Species diversity in restoration plantings: Important factors for increasing the diversity of threatened tree species in the restoration of the Araucaria forest ecosystem

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ABSTRACT

The Araucaria forest ecosystem in southern Brazil is highly threatened: less than one percent of the original forest remains, and what is left is a fragmented agro-mosaic of mostly early-to-late secondary forest patches among high-yield agriculture and timber monocultures. Forest restoration initiatives in this region aim to restore degraded areas, however the limited number of species used in restoration projects represents a missed opportunity for species-rich plantings. High diversity plantings represent a larger number of functional groups and provide a targeted conservation strategy for the high number of threatened species within this ecosystem. This study interviewed nurseries (Ns) and restoration practitioners (RPs) in Paraná and Santa Catarina states to identify what species are being cultivated and planted, and what factors are driving the species selection process. An average of 20 species were reportedly used in restoration plantings, most of which are common, widespread species. Baseline data confirms that Ns and RPs have disproportionately low occurrences of threatened species in their inventories and plantings, supporting findings from previous research. Questionnaire responses reveal that opportunities for seed acquisition are an extremely important factor in order for nurseries to increase their diversity of cultivated species. Results also suggest that facilitating species-rich plantings for restoration practitioners would only be feasible if it did not increase the time required to complete planting projects, as it would minimize their ability to keep costs low. This study proposes solutions for increasing the number of species used in restoration practice—such as developing a comprehensive species list, fostering knowledge-sharing between actors, creating seed sharing programs, and increasing coordination of planting projects. Long-term strategies involve complimenting traditional ex situ approaches with emerging inter-situ and quasi in situ conservation strategies which simultaneously provide long-term preservation of genetic diversity and increase seed production of target species.

1. Introduction

1.1. Restoration of degraded land and fragmented forests

Over 20% of forest and agricultural lands in Latin America are degraded: 300 million hectares of the region's forests are considered degraded, and about 350 million hectares are classified as deforested, leaving many remaining forests fragmented (Vergara et al., 2016). Small forest fragments tend to retain a degraded structure (Tabanez and Viana, 2000) as fragmentation promotes a decrease in species richness, a shift in the relative abundance of tree reproductive traits, and a reduction in the functional diversity of tree assemblages in fragmented landscapes (Girão et al., 2007). These effects drive fragments toward early-successional states (Pütz et al., 2011), leading to tree species impoverishment. Governments in Latin America and the Caribbean have committed to bringing 20 million hectares of degraded land into restoration by 2020 (WRI, 2017). In Brazil targets have been set to restore twelve million hectares of deforested and degraded forest land by 2030 through forest restoration initiatives (WRI, 2016), and forest restoration is mandatory under the Native Vegetation
Protection Law of Brazil (Law #12,651/2012). As a result there are a number of state, NGO, and corporate land restoration initiatives underway throughout the country (IUCN, 2016; AFRP, 2016). This level of restoration can provide myriad benefits to degraded land, such as restored biodiversity (including recovery of threatened species), increased ecological functioning, the supply of goods and ecological services, and the amelioration of rural poverty (Lamb et al., 2005).

Land can be restored passively or actively. Passive restoration is the spontaneous recovery of native tree species, whereas active restoration requires planting nursery-grown seedlings, direct seeding, or mimicking disturbance regimes to speed up recovery processes. Although passive regeneration has been demonstrated to promote richer regeneration than active restoration at a fraction of the cost, it is not more effective in highly fragmented areas where population levels are low and species rich communities cannot be naturally recruited (Crouzeilles et al., 2017). Because active restoration is most appropriate for fragmented forests, this paper is limited to the role of nursery-grown seedlings in restoration plantings.

1.2. Species selection in restoration interventions

There are differing recommendations for the ideal number of native species to be included in restoration plantings, each of which depend on particular restoration objectives. The “Framework Species Approach” recommends 20 to 30 species (Goossem and Tucker, 1995). However, high-diversity plantings, defined by 80 to 90 species per hectare, are preferable to lower-diversity plantings as this number of species represents multiple functional groups that a smaller number of common and fast-growing species lacks (Rodrigues et al., 2009). When restoration includes a limited set of 20 to 30 taxa, the “restored” area cannot achieve maximal functionality; it cannot recruit threatened species under pressures such as lack of seed flow from neighboring locations, small population sizes, competition, and encroachment (Volis, 2016b). Conversely, the more threatened species included, the more representation for taxa with narrow regeneration niches and limited dispersal abilities (Volis, 2016b).

