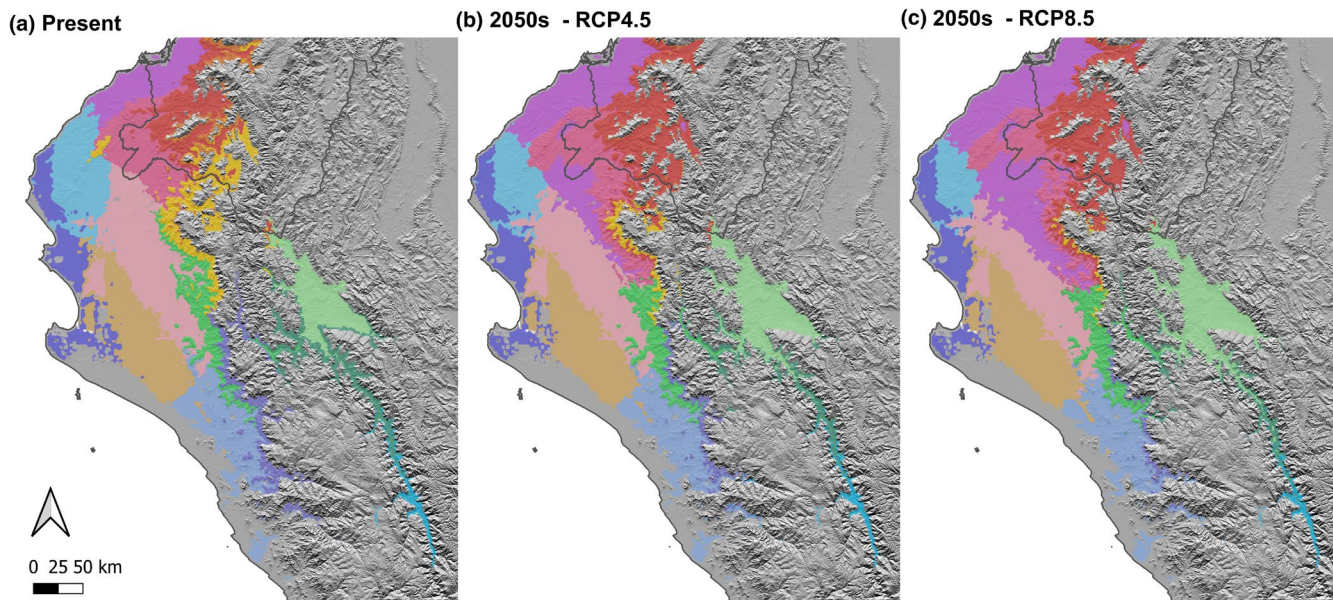
**FIGURE 3** Illustration of the trait-based species matching to the restoration objectives 'erosion control' (left) and 'silvopastoral systems' (right). Trait weights are indicated by shades of blue and aptness scores by green–yellow–red (see legend in the middle), with scores of 0.5 corresponding to a 'neutral' score. A hypothetical species aptness score is given for both restoration objectives, calculated using the trait levels indicated with an 'x'. The calculation is further detailed in Appendix S2.1 (Supporting Information 2)

among others (Godefroid et al., 2011; Höhl et al., 2020; Kodikara et al., 2017; Le et al., 2014). While these experiences provide learning opportunities to improve restoration practices, failing restoration initiatives are likely to diminish the interest and support of local communities, governments, donors and other stakeholders (Höhl et al., 2020), and time is running short to mitigate the ongoing biodiversity and climate crisis. Carefully planning restoration efforts is therefore crucial, and potential problems should be avoided as much as possible (Brancaion et al., 2020; Thomas et al., 2017). The D4R tool does not tackle all these problems, but supports planning species and seed choices in restoration initiatives once restoration sites have been identified, objectives have been agreed upon, and active planting is among the planned interventions. As such, it complements a wide array of existing tools to support decision making in different stages of the restoration process, recently reviewed by Chazdon and Guariguata (2018). Table 3 provides an updated overview of available tools, focusing on those that are scalable and ready-to-use. The D4R tool is unique in that it is—to the best of our knowledge—the only spatially explicit tool that provides recommendations on both the selection of tree species and seed sources while also taking into account climate change. Adding to this comprehensiveness, the tool

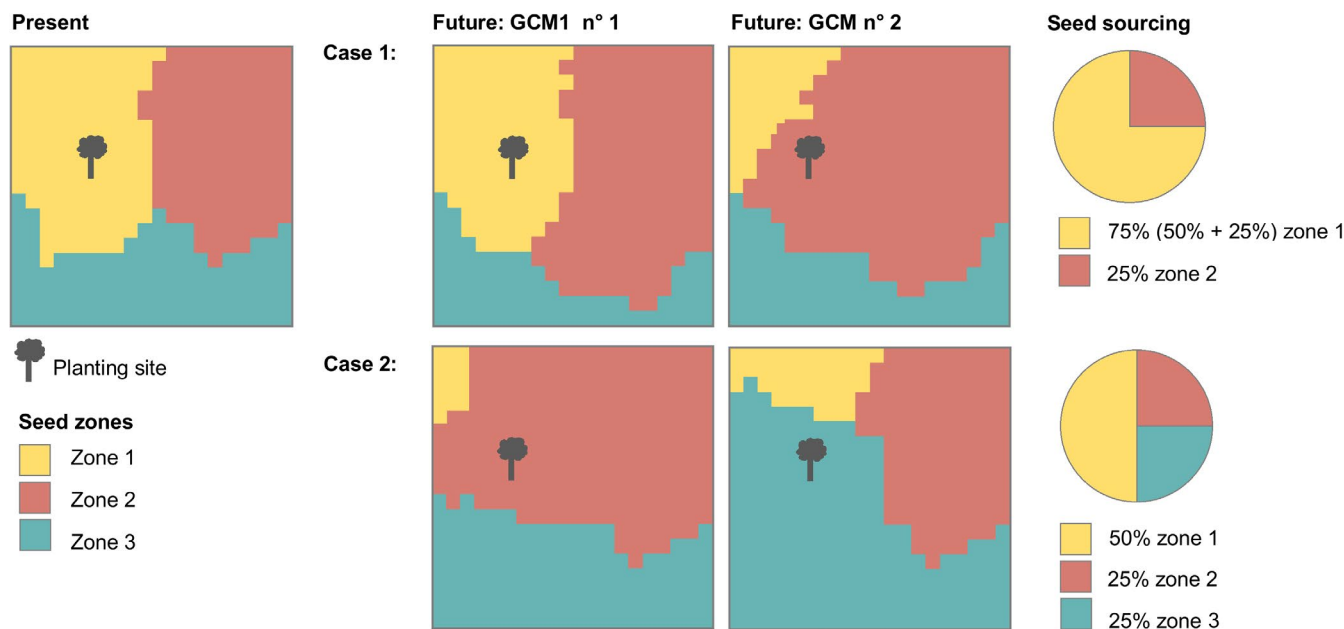
is also the only tool that includes such a wide range of local site conditions and restoration objectives.

