THE IMPORTANCE OF SPECIES SELECTION AND SEED SOURCING IN FOREST RESTORATION FOR ENHANCING ADAPTIVE CAPACITY TO CLIMATE CHANGE: COLOMBIAN TROPICAL DRY FOREST AS A MODEL

Evert Thomas[1], Carolina Alcazar[1], Luis Gonzalo Moscoso H. [2], Alvaro Vasquez[3], Luis Fernando Osorio[3], Beatriz Salgado-Negret[4], Mailyn Gonzalez[4], Mauricio Parra-Quijano[5], Michele Bozzano[6], Judy Loo[6], Riina Jalonen[7], Wilson Ramirez[4]

[1] *Bioversity International, Lima, Peru*
[2] *Forestpa SAS, Medellin, Colombia*
[3] *Universidad Nacional de Colombia, sede Medellin, Colombia*
[4] *Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogota, Colombia*
[5] *Fundación Agrobiodiversidad Colombiana, Bogotá, Colombia.*
[6] *Bioversity International, Rome, Italy*
[7] *Bioversity International, Serdang, Malaysia*

SUMMARY

- Forest restoration projects can derive great benefit from integrating climate modeling, functional trait analysis and genetic considerations in the selection of appropriate tree species and sources of forest reproductive material, for their critical importance for the delivery of ecosystem services and the viability and adaptive capacity of restored forests.
- Targets in restoration projects are not only quantitative but also qualitative. There is need for political commitment to create demand for good quality forest reproductive material of native species through regulatory frameworks and resource allocations.
- User friendly knowledge-based decision making tools need to be developed and mainstreamed to assist emerging restoration practitioners with the choice of tree species and sources of forest reproductive material.
- Countries need to increase experimental field setups such as provenance and progeny trials for native species to validate decision tools and apply adaptive management under climate change.
- Seed supply systems for restoration need to be diversified by involving and training stakeholders at different levels of society.

Keywords: climate change, functional traits, genetic diversity, seed transfer zones, restoration.

INTRODUCTION

The search for workable solutions to mitigate and adapt to climate change is onerous. In spite of concerted global efforts over decades to reduce the emission of greenhouse gasses, the atmospheric concentrations of these gasses, and the associated effects of climate change, have continued to increase (Stocker et al., 2013). Forest restoration including tree planting is increasingly seen by policy makers around the world as a fundamental part of the solution, for its enormous potential to tackle environmental crises related to climate change, biodiversity loss and desertification, while simultaneously boosting economic and rural development (Aronson & Alexander, 2013). Forest restoration, done properly, can do all that. With approximately 2 billion hectares of degraded land waiting to be restored globally, the potential scale of restoration activities is enormous (Laestadius et al., 2012). As in most countries large-scale restoration is a completely new undertaking, making mistakes will be unavoidable. While mistakes provide opportunities to reassess and continuously improve restoration practices, where possible, potential problems should be anticipated and avoided. Aside from putting in place the necessary human, technical and logistic capacity, one important, but often overlooked, aspect of ensuring the success of restoration projects relates to the selection of appropriate forest reproductive material (FRM), at least for active restoration activities that involve tree planting. As a minimum condition, FRM should be selected to (i) correspond to the restoration objectives, (ii) be well adapted to survive and thrive under the degraded site conditions and (iii) have sufficient genetic diversity to ensure the potential to adapt to changing conditions in the future (Thomas et al., 2014a).

Here we present a scalable approach which is intended to assist restoration practitioners of tropical dry forest (TDF) in Colombia with the identification of appropriate tree species and sources of FRM. Decision making combines information on (i) suitability modeling under current and future climate conditions; (ii) the intended future use of the forest under restoration; (iii) locally prevailing stress conditions; (iv) functional trait diversity of tree species; and (v) the genetic quality of FRM. Of all Colombian ecosystems, TDF is most threatened. Approximately 90% of its original cover has disappeared and less than 4% of old growth forest remains, while another 5% show some degree of degradation. With most forest fragments being located on private lands and less than 5% being represented in the national system of protected areas, the risks of further forest loss remain high (Pizano & García 2014). In response to this unsettling reality, the conservation and restoration of TDF has become a national priority in Colombia. The national research institute Alexander Von Humboldt plays a key facilitating role in this endeavor. The institute has recently published a very detailed map of the remaining TDF fragments and restoration priorities, based on remote sensing imaginary and exhaustive field validation (García et al., 2014). As a result of these efforts, approximately 345,000 hectares of degraded land have been identified as having the highest priority for dry forest restoration in the country, mainly located in Caribbean and Andean regions. The recently adopted Colombian law for the compensation for biodiversity loss (MADS, 2012) has great potential for providing part of the financial means to trigger large-scale restoration activities. Given the delicate conservation state of Colombian TDF, a growing body of scientific knowledge on its biology (Pizano & García, 2014), and the existing political momentum in support of efforts to reverse degradation trends (see Aguilar et al., 2015), we consider this ecosystem an ideal model case for testing our protocol for the selection of appropriate species and sources of FRM which we hope will be scaled out and up to other ecosystems and countries.

In what follows we outline the rationale and implementation of the elements considered in our protocol, which are summarized in figure 1. To facilitate accessibility to the information generated, we propose a map-based tool, available at www.restool.org, which allows the user to select any area (resolution of 30 arc seconds or ~1km2 at the equator) with potential for restoring TDF and extracting area-specific information about possible options regarding the selection of tree species and sources of FRMs that are best matched to user-defined restoration goals and the specific environmental conditions of the restoration site, now and in the future. The concept of restoration has different, audience-specific meanings and interpretations, ranging from recovering a pre-disturbance situation (ecological restoration) to establishing biodiversity-friendly land-use practices with a principally productive focus (forest landscape restoration). Our tool is intended to support the decision making of anyone interested in planting trees on land that is suitable for tropical dry forest for whichever purpose, and hence our use of the word restoration in what follows should be interpreted as such.