As illustrated in Table 3, while the D4R tool supports decisions across multiple aspects of the restoration process, several other building blocks are crucial for successful restoration. For example, many countries still have a long way to go to deliver the enormous quantities of site-adapted and genetically diverse seeds that will be needed to meet ambitious restoration targets (Atkinson et al., 2021; Jalonen et al., 2018). Without existing tree seed networks that can deliver such seeds for a diversity of native species, the use of the D4R tool, and diverse and climate-resilient restoration in general, becomes more challenging (Wiederkehr-Guerra & Gotor, 2020), as restoration projects then have to set up such networks themselves. Another important bottleneck for successful long-term restoration consists of the mismatch between limited and short-term funding available and the long-term funding needed for maintaining trees, monitoring and adaptive management (Höhl et al., 2020; Holl & Brancaion, 2020). Importantly, the necessary building blocks are not limited to those listed in Table 3, but also include an enabling environment with financial sustainability, protection of land rights and tenure, etc. (Perring et al., 2018).





**FIGURE 4** Seed zones ( $n = 15$ ) for the tropical dry forests of northwestern Peru-southern Ecuador under present climatic conditions (panel a) and future climatic conditions for the 2050s under the representative concentration pathways RCP4.5 and RCP8.5 (panels b and c). The seed zones are based on the clustering of climate and soil variables (Fremout, Thomas, Bocanegra-González, et al., 2021). Note that it is possible that specific seed zones disappear under climate change, as is almost the case for the yellow seed zone along the Andean foothills under the RCP8.5 scenario. The future seed zones shown here are those predicted by the *HadGEM2-ES* model, one of the five selected general circulation models (GCMs), but note that the tool combines the predictions of five GCMs





**FIGURE 5** Illustration of the climate-resilient seed sourcing strategy proposed in the tool. The squares represent maps with seed zones indicated in different colours, with case 1 and case 2 depicting two different hypothetical climate change scenarios as predicted by two general circulation models (GCMs), and the pie charts indicating the relative proportion of seeds to be sourced from the different seed zones. The recommended approach involves sourcing 50% of the seeds from the present seed zone, and 50% from the future seed zone(s), the latter of which consist of seed zones 1 and 2 for case 1, and of seed zones 2 and 3 for case 2. This is illustrated here with two GCMs for simplicity, but note that more GCMs were used in the tool

**TABLE 3** Selected tools and methods to guide decision making in different (chronological) phases of the forest restoration process. For each of the tools/methods, we indicate between brackets the scale (predominantly national/subnational level or local level) and whether it is spatially explicit or not. Tools specifically focused on engaging stakeholders and seeking financing for restoration initiatives are not included (please refer to Chazdon and Guariguata (2018) for this), nor are platforms bundling information of specific restoration projects

Type of tool according to phases across the forest restoration process	Tool/methodology with short description
<p>Tools for identifying readiness and bottlenecks for restoration</p> 	<ul style="list-style-type: none"> <li>• Restoration Diagnostic (WRI, 2015): a methodology for developing strategies for successful restoration, based on an evaluation of success factors and identification of policies, incentives or practices to address the missing factors (<i>national or subnational level; not spatially explicit</i>)</li> <li>• Restoration Opportunities Assessment Methodology—ROAM (IUCN &amp; WRI, 2014): a holistic set of methods including methods to evaluate readiness for restoration, identify priority areas and restoration intervention types, quantify costs and benefits and analyse finance and investment options (<i>national or subnational level; spatially explicit</i>)</li> <li>• Atkinson et al. (2021): a five-component indicator system to evaluate national seed supply systems, evaluating readiness and bottlenecks for the supply of large quantities of diverse, locally adapted seeds for climate-resilient restoration (<i>national level; not spatially explicit</i>)</li> </ul>
<p>Tools for spatial prioritization of areas to restore</p> 	<ul style="list-style-type: none"> <li>• Restoration Opportunities Assessment Methodology (ROAM; IUCN &amp; WRI, 2014): see above</li> <li>• Restoration Opportunities Optimization Tool (ROOT; Beatty et al., 2018): a software-based tool that uses information about potential restoration impacts together with spatial prioritization maps to identify priority areas for ecosystem service provision (<i>national or subnational level; spatially explicit</i>)</li> <li>• WePlan-Forests (weplan-forests.org): a web-based tool that considers trade-offs between carbon sequestration, species-specific extinction reduction benefits, opportunity and establishment costs and five restoration area targets (Strassburg et al., 2019) (<i>national or subnational level; spatially explicit</i>)</li> </ul>
<p>Tools for assessing ecosystem degradation status</p> 	<ul style="list-style-type: none"> <li>• Forest Landscape Assessment Tool (FLAT; Cieccko et al., 2016): a methodology to assess forest ecological baseline conditions and to determine and prioritize restoration needs (<i>local level; spatially explicit</i>)</li> <li>• ENVI Forest health tool (L3Harris Geospatial, 2020): software-based forest health assessment using multispectral remote sensing data in ENVI software (<i>typically local level; spatially explicit</i>)</li> <li>• Collect Earth (openforis.org/tools/collect-earth.html): a software-based tool that enables data collection through visual interpretation of Google Earth imagery, which can be used for assessing ecosystem conditions or monitoring restoration progress (<i>local level; spatially explicit</i>)</li> </ul>
<p>Tools for deciding on the type of restoration intervention (e.g. assisted natural regeneration or active planting)</p> 	<ul style="list-style-type: none"> <li>• Restoration Opportunities Assessment Methodology (ROAM; IUCN &amp; WRI, 2014): see above (<i>national or subnational level; recommendations for the types of restoration interventions are not spatially explicit</i>)</li> <li>• Crouzeilles et al. (2020): spatial modelling methodology to predict regeneration success in the Atlantic Forest in Brazil (<i>subnational level; spatially explicit</i>)</li> <li>• Quanto é Plantar Floresta (quantoefloresta.escolhas.org): web-based tool that estimates the costs and economic returns of different restoration intervention types, for example direct seeding, plantations with 50% eucalypt, agroforestry (<i>subnational level; not spatially explicit</i>)</li> <li>• Greener Land (greener.land): web-based tool that gives recommendations on restoration interventions depending on the site conditions (<i>local level; not spatially explicit</i>)</li> </ul>
<p>Tools to guide species selection (for initiatives involving active planting)</p> 	<ul style="list-style-type: none"> <li>• <b>Diversity for Restoration</b> (diversityforrestoration.org): this paper (<i>local level; spatially explicit</i>)</li> <li>• Useful Tree Species for Eastern Africa and Africa Tree Finder: a web-based tool and Android application, respectively, both based on Vegetationmap4Africa (vegetationmap4africa.org; Kindt et al., 2015), linking potential natural vegetation (PNV) types with native species and their uses (<i>local level; spatially explicit</i>)</li> <li>• Agroforestry Species Switchboard (apps.worldagroforestry.org/products/switchboard; Kindt et al., 2016): a website bundling links to a wide range of online information sources and databases for thousands of species used in agroforestry and restoration (<i>local level; not spatially explicit</i>)</li> <li>• Multi-criteria Tree Selection (MCTS) tool (Reubens et al., 2011): An Excel-based multi-criteria decision support tool to select species for land rehabilitation in Ethiopia (<i>local level; not spatially explicit</i>)</li> <li>• plantevalg.dk: a web-based tool for selecting species and seed sources in Denmark (<i>local level; spatially explicit</i>)</li> <li>• Shade tree ICT tool (shadetreeadvice.org; Van Der Wolf et al., 2017): a web-based tool to select tree species in cacao and coffee agroforestry systems based on local ecological knowledge (<i>local level; not spatially explicit</i>)</li> <li>• i-Tree species (species.itreetools.org/): a web-based tool to help urban foresters select the most appropriate tree species based on potential environmental services and geographic area (<i>local level; not spatially explicit</i>)</li> <li>• Tree Species Selector (greeningcanadianlandscape.ca/tree-species-selector): a web-based tool to select tree species in urban forestry, with a focus on restoring degraded soils (<i>local level; not spatially explicit</i>)</li> <li>• Select (Laughlin et al., 2018): an R package that can be used to generate species assemblages for restoration, simultaneously converging on average trait values and maximizing functional diversity (<i>local level; not spatially explicit</i>)</li> </ul>