1. SUITABILITY MODELING TO ASSESS SPECIES' ADAPTIVE POTENTIAL UNDER CLIMATE CHANGE

Climate change will increasingly affect the habitat suitability of the TDF ecosystem and the tree species that are part of it. To gauge potential future climate impacts we carried out suitability modeling, using an ensemble approach (following the protocol described in Thomas et al., 2014b) both for the TDF biome as a whole and for the tree species known to occur in it (Figure 1 section 1). For assessing potential range expansions or contractions of TDF as a biome, we carried out model calibrations using the historical distribution of TDF as a reference. Model quality was evaluated based on its discriminatory power to distinguish historical distribution areas from non-TDF areas, based on climatic, edaphic and terrain variables. Model projections to different future climate scenarios and time horizons allowed developing worst- and best-case scenarios (Figure 2a and 2b, respectively), the worst-case scenario being useful for the identification of priority areas for restoration. In spite of its degraded and fragmented state, TDF in Colombia is home to more than 900 tree species, including numerous exotic ones which are naturalized in Colombian vegetation (Pizano et al., 2014). We modeled all species for which sufficient presence data were available, including some exotics for their proven usefulness for restoration such as *Acacia mangium* (Moscoso Higuita, 2005; Thomas, 2014). We used only presence points located in the historical distribution range of TDF (based on Etter et al., 2008), since many species also occur in other ecosystems. By combining individual species suitability maps under present and different future climate scenarios and time horizons, a distinction can be made between areas that are likely to be able to sustain higher numbers of tree species now and in the future (considered priority areas for restoration efforts) from less suitable areas (Figure 2).

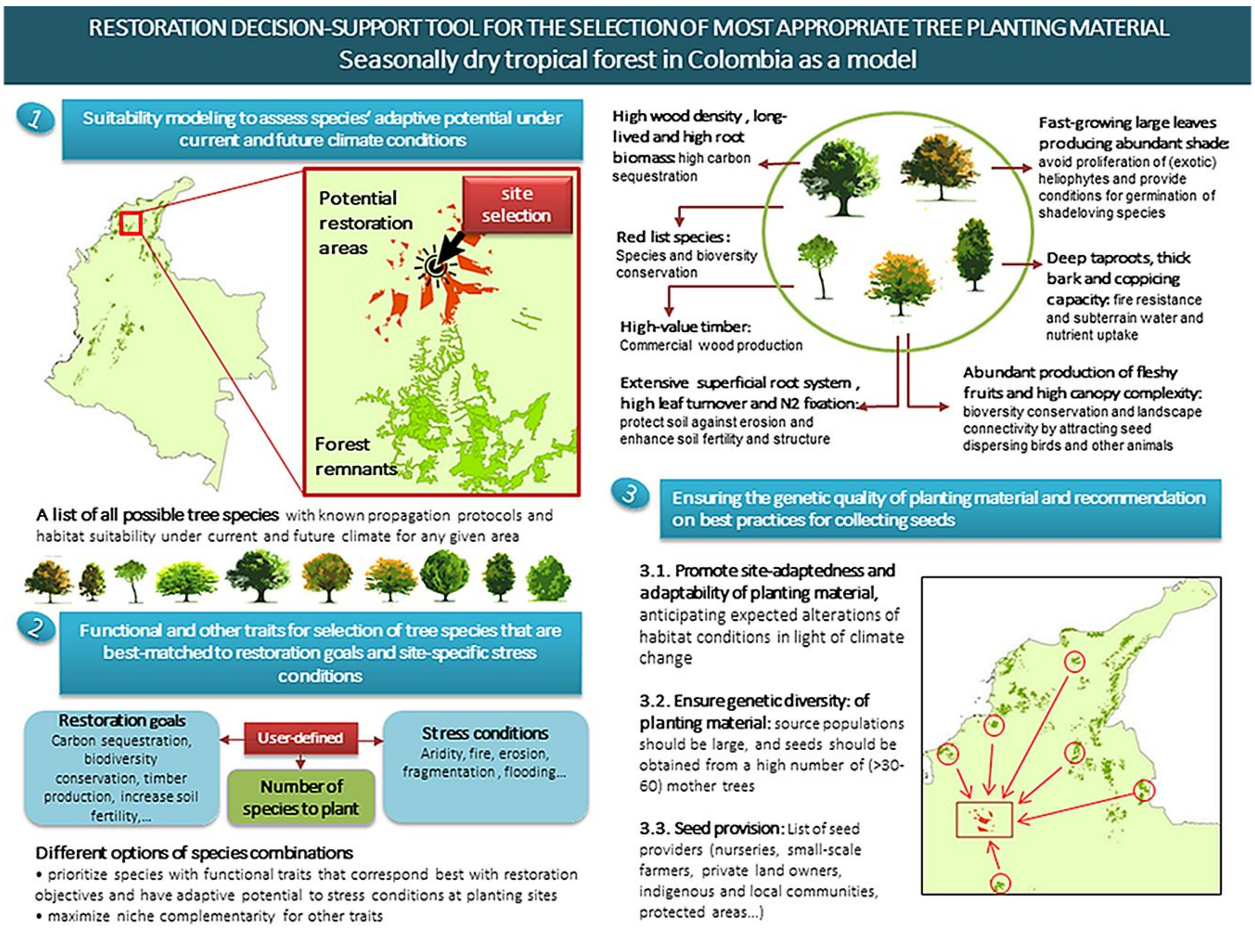

Figure 1: Schematic representation of the different elements considered in our protocol for the selection of appropriate tree species and sources of FRM that are best matched to the restoration goals and the specific environmental conditions of a selected restoration site

The outcome of the above modeling exercise is a list of tree species that are likely to be able to grow in any given area with restoration potential, now and in the coming decades (Figure 1 section 1). In many areas the list of potential species is very extensive (often >250), stressing the need for additional filters. A first filter we use is the existence of information on the propagation of the different tree species under consideration. We compiled information on existing propagation protocols for approximately 340 species which will be made freely available both on-line and as a printed manual targeting restoration practitioners. The user is offered the possibility to further limit the potential species list to best respond to specific restoration objectives or local preferences. For example if the aim is to restore vegetation to pre-disturbance conditions, only species known to occur in reference lists of local vegetation can be given priority.

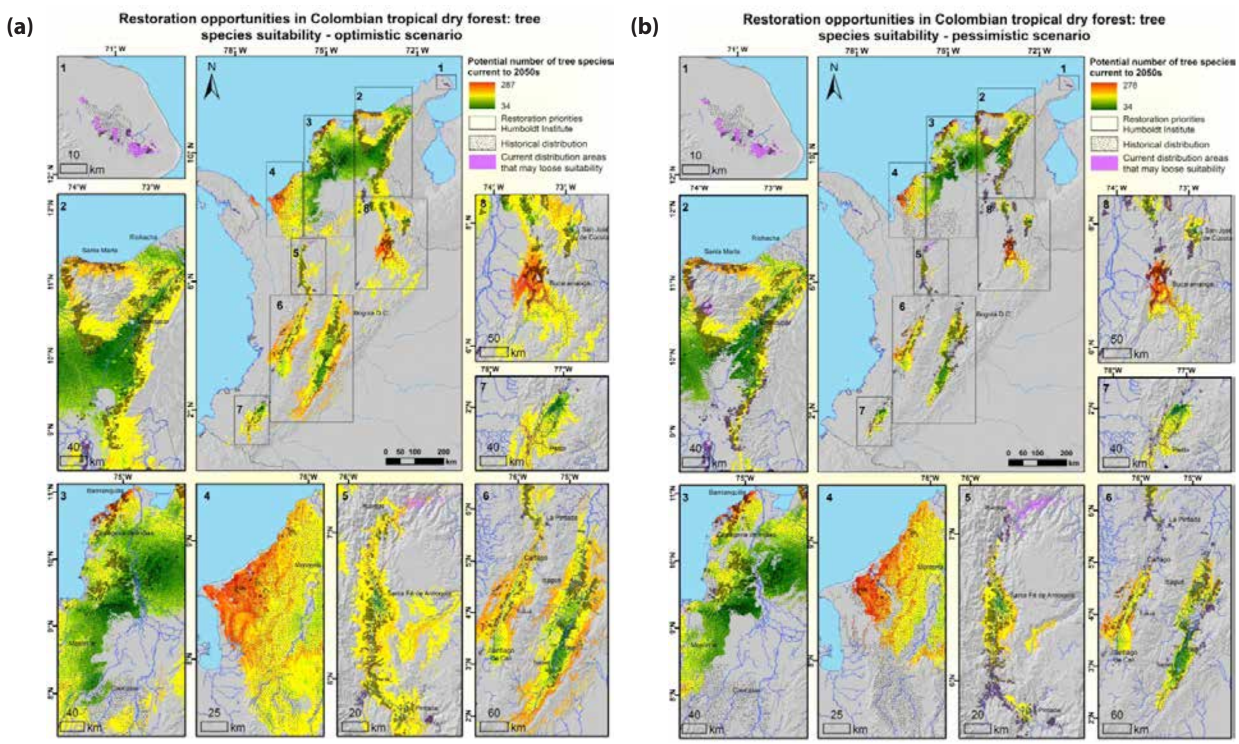

Figure 2: Maps showing TDF tree species suitability in Colombia under future climate conditions (2050s) based on suitability maps of 437 tree species and using the intersect of suitability models of TDF as an ecosystem for different emission scenarios (rcp4.5 and rcp8.5) and time horizons (2030s and 2050s) as a mask; (a) and (b) represent best and worst case scenarios, respectively.

2. FUNCTIONAL TRAITS FOR OPTIMIZING SPECIES COMBINATIONS

To optimize further species selection, we use their functional trait profiles (Figure 1, section 2), a fairly new but growing approach in restoration science (Sandel et al., 2011; Clark et al., 2012; Ostertag et al., 2015). A functional trait is a feature of a species that is linked to a specific role that it plays in the ecosystem and/or its capacity to respond to a given disturbance factor or environmental change. Traits include morphological, ecophysiological, biochemical and reproductive factors and they may be associated with multiple processes and ecosystem services (de Bello et al., 2010). A first criterion in species selection based on functional traits is the restoration objective. The properties of some species will be better aligned with specific restoration goals than others. For example if the objective is to enhance soil fertility, species producing abundant leaf litter and/or able to fix nitrogen through symbiosis with *Rhizobium* bacteria may be most appropriate, while to eliminate hazardous substances from degraded sites, species that hyperaccumulate these substances in plant tissue are to be preferred (Kramer, 2010). Species must also have the necessary adaptive traits be able to survive under the particular conditions of a restoration site. For example, on steep slopes species with extensive root systems may be preferred, or in areas where natural or anthropogenic fires are frequent, species with thicker bark may be appropriate.