TABLE 3 (Continued)

Type of tool according to phases across the forest restoration process	Tool/methodology with short description
<p>Tools for supporting seed sourcing (for initiatives involving active planting)</p> 	<ul style="list-style-type: none"> <li>• <b>Diversity for Restoration</b> (diversityforrestoration.org): this paper (<i>local level; spatially explicit</i>)</li> <li>• Seedlot selection tool (seedlotselectiontool.org/sst): a web-based tool to help forest managers to match seedlots with planting site based on current or future climatic conditions in the United States (<i>local level; spatially explicit</i>)</li> <li>• Climate Smart Restoration Tool (climaterestorationtool.org/csrt): a web-based tool for mapping current and future seed transfer limits for plant species using climate data in the United States (<i>local level; spatially explicit</i>)</li> <li>• plantevalg.dk: see above (<i>local level; spatially explicit</i>)</li> <li>• Climate Distance Mapper (usgs-werc-shinytools.shinyapps.io/Climate_Distance_Mapper; Shryock et al., 2018): a web-based tool to support the selection of seed sources by mapping the multivariate climate distances to the seed sources in the Desert Southwest of the United States (<i>local level; spatially explicit</i>)</li> <li>• Restore and Renew (restore-and-renew.org.au; Rossetto et al., 2019): a web-based tool for delimiting seed sourcing areas and identifying similar climates under present and future conditions in the southeast of Australia (<i>local level; spatially explicit</i>)</li> <li>• Capfitogen (capfitogen.net; Parra-Quijano et al., 2012): a software-based tool that provides seed zones based on ecogeographical clustering (<i>local level; spatially explicit</i>)</li> <li>• SeedIT (seedit.io): a smartphone application to track, manage and diversify seed collections (<i>local level; spatially explicit only in the sense that it allows recording coordinates</i>)</li> </ul>
<p>Tools to guide monitoring and adaptive management</p> 	<ul style="list-style-type: none"> <li>• FAO Forest Restoration Monitoring Tool (FAO, 2012): a survey-like template for monitoring restoration projects, focused on dryland forests (<i>local level; not spatially explicit</i>)</li> <li>• SER 5-Star Recovery System tool (Gann et al., 2016): a visual methodological tool to record and communicate ecological recovery in restoration projects, using 5 levels of progress (<i>local level; not spatially explicit</i>)</li> <li>• Collect Earth (openforis.org/tools/collect-earth): see above (<i>local level; spatially explicit</i>); also other environmental monitoring tools available at openforis.org</li> <li>• Regreening Africa App (regreeningafrica.org): a smartphone application to collect data on tree planting/protecting and tree management by farmers (<i>local level; spatially explicit only in the sense that it allows recording coordinates</i>)</li> <li>• Restor (restor.eco): a web-based open data platform to access and share ecological spatial data and to monitor restoration initiatives (<i>local level; spatially explicit</i>)</li> <li>• Sustainability Index for Landscape Restoration (Zamora-Cristales et al., 2020): a methodological framework for monitoring the biophysical and socio-economic impacts of landscape restoration through the construction of an index (<i>local level; to be applied across a landscape but results not spatially explicit</i>)</li> </ul>