To select appropriate tree species according to restoration goals and adaptation to the site conditions, we developed a database establishing the relationship between traits, or trait states, and specific restoration objectives and resistance against site-specific stress conditions, and use this to screen the potential tree species for any given site which best match the defined trait targets. Species are assigned lower or higher scores, in terms of how well their traits align with either the restoration objectives or the desired adaptive potential to stress conditions. Scoring is based on a combination of literature data and restoration experts' judgements (cf. Graff & McIntyre, 2014). Non-biological traits of species are also considered where relevant. For example, one of the traits associated with a restoration objective to harvest timber is the average market price of a standardized unit of wood for commercially exploited timber species, while the red list classification of species is used among the traits to guide restoration goals associated with biodiversity conservation.

In a next step, the resulting subset of tree species is used to assemble species combinations that maximize both scores associated with restoration goals and diversity in other response and effect traits. Response traits are the response of plant species to environmental conditions (e.g. resource availability, disturbance), whereas effect traits refer to the effects species exert on the ecosystem (e.g. biogeochemical cycling) (Lavorel & Garnier, 2002; Suding et al., 2008). Maximizing diversity in functional traits promotes niche complementarity this refers to the combination of *resource partitioning*, i.e. how species use resources and adapt to planting sites, which is particularly critical in degraded areas which by definition are resource-limited, and *facilitation* i.e. impacts on other species through modification of the growth environment (Loreau & Hector, 2001). Maximizing niche complementarity in restoration projects can be useful as it is positively related not only to primary production (communities with high diversity of plant traits have high primary productivity (Wood et al 2015)) but also to the speed and success of establishment of nascent ecosystems (Verheyen et al., 2015). Furthermore, niche complementarity can increase functional redundancy between native and invasive species hence reducing invasiveness risk (Funk et al., 2008).

Based on the species-selection protocol outlined above, the user of our decision-support tool is provided with different options of species combinations that are best aligned with the restoration objectives and the planting site conditions, and maximize additional trait diversity. This allows one to match the most appropriate species combination to local realities, e.g. in terms of local preferences for species, and availability of germplasm. Cost associated with the use of a large number of species should not be considered a disincentive, at least not in the mid to longer term. Experiences from the Brazilian Atlantic Forest restoration pact which aims to restore 15 million hectares by 2050, have shown that with the right (political and economic) incentives, the cost of seedling production does not necessarily inhibit the use of diverse species combinations, so there is no plausible justification to avoid using high diversity of native species (Brancalion et al., 2010), as long as there is an adequate supply chain of native tree seedlings grown in nurseries.

3. ENSURING THE GENETIC QUALITY OF FRM

Once the species combination to be planted in a given area has been decided upon, information is provided on recommended (mixes) of appropriate sources of FRM. The origin and genetic quality of FRM is positively related not only to the survival, growth, productivity and adaptive capacity of tree populations (Reed & Frankham, 2003; Schaberg et al., 2008; Reynolds et al., 2012), but also to wider ecosystem functioning and resilience (Gregorius, 1996; Reusch et al., 2005; Whitham et al., 2006; Bailey, 2011) which is increasingly important in light of climate change (Sgrò et al 2011; Bozzano et al., 2014; Havens et al., 2015). In a meta-analysis of almost 250 plant species reintroductions worldwide, Godefroid et al (2011) found that when restoration practitioners had some knowledge of the genetic variation of the target species this significantly enhanced the survival rate from the first year after reintroduction, and this difference increased over time.

Two main considerations in the selection of germplasm are crucial to avoid problems and bolster the adaptive potential of planted forests. FRM should be (1) well-matched to the (present and expected future) conditions of the planting site to ensure survival, growth and reproduction of planted trees and (2) genetically diverse enough to avoid adverse effects of inbreeding, provide sufficient building blocks for adaptation to changing conditions through natural selection, and enhance populations' resistance to acute and chronic stressors, such as pests and diseases, drought and other effects of progressive climate change (Thomas et al., 2014a). Inadequate attention to these considerations can result in different degrees of failure in restoration (Gregorio et al., 2016). High initial mortality is a type of failure that is often manifested early on and may still be 'fixed ' during the planting, maintenance or guarantee periods of restoration projects by replanting with quality FRM. However, most other types of failure are manifested on much longer time scales, often long after the monitoring phase has ended and project funds have dried up. One example is that trees do survive but show suboptimal or poor growth when not well adapted to site conditions, an outcome consistently demonstrated by provenance trials around the world (FAO, 2014). Another type of failure is delayed mortality, which may manifest itself only after certain exceptional events such as the strong winter of 1984/1985 in the Landes region of France which destroyed a 30,000 ha plantation of *Pinus pinaster* Aiton, established with non-frost-resistant material from the Iberian Peninsula (Timbal et al., 2005). A last example of failure is when there is a decrease in the quality and quantity of seed production in planted forests -a typical effect of inbreeding (Broadhurst et al 2008)- which may jeopardize the long term viability and resilience of plantations. For example, a comparison of self-pollinated and outcrossed offspring of Douglas-fir (*Pseudotsuga menziesii*), 33 years after seedling establishment showed that the survival of selfed trees was 61% lower than that of the outcrossed trees and that the diameter at breast height of selfed trees was 41% smaller than that of the outcrossed trees (for surviving trees) (White et al., 2007).

Good genetic quality of FRM can be achieved by application of seed collection protocols and adequate planning to identify the seed sources best matched to the conditions of the restoration site (Thomas et al., 2015). For ensuring genetic diversity in planting stock, among a series of other considerations recently summarized by Basey et al. (2015), source populations should be large (at least 500 reproductively mature individuals), and seeds should be obtained from a high number (ideally 30-60, but minimally >15) of mother trees per population; ideally collecting and mixing seed from multiple suitable populations. It is important to note that quality seeds are unlikely to excessively raise the costs of restoration efforts. In a review based on 40-50 years of experiences with tree seed supply systems in the global South, Graudal & Lilleso (2007) estimated that (good quality) seed generally represents only 2-4% of total plantation establishment costs. Also the cost of producing quality seed, for example harvested from a minimum of 40 mother trees as compared to random collection from a few trees, is for most species, less than 5% per unit of seed collected (Graudal and Lilleso 2007). When this is compared with the opportunity costs associated with failed plantings, the cost is small indeed. In Atlantic Forest regions, many of the native tree nurseries work collaboratively and swap their material so they have diverse genotypes represented in their nursery stock (Robin Chazdon, pers. comm.).

To ensure suitability of planting material (Figure 1, section 3), identification and selection of FRM should ideally be guided by the strength of the interaction between genotype performance and current and future environmental conditions (genotype-by-environment, GXE interactions), which are studied using multi-location progeny or provenance trials and climate modeling, respectively (Sgrò et al., 2011; Breed et al., 2013). However provenance and progeny trials of native species in tropical dry forest conditions currently either do not exist in Colombia, or are not yet mature enough to guide decision making. Therefore, recommendations for seed sourcing in our approach are based on a combination of available genetic data and ecogeographic assessments. Neutral genetic characterization data of a number of model species' populations at representative sites across Colombian tropical dry forest remnants are used to identify areas that are relatively genetically homogenous which, in combination with an ecogeographical analysis, is used to construct seed transfer zones (Azpilicueta et al., 2013, Thomas et al. 2017). Seed transfer zones are geographical areas within which plant materials can be expected to be moved freely with little disruption of genetic patterns or loss of local adaptation.

It has been shown that (i) ecogeographical boundaries can be useful proxies for delineating seed transfer zones (Miller et al., 2011; Potter & Hargrove, 2012), and (ii) that genetic studies in model species can provide useful resources to infer seed source guidelines from life history properties for species with no population genetic knowledge (Williams et al., 2014). Accordingly, we constructed seed zones for species lacking genetic data through a combination of their ecogeographic distribution profile and some of their life history traits, notably those related to mating system which have been shown to correlate with patterns in neutral genetic diversity (Duminil et al., 2007). We acknowledge that delineating seed transfer zones based on neutral marker data is not ideal since neutral and adaptive genetic diversity are generally not ecologically equivalent measures of intraspecific variation (Whitlock, 2014), and neutral molecular markers may or may not reflect the same genetic patterns as traits under natural selection (Mijangos et al., 2015). Therefore, this approach has to be considered as a due diligence approach, given the absence of reliable GxE data for most if not all tree species for Colombian TDF.

Climate change will increasingly affect seed sourcing strategies (Havens et al., 2015). For example if temperature is expected to increase by 2°C at a given restoration site, it may be wise to use at least some FRM from populations of a target species which presently already grow under hotter conditions. A growing number of studies recommend the use of seed from mixed sources, in different compositions to anticipate the potential impacts of climate change (Broadhurst et al., 2008; Sgro et al., 2011; Breed et al., 2013; Prober et al., 2015). We use a decision tree which builds on those developed by Breed et al. (2013) and Byrne et al. (2011) to select the most appropriate seed sourcing approach, depending on the evidence and confidence limits surrounding climate distribution modeling, and the knowledge of population genetic and/or environmental differences between populations. For identifying TDF sites where current environmental conditions are likely to be similar to those under future climate scenarios at a given restoration site, we applied the Ecogeographical Land Characterization (ELC) maps approach (Parra-Quijano et al., 2012, 2014). ELC maps identify zones with similar abiotic growth conditions based on selected variables grouped in bioclimatic, edaphic and geophysic components. ELC maps can be used as proxies for delineating seed zones and can be projected to future climate conditions. For Colombian TDF seed zones, we created an ELC map under present climate conditions covering the current TDF remnants using non-collinear abiotic variables such as rainfall during the driest month, average daytime temperature range, soil pH and cation exchange capacity, terrain slope, sunshine, among others. This ELC map was projected to future climate scenarios (representative concentration pathways RCPs 4.5 and 8.5) using a Random Forest model. Joint interpretation of current and future ELC maps allows identifying the current location seed zones that are expected to appear at a given restoration site in the future.

The combined outcome of all the above analyses result in recommendations of most suitable seed sources and mixes thereof for a given restoration site and tree species. Different options are always provided to enhance the convenience of actually obtaining FRM in sufficient quantities within determined periods of time. Availability of seed is a constraining factor in many restoration endeavors around the world, and this is no different for Colombian TDF, a situation which is very likely to increase as the demand for restoration will continue to grow. To alleviate this situation we are compiling a list of contact details of land owners, indigenous and local communities, individuals or institutions such as arboreta, interested in contributing to providing seeds from TDF forest patches under their control. We plan to make contact details of seed providers publicly available to potential buyers.