## 4 | PRACTICAL CONSIDERATIONS AND PROSPECTS

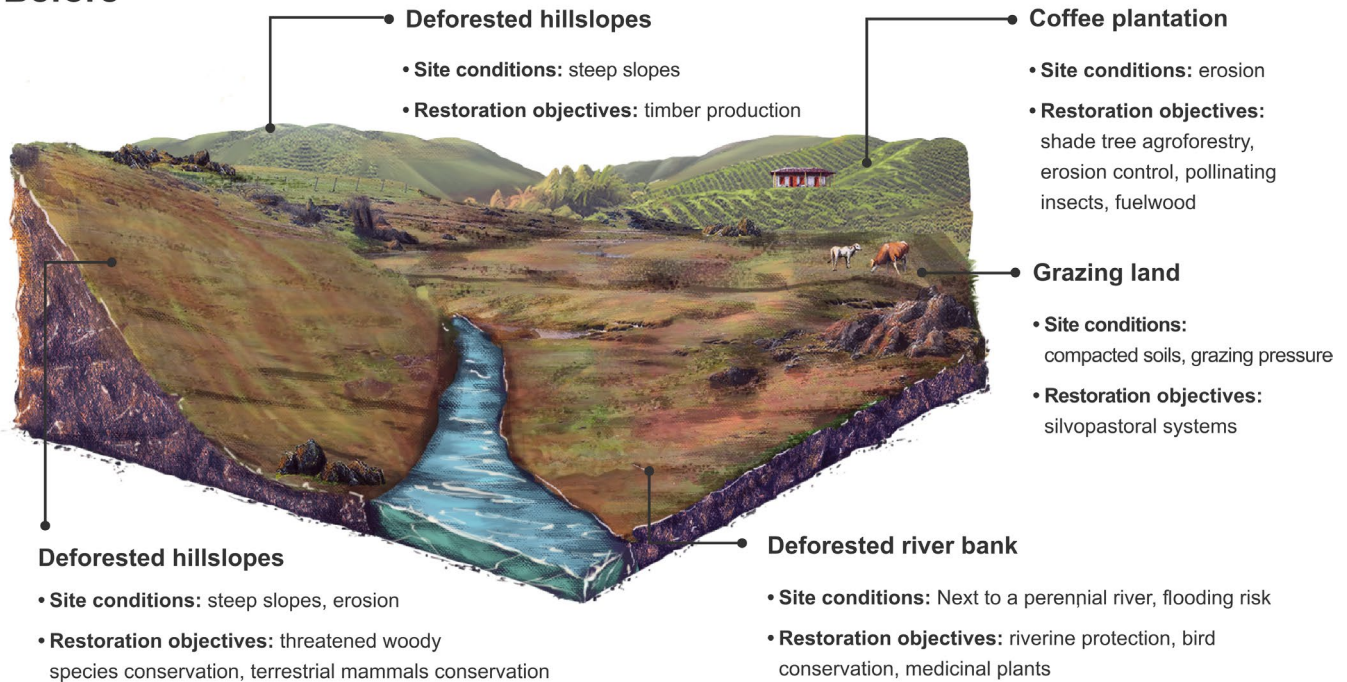
The D4R tool is aligned with the forest landscape restoration (FLR) approach, defined as a 'planned process that aims to regain ecological integrity and enhance human wellbeing in deforested or degraded landscapes' (WWF & IUCN, 2000). Similar to the flexible and pragmatic FLR approach, the tool is meant to support tree planting efforts for various purposes, ranging from biodiversity conservation to timber production and agroforestry. While the tool does not provide landscape-scale recommendations, it is meant to be run separately for different land units within the landscape mosaic, as local site conditions and restoration objectives usually differ in different parts of the landscape (Figure 6). Users are free to select the number of species according to their objectives while considering practical and financial limitations, but we do recommend to always use multiple species for the reasons mentioned in Section 2.3. Another important consideration is that the species recommendations provided by the tool should not be seen as a cook book recipe; they merely

provide a starting point based on the best information available and should be discussed with relevant stakeholders including local communities, assessed in light of what is logistically possible, and adjusted where necessary.

Once an appropriate combination of species and seed zones has been identified, restoration planners need to identify at least one seed source or seed provider in each of the seed zones (more is better to increase adaptive potential, but logistics and costs may make this unrealistic). To mitigate the issue of seed availability, the tool proposes different options of tree species for a particular set of site conditions and restoration objectives (Section 2.3). Furthermore, wherever possible, contact details are provided of people or institutions who can provide seeds of selected species from particular seed sources. This is currently already implemented for the TDFs of Peru (Cerrón et al., 2019), and planned for other regions.

Choosing tree species and seed sources are not the only practical decisions to make when planting trees: other decisions need to be made on the planting strategy (e.g. planting in nuclei, along contour lines, etc.) and the spatial configuration of the selected species. Similarly, when trees die, a choice needs to be made between replanting and letting

## Before



## After



**FIGURE 6** Illustration of the use of the Diversity for Restoration tool for different land units, with differing site conditions and restoration objectives

further community assembly occur naturally, a decision which depends on budgetary flexibility and how dependent the desired ecosystem services are on the presence of specific species, among other aspects. While the tool currently does not include these aspects, we are planning to include some guidance on them in the future.

D4R is a dynamic and scalable tool, both in terms of the inclusion of additional restoration objectives and the expansion to other countries. Among the new restoration objectives being rolled out are those related to nutrition and food security, and shade tree selection in cacao and coffee agroforestry systems. Application of

the tool in other countries and ecosystems is underway in western Ethiopia, northern Thailand, the Sabah state of Malaysia and the Western Ghats in India, which will also allow the addition of context-specific restoration objectives (e.g. conservation of sun bear, orangutan and hornbills in Sabah, Malaysia). While these are all forest ecosystems, the tool can be extended to other ecosystems as well. Furthermore, we plan to integrate an economic simulation module to provide users with additional information about which of the possible species combinations simultaneously maximize the benefit-cost ratio, considering a series of threats (e.g. extreme drought, fire, pests

and diseases) that may affect a restoration site over a given period of time.

Ultimately, the success of the D4R tool ([www.diversityforrestoration.org](http://www.diversityforrestoration.org)) will be measured through its uptake by restoration planners. We hope that the explanation of the mechanics behind the tool can contribute to this, as the recommendations of 'black box' approaches are less likely to be accepted by users. While the expected usefulness of the tool has been positively evaluated by both scientists and restoration practitioners (Wiederkehr-Guerra & Gotor, 2020), its application on the ground is only starting (Aping, 2019). One of the main priorities now is therefore to test the tool through the network that has been established in the different regions where the tool is functional.

Long-term monitoring of restoration plantings based on the recommendations of the D4R tool will be important to improve the quality of these recommendations. For example, it remains unclear how well our habitat distribution models can predict the realized long-term community composition, as they do not consider biotic interactions and therefore have their limitations in predicting species co-occurrence. While the tool allows to maximize functional diversity (Section 2.3), which is expected to promote niche complementarity and reduce competition between species (Wagg et al., 2017), such long-term monitoring is needed to better understand how we can predict community assembly based on habitat suitability models and functional traits.

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## CONFLICT OF INTEREST

No conflict of interest has been declared by the authors.

## AUTHORS' CONTRIBUTIONS

T.F., E.T. and B.M. conceived the ideas and designed the methodology; T.F., E.T., H.T., S.B., C.E.G.-M., C.A.-C., A.L. and H.M.K. collected and compiled trait data; T.F., E.T., H.G., B.V., E.B., V.C. and A.V. compiled occurrence data; T.F., E.T., S.B., E.B., V.C. and A.V. contributed to data analysis; T.F. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

The R scripts behind the tool are available at <https://github.com/tobiasfremout/D4R>, data to test the scripts are available via Figshare (<https://doi.org/10.6084/m9.figshare.16764628>) (Fremout, Thomas, Taedoumg, et al., 2021).

## ORCID

Tobias Fremout  <https://orcid.org/0000-0002-0812-3027>

Evert Thomas  <https://orcid.org/0000-0002-7838-6228>

Hermann Taedoumg  <https://orcid.org/0000-0002-8137-2396>

Carolina Alcázar-Caicedo  <https://orcid.org/0000-0002-9366-8098>

Hubert Mounmemi Kpoumie  <https://orcid.org/0000-0003-1920-6116>

Barbara Vinceti  <https://orcid.org/0000-0001-8908-2994>

Chris Kettle  <https://orcid.org/0000-0002-9476-0136>

Marius Ekué  <https://orcid.org/0000-0002-5829-6321>

Rachel Atkinson  <https://orcid.org/0000-0001-8977-5707>

Riina Jalonen  <https://orcid.org/0000-0003-1669-9138>

Hannes Gaisberger  <https://orcid.org/0000-0002-6023-1236>

Stephen Elliott  <https://orcid.org/0000-0002-5846-3353>

Viviana Ceccarelli  <https://orcid.org/0000-0003-2160-9483>

Smitha Krishnan  <https://orcid.org/0000-0002-2851-6813>

Harald Vacik  <https://orcid.org/0000-0002-5668-6967>

Gabriela Wiederkehr-Guerra  <https://orcid.org/0000-0002-2742-6285>

Beatriz Salgado-Negret  <https://orcid.org/0000-0002-3103-9878>

Colin Maycock  <https://orcid.org/0000-0002-4368-2545>

Bart Muys  <https://orcid.org/0000-0001-9421-527X>

## REFERENCES

- Aping, P. J. (2019). *Testing the effectiveness of different restoration interventions of the tropical dry forest in the hidroituango compensation zone Antioquia, Colombia* (MSc thesis). Department of Biology, Faculty of Mathematics and Natural Sciences, University of Hamburg.
- Araújo, M. B., & Peterson, A. T. (2012). Uses and misuses of bioclimatic envelope modeling. *Ecology*, 93(7), 1527–1539. <https://doi.org/10.1890/11-1930.1>
- Aronson, J., & Alexander, S. (2013). Ecosystem restoration is now a global priority: Time to roll up our sleeves. *Restoration Ecology*, 21(3), 293–296. <https://doi.org/10.1111/rec.12011>
- Atkinson, R. J., Thomas, E., Roscioli, F., Cornelius, J. P., Zamora-Cristales, R., Franco Chuaire, M., Alcázar, C., Mesén, F., Lopez, H., Ipinza, R., Donoso, P. J., Gallo, L., Nieto, V., Ugarte, J., Sáenz-Romero, C., Fremout, T., Jalonen, R., Gaisberger, H., Vinceti, B., ... Kettle, C. (2021). Seeding resilient restoration: An indicator system for the analysis of tree seed systems. *Diversity*, 13, 367. <https://doi.org/10.3390/d13080370>
- Beatty, C. R., Raes, L., Vogl, A. L., Hawthorne, P. L., Moraes, M., Saborio, J. L., & Meza-Prado, K. (2018). *Landscapes, at your service: Applications of the Restoration Opportunities Optimization Tool (ROOT)*. IUCN. <https://doi.org/10.2305/iucn.ch.2018.17.en>
- Boshier, D., Broadhurst, L., Cornelius, J., Gallo, L., Koskela, J., Loo, J., Petrokofsky, G., & St Clair, B. (2015). Is local best? Examining the evidence for local adaptation in trees and its scale. *Environmental Evidence*, 4, 20. <https://doi.org/10.1186/s13750-015-0046-3>
- Brancalion, P. H. S. S., Holl, K. D., & Cruz, S. (2020). Guidance for successful tree planting initiatives. *Journal of Applied Ecology*, 57(12), 2349–2361. <https://doi.org/10.1111/1365-2664.13725>