Seed provision can be a profitable business in Colombia, where one kilogram of seeds of certain tree species such as Colombian mahogany (*Cariniana pyriformis*) can be worth more than twice a monthly wage. As people in rural areas often do not earn even the minimum wage, such amounts can be attractive. For private landowners, seed provision can be considered to be a type of payment for ecosystem services and hence can serve as an incentive to continue to conserve TDF patches for the seeds they produce. Experiences from the Brazilian Atlantic Forest restoration pact have shown that diversified strategies for obtaining planting stock are important to guarantee seed availability (Brancalion et al., 2012a) and that harvesting of FRM can be a good avenue for generating income and jobs in rural contexts (Brancalion et al., 2012b). However it is important that seed providers are trained in proper collection of FRM so it adequately captures the diversity of local tree populations (Basey et al., 2015). In the longer term a certification system for seed providers may be developed.

4. CONCLUSIONS AND RECOMMENDATIONS

Today, many if not most restoration projects in Colombia and beyond are opportunistic in the way they select and collect FRM, using material that is easily available, but often of poor quality, putting at risk long-term success (Jalonen et al. in press). Use of inadequate FRM may be even more likely as a consequence of limited restoration experience of the many new actors emerging in response to the enormous restoration goals in Colombia and worldwide. Policy has an important role in avoiding these risks. Decision makers first need to acknowledge that the targets in restoration projects are not only quantitative but also qualitative, meaning that adequate attention needs to be given to the identity and genetic quality of FRM. This was recognized by the 12th Conference of the Parties to the United Nations Convention on Biological Diversity, which, in decision XII/19, indent 4(h), called for due attention to genetic diversity and the use of native species in ecosystem restoration (http://www.cbd.int/doc/decisions/cop-12/cop-12-dec-19-en.pdf) (2014). The implementation of this decision will require political commitment to create demand for good quality seeds of native species through regulatory frameworks and resource allocations. As most restoration practitioners lack the capacity to plan adequately for the selection of species and seed sources that best respond to the restoration goals, while enhancing resilience against climate change and other stress factors, the development and use of user-friendly knowledge-based tools and protocols such as the one we have outlined here (www.restool.org) should be promoted. Such tools and protocols can then be used by governments, donors or implementers of restoration projects to ensure due diligence is applied in the selection of appropriate species and seed sources.

However, as these tools and protocols make extensive use of modeling, which have inherent uncertainties; they have to be complemented with robust field experimentation. The time is now for Colombia and other countries, particularly in the tropics, to invest in the establishment of provenance and progeny trails, arboreta and demonstration plantings with native species across different environmental gradients, as such trials generate the most reliable data on site adaptability and how this may change as a consequence of global warming. It will be critical to apply adaptive management and learn from mistakes and failures and continuously integrate new knowledge in decision–making as it becomes available. Countries also need to invest more in the establishment of functional seed distribution systems at different scales, to ensure the availability of appropriate FRM at any given restoration site (Atkinson et al. 2017). This includes diversifying seed supply by involving stakeholders at different levels of society, including small scale farmers, private land owners, indigenous and local communities, and protected areas. Ensuring the quality of FRM harvested by these actors will require capacity strengthening and possibly the development of certification schemes.

ACKNOWLEDGEMENTS

The authors wish to thank Ecopetrol, Empresas Públicas de Medellín, the government of Antioquia, Colombia, the Forest Ecosystem Restoration Initiative (FERI), the CGIAR Fund Donors (http://www.cgiar.org/who-we-are/cgiar-fund/fund-donors-2) and the CGIAR Research Program on Forests, Trees and Agroforestry for financial support. We are grateful to Robin Chazdon and Holm Tiessen for helpful comments on a previous version of this chapter.

REFERENCES

Aguilar M., Sierra J., Ramirez W., Vargas O., Calle Z., Vargas W., Murcia C., Aronson J., & Barrera Cataño J.I. (2015) Toward a post-conflict Colombia: restoring to the future. *Restoration Ecology*, **23**, 4–6.

Aronson J. & Alexander S. (2013) Ecosystem Restoration is Now a Global Priority: Time to Roll up our Sleeves. *Restoration Ecology*, **21**, 293–296.

Atkinson R., Thomas E., Cornelius J., Zamora R. & M. Franco (2017) Fit for purpose seed supply systems for the implementation of landscape restoration under Initiative 20x20: An analysis of national seed systems in Mexico, Guatemala, Costa Rica, Colombia, Peru, Chile and Argentina. World Resources Institute, Bioversity International, ICRAF

Azpilicueta M.M., Gallo L.A., Van Zonneveld M., Thomas E., Moreno C., & Marchelli P. (2013) Management of Nothofagus genetic resources: Definition of genetic zones based on a combination of nuclear and chloroplast marker data. *Forest Ecology and Management*, **302**, 414–424.

Bailey J.K. (2011) From genes to ecosystems: a genetic basis to ecosystem services. *Population Ecology*, **53**, 47–52.

Basey A.C., Fant J.B., & Kramer A.T. (2015) Producing native plant materials for restoration: 10 rules to collect and maintain genetic diversity. *Native Plants Journal*, **16**, 37–53.

De Bello F., Lavorel S., Díaz S., Harrington R., Cornelissen J.H.C., Bardgett R.D., Berg M.P., Cipriotti P., Feld C.K., Hering D., da Silva P.M., Potts S.G., Sandin L., Sousa J.P., Storkey J., Wardle D. a., & Harrison P. a. (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, **19**, 2873–2893.

Bozzano M., Jalonen R., Thomas E., Boshier D., Gallo L., Cavers S., Bordács S., Smith P., & Loo J. (2014) *Genetic considerations in ecosystem restoration using native tree species. State of the World's Forest Genetic Resources – Thematic Study.* FAO and Bioversity International, Rome.