- Breed, M. F., Cross, A. T., Wallace, K., Bradby, K., Flies, E., Goodwin, N., Jones, M., Orlando, L., Skelly, C., Weinstein, P., & Aronson, J. (2020). Ecosystem restoration: A public health intervention. *EcoHealth*. <https://doi.org/10.1007/s10393-020-01480-1>
- Broadhurst, L. M., North, T., & Young, A. G. (2006). Should we be more critical of remnant seed sources being used for revegetation? *Ecological Management and Restoration*, 7(3), 211–217. <https://doi.org/10.1111/j.1442-8903.2006.00311.x>
- Cadotte, M. W., Cavender-Bares, J., Tilman, D., & Oakley, T. H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE*, 4(5), e5695. <https://doi.org/10.1371/journal.pone.0005695>
- Cadotte, M. W., Dinnage, R., & Tilman, D. (2012). Phylogenetic diversity promotes ecosystem stability. *Ecology*, 93(8), S223–S233. <https://doi.org/10.1890/11-0426.1>
- Cerrón, J., Fremout, T., Atkinson, R., Thomas, E., & Cornelius, J. (2019). *Experiencias de restauración y fuentes semilleras en el bosque seco tropical del norte del Perú*. Bioversity International, World Agroforestry. <https://doi.org/10.13140/RG.2.2.13126.63040>
- Chazdon, R. L., & Guariguata, M. R. (2018). *Decision support tools for forest landscape restoration: Current status and future outlook (No. 183)*. CIFOR <https://doi.org/10.17528/cifor/006792>
- Ciecko, L., Kimmett, D., Saunders, J., Katz, R., Wolf, K. L., Bazinet, O., Richardson, J., Brinkley, W., & Blahna, D. J. (2016). *Forest Landscape Assessment Tool (FLAT): Rapid assessment for land management*. General Technical Report, US Forest Service
- Crouzeilles, R., Beyer, H. L., Monteiro, L. M., Feltran-Barbieri, R., Pessôa, A. C. M., Barros, F. S. M., Lindenmayer, D. B., Lino, E. D. S. M., Grelle, C. E. V., Chazdon, R. L., Matsumoto, M., Rosa, M., Latawiec, A. E., & Strassburg, B. B. N. (2020). Achieving cost-effective landscape-scale forest restoration through targeted natural regeneration. *Conservation Letters*, 13(3), e12709. <https://doi.org/10.1111/conl.12709>
- Crow, T. M., Albeke, S. E., Buerkle, C. A., & Hufford, K. M. (2018). Provisional methods to guide species-specific seed transfer in ecological restoration. *Ecosphere*, 9(1), e02059. <https://doi.org/10.1002/ecs2.2059>
- Crowe, K. A., & Parker, W. H. (2008). Using portfolio theory to guide reforestation and restoration under climate change scenarios. *Climatic Change*, 89(3–4), 355–370. <https://doi.org/10.1007/s10584-007-9373-x>
- Durka, W., Michalski, S. G., Berendzen, K. W., Bossdorf, O., Bucharova, A., Hermann, J.-M., Hölzel, N., & Kollmann, J. (2017). Genetic differentiation within multiple common grassland plants supports seed transfer zones for ecological restoration. *Journal of Applied Ecology*, 54(1), 116–126. <https://doi.org/10.1111/1365-2664.12636>
- FAO. (2012). *Forest restoration monitoring tool*. Draft version for field test. Rome, Italy. Retrieved from <http://www.fao.org/sustainable-forest-management/toolbox/tools/tool-detail/en/c/233276/>
- FAO. (2020). *Restoring the Earth—The next decade (Vol. 71)*. FAO. <https://doi.org/10.4060/cb1600en>
- Flynn, D. F. B., Mirotnick, N., Jain, M., Palmer, M. I., & Naeem, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity - ecosystem function relationships. *Ecology*, 92(8), 1573–1581. <https://doi.org/10.1890/10-1245.1>
- Fremout, T., Gutiérrez-Miranda, C. E., Briers, S., Marcelo-Peña, J. L., Cueva-Ortiz, E., Linares-Palomino, R., La Torre-Cuadros, M. D. L. Á., Chang-Ruiz, J. C., Villegas-Gómez, T. L., Acosta-Flota, A. H., Plouvier, D., Atkinson, R., Charcape-Ravelo, M., Aguirre-Mendoza, Z., Muys, B., & Thomas, E. (2021). The value of local ecological knowledge to guide tree species selection in tropical dry forest restoration. *Restoration Ecology*, 29(4), e13347. <https://doi.org/10.1111/rec.13347>
- Fremout, T., Thomas, E., Bocanegra-González, K. T., Aguirre-Morales, C. A., Morillo-Paz, A. T., Atkinson, R., Kettle, C., González-M., R., Alcázar-Cacedo, C., González, M. A., Gil-Tobón, C., Gutiérrez, J. P., Gonzalo Moscoso-Higueta, L., López-Lavalle, L. A. B., de Carvalho, D., & Muys, B. (2021). Dynamic seed zones to guide climate-smart seed sourcing for tropical dry forest restoration in Colombia. *Forest Ecology and Management*, 490, 119127. <https://doi.org/10.1016/j.foreco.2021.119127>
- Fremout, T., Thomas, E., Gaisberger, H., Van Meerbeek, K., Muenchow, J., Briers, S., Gutierrez-Miranda, C. E., Marcelo-Peña, J. L., Kindt, R., Atkinson, R., Cabrera, O., Espinosa, C. I., Aguirre-Mendoza, Z., & Muys, B. (2020). Mapping tree species vulnerability to multiple threats as a guide to restoration and conservation of tropical dry forests. *Global Change Biology*, 26(6), 3552–3568. <https://doi.org/10.1111/gcb.15028>
- Fremout, T., Thomas, E., Taedoum, H., Briers, S., Gutiérrez-Miranda, C. E., Alcázar-Cacedo, C., Lindau, A., Mounmeme Kpoumie, H., Vinceti, B., Kettle, C., Ekué, M., Atkinson, R., Jalonen, R., Gaisberger, H., Elliott, S., Brechbühler, E., Ceccarelli, V., Krishnan, S., Vacic, H., ... Muys, B. (2021). Test data to run the R scripts behind the Diversity for Restoration Tool. *figshare*. <https://doi.org/10.6084/m9.figshare.16764628>
- Funk, J. L., Cleland, E. E., Suding, K. N., & Zavaleta, E. S. (2008). Restoration through reassembly: Plant traits and invasion resistance. *Trends in Ecology & Evolution*, 23(12), 695–703. <https://doi.org/10.1016/j.tree.2008.07.013>
- Gann, G. D., McDonald, T., Walder, B., Aronson, J., Nelson, C. R., Jonson, J., Hallett, J. G., Eisenberg, C., Guariguata, M. R., Liu, J., Hua, F., Echeverría, C., Gonzales, E., Shaw, N., Decler, K., & Dixon, K. W. (2016). International standards for the practice of ecological restoration—Including principles and key concepts. *Restoration Ecology*, 27, S1–S46.
- Godefroid, S., Piazza, C., Rossi, G., Buord, S., Stevens, A. D., Aguruiju, R., Cowell, C., Weekley, C. W., Vogg, G., Iriondo, J. M., Johnson, I., Dixon, B., Gordon, D., Magnanon, S., Valentin, B., Bjoreke, K., Koopman, R., Vicens, M., Virevaire, M., & Vanderborcht, T. (2011). How successful are plant species reintroductions? *Biological Conservation*, 144(2), 672–682. <https://doi.org/10.1016/j.biocon.2010.10.003>
- Gray, L. K., & Hamann, A. (2011). Strategies for reforestation under uncertain future climates: Guidelines for Alberta, Canada. *PLoS ONE*, 6(8), e22977. <https://doi.org/10.1371/journal.pone.0022977>
- Gross, N., Bagousse-Pinguet, Y. L., Liancourt, P., Berdugo, M., Gotelli, N. J., & Maestre, F. T. (2017). Functional trait diversity maximizes ecosystem multifunctionality. *Nature Ecology & Evolution*, 1(5), 0132. <https://doi.org/10.1038/s41599-017-0132>
- Hallett, L. M., Stein, C., & Suding, K. N. (2017). Functional diversity increases ecological stability in a grazed grassland. *Oecologia*, 183(3), 831–840. <https://doi.org/10.1007/s00442-016-3802-3>
- Höhl, M., Ahimbisibwe, V., Stanturf, J. A., Elsasser, P., Kleine, M., & Bolte, A. (2020). Forest landscape restoration—What generates failure and success? *Forests*, 11, 938. <https://doi.org/10.3390/F11090938>
- Holl, K. D., & Brancalion, P. H. S. (2020). Tree planting is not a simple solution. *Science*, 368(6491), 580–581. <https://doi.org/10.1126/science.aba8232>
- Huang, X., Su, J., Li, S., Liu, W., & Lang, X. (2019). Functional diversity drives ecosystem multifunctionality in a *Pinus yunnanensis* natural secondary forest. *Scientific Reports*, 9, 6979. <https://doi.org/10.1038/s41598-019-43475-1>
- IUCN & WRI. (2014). *A guide to the Restoration Opportunities Assessment Methodology (ROAM): Assessing forest landscape restoration opportunities at the national or sub-national level*. Working Paper (Road-test edition). IUCN.
- Jalonen, R., Valette, M., Boshier, D., Duminil, J., & Thomas, E. (2018). Forest and landscape restoration severely constrained by a lack of attention to the quantity and quality of tree seed: Insights from a global survey. *Conservation Letters*, 11, e12424. <https://doi.org/10.1111/conl.12424>
- Jiang, S., Luo, M.-X., Gao, R.-H., Zhang, W., Yang, Y.-Z., Li, Y.-J., & Liao, P.-C. (2019). Isolation-by-environment as a driver of genetic