Brancalion P.H.S., Rodrigues R.R., Gandolfi S., Kageyama P.Y., Nave A.G., Gandara F.B., Barbosa L.M., & Tabarelli M. (2010) Instrumentos legais podem contribuir para a restauração de florestas tropicais biodiversas. *Revista Árvore*, **34**, 455–470.

Brancalion P.H.S., Viani R. a G., Aronson J., Rodrigues R.R., & Nave A.G. (2012a) Improving Planting Stocks for the Brazilian Atlantic Forest Restoration through Community-Based Seed Harvesting Strategies. *Restoration Ecology*, **20**, 704–711.

Brancalion P.H.S., Viani R. a G., Strassburg B.B.N., & Rodrigues R.R. (2012b) Finding the money for tropical forest restoration. *Unasylva*, **63**, 41–50.

Breed M.F., Stead M.G., Ottewell K.M., Gardner M.G., & Lowe A.J. (2013) Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conservation Genetics*, **14**, 1–10.

Broadhurst L.M., Lowe A., Coates D.J., Cunningham S. a., McDonald M., Vesk P. a., & Yates C. (2008) Seed supply for broadscale restoration: maximizing evolutionary potential. *Evolutionary Applications*, **1**, 587–597.

Byrne M., Stone L., & Millar M. a. (2011) Assessing genetic risk in revegetation. *Journal of Applied Ecology*, **48**, 1365–1373.

Clark D.L., Wilson M., Roberts R., Dunwiddie P.W., Stanley A., & Kaye T.N. (2012) Plant traits - a tool for restoration? *Applied Vegetation Science*, **15**, 449–458.

Díaz S. & Cabido M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, **16**, 646–655.

Duminil J., Fineschi S., Hampe A., Jordano P., Salvini D., Vendramin G.G., & Petit R.J. (2007) Can population genetic structure be predicted from life-history traits? *The American naturalist*, **169**, 662–672.

Etter A., McAlpine C., & Possingham H. (2008) Historical Patterns and Drivers of Landscape Change in Colombia Since 1500: A Regionalized Spatial Approach. *Annals of the Association of American Geographers*, **98**, 2–23.

FAO (2014) *Report on the State of the World's Forest Genetic Resources.* United Nations Food and Agriculture Organization, Rome, Italy.

Funk J.L., Cleland E.E., Suding K.N., & Zavaleta E.S. (2008) Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology and Evolution*, **23**, 695–703.

García H., Corzo G., Isaacs P., & Etter A. (2014) Distribución y estado actual de los remanentes del bioia: insumos para su gestiónma de bosque seco tropical en Colomb. *En Bosque seco tropical en Colombia* (ed. by C. Pizano and H. García), Instituto de Investigación de recursos Biológicos Alexander von Humboldt, Bogota D.C. Colombia.

Godefroid S., Piazza C., Rossi G., Buord S., Stevens A.-D., Aguraiuja R., Cowell C., Weekley C.W., Vogg G., Iriondo J.M., Johnson I., Dixon B., Gordon D., Magnanon S., Valentin B., Bjureke K., Koopman R., Vicens M., Virevaire M., & Vanderborght T. (2011) How successful are plant species reintroductions? *Biological Conservation*, **144**, 672–682.

Graff P. & McIntyre S. (2014) Using ecological attributes as criteria for the selection of plant species under three restoration scenarios. *Austral Ecology*, **39**, 907–917.

Graudal L. & Lilleso J. (2007) *Experiences and Future Prospects for Tree Seed Supply in Agricultural Development Support Working Paper 2007.*

Gregorio N., Herbohn J., Harrison S., Pasa A., & Ferraren A. (2016) Regulating the Quality of Seedlings for Forest Restoration: Lessons from the National Greening Program in the Philippines. *Small-scale Forestry*, 1–20.

Gregorius H. (1996) The contribution of the genetics of populations to ecosystem stability. *Silvae Genetica*, **45**, 267–271.

Havens K., Vitt P., Still S., Kramer A.T., Fant J.B., & Schatz K. (2015) Seed Sourcing for Restoration in an Era of Climate Change. *Natural Areas Journal*, **35**, 122–133.

Jalonen, R., Valette, M., Boshier, D., Duminil, J., Thomas, E. 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 (in press)

Kramer U. (2010) Metal hyperaccumulation in plants. *Annual Review of Plant Biology*, **61**, 517–534.

Laestadius L., Maginnis S., Minnemeyer S., Potapov P., Saint-Laurent C., & Sizer N. (2012) Mapping opportunities for forest landscape restoration. *Unasylva*, **62**, 47–48.

Lavorel S. & Garnier E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: *Functional Ecology*, **16**, 545–556.

Loreau M. & Hector A. (2001) Partitioning selection and complementarity in biodiversity experiments. Nature 412: 72–76.

MADS (Ministerio de Ambiente y Desarrollo Sostenible de Colombia) (2012) Manual para la Asignación de Compensaciones por Pérdida de Biodiversidad. .

Mijangos J.L., Pacioni C., Spencer P.B.S., & Craig M.D. (2015) Contribution of genetics to ecological restoration. *Molecular Ecology*, **24**, 22–37.

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**, 268–276.

Moscoso Higuita L. (2005) *Reforestation: A Natural Process.* Editorial Colina, Medellín, Colombia.

Ostertag R., Warman L., Cordell S., & Vitousek P.M. (2015) Using plant functional traits to restore Hawaiian rainforest. *Journal of Applied Ecology*, 52:805-809.