- differentiation among populations of the only broad-leaved evergreen shrub *Ammopiptanthus mongolicus* in Asian temperate deserts. *Scientific Reports*, 9(1), 12008. <https://doi.org/10.1038/s41598-019-48472-y>
- Jin, Y., & Qian, H. (2019). VPhyloMaker: An R package that can generate very large phylogenies for vascular plants. *Ecography*, 42(8), 1353–1359. <https://doi.org/10.1111/ecog.04434>
- Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar, C. C., Aleixo, I., Ali, H., ... Wirth, C. (2020). TRY plant trait database—Enhanced coverage and open access. *Global Change Biology*, 26(1), 119–188. <https://doi.org/10.1111/gcb.14904>
- Keesing, F., & Ostfeld, R. S. (2021). Impacts of biodiversity and biodiversity loss on zoonotic diseases. *Proceedings of the National Academy of Sciences of the United States of America*, 118(17), 1–4. <https://doi.org/10.1073/pnas.2023540118>
- Kindt, R. (2018). Ensemble species distribution modelling with transformed suitability values. *Environmental Modelling & Software*, 100, 136–145. <https://doi.org/10.1016/j.envsoft.2017.11.009>
- Kindt, R., Blanchet, F. G., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. V., Solymos, P., Stevens, M. H. H., & Wagner, H. (2016). *Agroforestry species switchboard*. Retrieved from <http://apps.worldagroforestry.org/products/switchboard>
- Kindt, R., Graudal, L., Jaminadass, R., Lillesø, J.-P.-B., Orwa, C., & van Breugel, P. (2015). *Useful tree species for Eastern Africa: A species selection tool based on the VECEA map*. Version 2.0. Retrieved from <https://vegetationmap4africa.org/>
- Kodikara, K. A. S., Mukherjee, N., Jayatissa, L. P., Dahdouh-Guebas, F., & Koedam, N. (2017). Have mangrove restoration projects worked? An in-depth study in Sri Lanka. *Restoration Ecology*, 25(5), 705–716. <https://doi.org/10.1111/rec.12492>
- Kramer, A. T., & Havens, K. (2009). Plant conservation genetics in a changing world. *Trends in Plant Science*, 14(11), 599–607. <https://doi.org/10.1016/j.tplants.2009.08.005>
- Kramer, A. T., Larkin, D. J., & Fant, J. B. (2015). Assessing potential seed transfer zones for five forb species from the Great Basin Floristic Region, USA. *Natural Areas Journal*, 35(1), 174–188. <https://doi.org/10.3375/043.035.0119>
- L3Harris Geospatial. (2020). *Forest health tool*. Retrieved from <https://www.l3harrisgeospatial.com/docs/ForestHealthTool.html>
- Laliberté, E., Legendre, P., & Shipley, B. (2014). *FD: Measuring functional diversity from multiple traits, and other tools for functional ecology*. R package version 1.0-12.
- Laughlin, D. C., Chalmandrier, L., Joshi, C., Renton, M., Dwyer, J. M., & Funk, J. L. (2018). Generating species assemblages for restoration and experimentation: A new method that can simultaneously converge on average trait values and maximize functional diversity. *Methods in Ecology and Evolution*, 9(7), 1764–1771. <https://doi.org/10.1111/2041-210X.13023>
- Le, H. D., Smith, C., & Herbohn, J. (2014). What drives the success of reforestation projects in tropical developing countries? The case of the Philippines. *Global Environmental Change*, 24(1), 334–348. <https://doi.org/10.1016/j.gloenvcha.2013.09.010>
- Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412(6842), 72–76. <https://doi.org/10.1038/35083573>
- Lowe, A. J., Hoffmann, A. A., Sgro, C. M., Sgrò, C. M., Lowe, A. J., Hoffmann, A. A., & Sgro, C. M. (2011). Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications*, 4(2), 326–337. <https://doi.org/10.1111/j.1752-4571.2010.00157.x>
- Mansourian, S. (2018). In the eye of the beholder: Reconciling interpretations of forest landscape restoration. *Land Degradation and Development*, 29(9), 2888–2898. <https://doi.org/10.1002/ldr.3014>
- McKay, J. K., Christian, C. E., Harrison, S., & Rice, K. J. (2005). 'How local is local?'—A review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology*, 13(3), 432–440. <https://doi.org/10.1111/j.1526-100X.2005.00058.x>
- Miller, S. A., Bartow, A., Gisler, M., Ward, K., Young, A. S., & Kaye, T. N. (2011). Can an ecoregion serve as a seed transfer zone? Evidence from a common garden study with five native species. *Restoration Ecology*, 19(201), 268–276. <https://doi.org/10.1111/j.1526-100X.2010.00702.x>
- Mori, A. S., Furukawa, T., & Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews*, 88(2), 349–364. <https://doi.org/10.1111/brv.12004>
- Orwa, C., Mutua, A., Kindt, R., Jaminadass, R., & Anthony, S. (2009). *Agroforestry Database: A tree reference and selection guide version 4.0*. [https://doi.org/10.1007/978-94-007-5628-1\\_11](https://doi.org/10.1007/978-94-007-5628-1_11)
- Paradis, E., & Schliep, K. (2018). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35, 526–528. <https://doi.org/10.1093/bioinformatics/bty633>
- Parra-Quijano, M., Iriondo, J. M., & Torres, E. (2012). Ecogeographical land characterization maps as a tool for assessing plant adaptation and their implications in agrobiodiversity studies. *Genetic Resources and Crop Evolution*, 59(2), 205–217. <https://doi.org/10.1007/s10722-011-9676-7>
- Perring, M. P., Erickson, T. E., & Brancalion, P. H. S. (2018). Rocketing restoration: Enabling the upscaling of ecological restoration in the Anthropocene. *Restoration Ecology*, 26(6), 1017–1023. <https://doi.org/10.1111/rec.12871>
- Platts, P. J., Omeny, P. A., & Marchant, R. (2014). AFRICLIM: High-resolution climate projections for ecological applications in Africa. *African Journal of Ecology*, 53, 103–108. <https://doi.org/10.1111/aje.12180>
- Qin, T. J., Zhou, J., Sun, Y., Müller-Schärer, H., Luo, F. L., Dong, B. C., Li, H. L., & Yu, F. H. (2020). Phylogenetic diversity is a better predictor of wetland community resistance to *Alternanthera philoxeroides* invasion than species richness. *Plant Biology*, 22(4), 591–599. <https://doi.org/10.1111/plb.13101>
- Reubens, B., Moeremans, C., Poesen, J., Nyssen, J., Tewoldeberhan, S., Franzel, S., Deckers, J., Orwa, C., & Muys, B. (2011). Tree species selection for land rehabilitation in Ethiopia: From fragmented knowledge to an integrated multi-criteria decision approach. *Agroforestry Systems*, 82(3), 303–330. <https://doi.org/10.1007/s10457-011-9381-8>
- Rossetto, M., Bragg, J., Kilian, A., McPherson, H., van der Merwe, M., & Wilson, P. D. (2019). Restore and renew: A genomics-era framework for species provenance delimitation. *Restoration Ecology*, 27(3), 538–548. <https://doi.org/10.1111/rec.12898>
- Sexton, J. P., Hangartner, S. B., & Hoffmann, A. A. (2014). Genetic isolation by environment or distance: Which pattern of gene flow is most common? *Evolution*, 68(1), 1–15. <https://doi.org/10.1111/evo.12258>
- Shryock, D. F., DeFalco, L. A., & Esque, T. C. (2018). Spatial decision-support tools to guide restoration and seed-sourcing in the Desert Southwest. *Ecosphere*, 9(10), e02453. <https://doi.org/10.1002/ecs2.2453>
- Strassburg, B. B. N., Beyer, H. L., Crouzeilles, R., Iribarrem, A., Barros, F., de Siqueira, M. F., Sánchez-Tapia, A., Balmford, A., Sansevero, J. B. B., Brancalion, P. H. S., Broadbent, E. N., Chazdon, R. L., Filho, A. O., Gardner, T. A., Gordon, A., Latawiec, A., Loyola, R., Metzger, J. P., Mills, M., ... Uriarte, M. (2019). Strategic approaches to restoring ecosystems can triple conservation gains and halve costs. *Nature Ecology & Evolution*, 3(January), 62–70. <https://doi.org/10.1038/s41559-018-0743-8>
- Suding, K., Higgs, E., Palmer, M., Callicott, J. B., Anderson, C. B., Baker, M., Gutrich, J. J., Hondula, K. L., Lavefor, M. C., Larson, B. M. H., Randall, A., Ruhl, J. B., & Schwartz, K. Z. S. (2015). Committing to ecological restoration. *Science*, 348(6235), 638–640. <https://doi.org/10.1126/science.aaa4216>

- Thomas, E., Alcazar, C., Moscoso, H. L. G., Vasquez, A., Osorio, L. F., Salgado-Negret, B., Gonzalez, M., Parra, M., Bozzano, M., Loo, J., Jalonen, R., & Ramirez, W. (2017). The importance of species selection and seed sourcing in forest restoration for enhancing adaptive potential to climate change: Colombian tropical dry forest as a model. In L. Rodríguez & I. Anderson (Eds.), *CBD Technical series N° 89: The lima declaration on biodiversity and climate change: Contributions from science to policy for sustainable development* (pp. 122–132). Convention on Biological Diversity.
- Thomas, E., Jalonen, R., Loo, J., Boshier, D., Gallo, L., Cavers, S., Bordács, S., Smith, P., & Bozzano, M. (2014). Genetic considerations in ecosystem restoration using native tree species. *Forest Ecology and Management*, 333, 66–75. <https://doi.org/10.1016/j.foreco.2014.07.015>
- Valette, M., Vinceti, B., Gregorio, N., Bailey, A., Thomas, E., & Jalonen, R. (2020). Beyond fixes that fail: Identifying sustainable improvements to tree seed supply and farmer participation in forest and landscape restoration projects. *Ecology and Society*, 25(4), 30. <https://doi.org/10.5751/ES-12032-250430>
- van der Plas, F., Manning, P., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M. A., Hector, A., Ampoorter, E., Baeten, L., Barbaro, L., Bauhus, J., Benavides, R., Benneter, A., Berthold, F., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., ... Fischer, M. (2016). Jack-of-all-trades effects drive biodiversity-ecosystem multifunctionality relationships in European forests. *Nature Communications*, 7, 11109. <https://doi.org/10.1038/ncomms11109>
- Van Der Wolf, J., Gram, G., Bukomeko, H., Mukasa, D., Giller, O., Kirabo, E., Angebault, C., Vaast, P., Asaré, R., & Jassogne, L. (2017). *The shade tree advice tool an ICT solution to advise coffee and cocoa farmers on shade tree selection*. CCAFS Info Note. <https://doi.org/10.13140/RG.2.2.25488.40960>
- Vander Mijnsbrugge, K., Bischoff, A., & Smith, B. (2010). A question of origin: Where and how to collect seed for ecological restoration. *Basic and Applied Ecology*, 11(4), 300–311. <https://doi.org/10.1016/j.baae.2009.09.002>
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116(5), 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Vitt, P., Havens, K., Kramer, A. T., Sollenberger, D., & Yates, E. (2010). Assisted migration of plants: Changes in latitudes, changes in attitudes. *Biological Conservation*, 143, 18–27. <https://doi.org/10.1016/j.biocon.2009.08.015>
- Vranckx, G., Jacquemyn, H., Muys, B., & Honnay, O. (2012). Meta-analysis of susceptibility of woody plants to loss of genetic diversity through habitat fragmentation. *Conservation Biology*, 26(2), 228–237. <https://doi.org/10.1111/j.1523-1739.2011.01778.x>
- Wagg, C., Ebeling, A., Roscher, C., Ravenek, J., Bachmann, D., Eisenhauer, N., Mommer, L., Buchmann, N., Hillebrand, H., Schmid, B., & Weisser, W. W. (2017). Functional trait dissimilarity drives both species complementarity and competitive disparity. *Functional Ecology*, 31(12), 2320–2329. <https://doi.org/10.1111/1365-2435.12945>
- Wiederkehr-Guerra, G., & Gotor, E. (2020). *Evaluation report: An assessment of the Diversity For Restoration (D4R) tool*. Retrieved from <https://hdl.handle.net/10568/111078>
- WRI. (2015). *The restoration diagnostic: A method for developing forest landscape restoration strategies by rapidly assessing the status of key success factors*. WRI.
- WWF and IUCN. (2000). *Minutes of the forests reborn workshop*. Segovia, Spain.
- Zamora-Cristales, R., Herrador, D., Cuellar, N., Díaz, O., Kandel, S., Quezada, J., de Larios, S., Molina, G., Rivera, M., Ramirez, W. M., Jimenez, A., Flores, E., Chuaire, M. F., Lomeli, L. G., & Vergara, W. (2020). *Sustainability index for landscape restoration. A tool for monitoring the biophysical and socioeconomic impacts of landscape restoration*. World Resources Institute.

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