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**, 205–217.

Parra-Quijano M., Torres E., Iriondo J.M., & López F. (2014) *CAPFITOGEN Tools. Programme to Strengthen National Plant Genetic Resource Capacities in Latin America. Version 1.2.* FAO, Rome, Italy.

Pizano C. & García H. (2014) En Bosque seco tropical en Colombia. Instituto de Investigación de recursos Biológicos Alexander von Humboldt, Bogota D.C. Colombia.

Pizano C., González-M. R., Gonzáles M.F., Castro-Lima F., Rodríguez N., Idárraga-Piedrahíta A., Vargas W., Vergara-Varela H., Castaño-Naranjo A., Devia W., Rojas A., Cuadros H., & Lázaro Toro J. (2014) Las plantas de los bosques secos de Colombia. *En Bosque seco tropical en Colombia* (ed. by C. Pizano and H. García), Instituto de Investigación de recursos Biológicos Alexander von Humboldt, Bogota D.C. Colombia.

Potter K.M. & Hargrove W.W. (2012) Determining suitable locations for seed transfer under climate change: A global quantitative method. *New Forests*, **43**, 581–599.

Prober S.M., Byrne M., McLean E.H., Steane D. a., Potts B.M., Vaillancourt R.E., & Stock W.D. (2015) Climate-adjusted provenancing: a strategy for climate-resilient ecological restoration. *Frontiers in Ecology and Evolution*, **3**: 65.

Reed D.H. & Frankham R. (2003) Correlation between fitness and genetic diversity. *Conservation Biology*, **17**, 230–237.

Reusch T., Ehler A., Hammerli A., & Worm B. (2005) Ecosystem recovery after climatic extremes enhanced by genetic diversity. *Proceedings of the National Academy of Sciences USA*, **102**, 2826–2831.

Reynolds L.K., McGlathery K.J., & Waycott M. (2012) Genetic diversity enhances restoration success by augmenting ecosystem services. *PLoS ONE*, **7**, 1–7.

Schaberg P., DeHayes D., Hawley G., & Nijensohn S. (2008) Anthropogenic alterations of genetic diversity within tree populations: Implications for forest ecosystem resilience. *Forest Ecology and Management*, **256**, 855–862.

Sgro C.M., Lowe A.J., & Hoffmann A.A. (2011) Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications*, **4**, 326–337.

Stocker T.F., D. Qin G.-K., Plattner L.V., Alexander S.K., Allen N.L., Bindoff F.-M., Bréon J. a., Church U., Cubasch S., Emori P., Forster P., Friedlingstein N., Gillett J.M., Gregory D.L., Hartmann E., Jansen B., Kirtman R., Knutti K., Krishna Kumar P., Lemke J., Marotzke V., Masson-Delmotte G. a., Meehl I.I., Mokhov S., Piao V., Ramaswamy D., Randall M., Rhein M., Rojas C., Sabine D., Shindell L.D., Talley D.G., & Xie V. and S.-P. (2013) Technical Summary.

Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (ed. by T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P.M. Midgley), pp. 33–115. Cambridge University Press, Cambridge United Kingdom and New York, NY, USA.

Suding K.N., Lavorel S., Chapin F.S., Cornelissen J.H.C., Díaz S., Garnier E., Goldberg D., Hooper D.U., Jackson S.T., & Navas M.L. (2008) Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*, **14**, 1125–1140.

Thomas E. (2014) Gold rush: forest devastated by mining is reborn. *Nature*, **511**, 155.

Thomas E., Jalonen R., Loo J., Boshier D., Gallo L., Cavers S., Bordács S., Smith P., & Bozzano M. (2014a) Genetic considerations in ecosystem restoration using native tree species. *Forest Ecology and Management*, **333**, 66–75.

Thomas, E., Gil Tobón, C., Gutierrez, J.P., Alcazar Caicedo, C., Moscoso Higuita, L.G., Becerra, L.A., Loo, J., Gonzales, M.A. (2017) Genetic diversity of Enterolobium cyclocarpum in Colombian seasonally dry tropical forest: implications for conservation and restoration. Biodiversity & Conservation 26, 825–842.

Thomas E., Alcázar Caicedo C., Loo J., & Kindt R. (2014b) The distribution of the Brazil nut (Bertholletia excelsa) through time: from range contraction in glacial refugia, over human-mediated expansion, to anthropogenic climate change. *Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais*, **9**, 267–291.

Thomas E., Jalonen R., Loo J., & Bozzano M. (2015) Avoiding failure in forest restoration: the importance of genetically diverse and site-matched germplasm. *Unasylva*, 245:29-36

White T.W., Adams W.T., & Neale D.B. (2007) *Forest Genetics.* CAB International 2007,

Whitham T.G., Bailey J.K., Schweitzer J. a, Shuster S.M., Bangert R.K., LeRoy C.J., Lonsdorf E. V, Allan G.J., DiFazio S.P., Potts B.M., Fischer D.G., Gehring C. a, Lindroth R.L., Marks J.C., Hart S.C., Wimp G.M., & Wooley S.C. (2006) A framework for community and ecosystem genetics: from genes to ecosystems. *Nature reviews. Genetics*, **7**, 510–523.

Whitlock R. (2014) Relationships between adaptive and neutral genetic diversity and ecological structure and functioning: A meta-analysis. *Journal of Ecology*, **102**, 857–872.

Williams A. V., Nevill P.G., & Krauss S.L. (2014) Next generation restoration genetics: Applications and opportunities. *Trends in Plant Science*, **19**, 529–537.