The delivery of high-diversity plantings is a challenge within the restoration industry, as the instability of native species markets and problems with the commercialization of native seedlings usually result in species bottlenecks (Bozzano et al., 2014; Silva et al., 2014). In Mexico 60 to 80 species have been demonstrated to be a financially feasible target number, but due to constraints within the market only 20 to 30 are typically used (Arroyo-Rodríguez et al., 2009).

It is valuable to include threatened species in high-diversity plantings, as they are exceedingly vulnerable in fragmented landscapes. Threatened populations are expected to continue decreasing due to time-lag biological responses even if no further degradation occurs (Metzger et al., 2009), compounded with bottlenecks in genetic diversity (Sork and Smouse, 2006). Furthermore, permanent distortions of species composition in favor of abundant dominant or dispersal-efficient subordinate species in fragmented landscapes makes rare and threatened species disproportionately vulnerable to extinction due to their limited immigration and colonization abilities (Maina and Howe, 2000; Tabarelli et al., 2005). Given the increased vulnerability of rare and threatened species in fragmented landscapes, therefore, their inclusion is an essential strategy to support their in situ conservation, which is a key goal in ongoing restoration projects in the Latin America region (Gill et al., 2017).

1.3. Constraints on species selection

Although high-diversity plantings are demonstrably more successful in terms of maximizing representation of functional groups and therefore ecosystem function, there are various practicalities imposing restraints on the ability of restoration actors to use a large number of species—including threatened species—in their plantings. Restoration actors attempting to balance species richness goals with their available resources must consider a multitude of factors in their species selection processes. The scope of this paper focuses on two primary actors in the restoration supply chain: nurseries who grow seedlings for restoration projects, and restoration practitioners who purchase seedlings from nurseries in order to carry out restoration plantings.

Nurseries encounter seed sourcing, collection, production, and storage of species as significant challenges to their use (Jalonen et al., 2017; Ladouceur et al., 2017), as well as adequate information on a wide range of species, preventing their ubiquity in plantings (Hoffmann et al., 2015). Nurseries are restricted by their ability to travel to seed sources and the technical feasibilities of wild seed collection in adequate quantities. Specific barriers include limited number of individuals and populations, difficulty and cost to access these populations, in addition to narrow collection windows, seed crops of mixed maturity, and atypical germination patterns (Broadhurst et al., 2016; Hoffmann et al., 2015). Currently native seed collection is forbidden in Protected Areas, which limits the inclusion of species with higher conservation value in restoration projects, especially in biomes with very low forest cover remaining such as the Atlantic Forest (Silva et al., 2016). Further restraints include low market prices for seedlings, which results in lack of motivation for nurseries to diversify their stock, and relationships with restoration practitioners who request a limited set of species (Jalonen et al., 2017; Volis, 2016a).

Restoration practitioners—those who purchase seedlings from nurseries—must choose species with ecological properties advantageous to plantings, such as high survival and growth rates in degraded sites, dense crowns that shade out herbaceous weeds, provision of resources that attract seed dispersers at early restoration stages, and natural regeneration capacity (Blakesley et al., 2002; Lindell et al., 2013; dos Santos et al., 2008). Restoration practitioners tend to use common and widespread species because they are ubiquitous in nurseries and have high success rates once planted (Aronson et al., 2011). Although the selection of a limited set of species produces successful plantings, it can lead to the homogenization of restored areas with few, widespread species dominating the landscape (Silva et al., 2016).

Given these competing considerations, diversity is seldom prioritized and typically only common or commercially important species are cultivated in large numbers and used for plantings (Jalonen et al., 2017). This leads to a species bias (Broadhurst et al., 2016), in which a few core species that can be reliably and readily sourced, easily stored and germinated are selected by nurseries, and these same reliable species are then purchased by practitioners. Biased selections deliver cost-effective outcomes with low risk to both nurseries and practitioners, but they represent only a fraction of species required to reconstruct diverse and resilient restoration outcomes (Volis, 2016b).

1.4. Restoration of the Araucaria forest

The subtropical Araucaria forest ecosystem in Brazil is a unique case for restoration as so little remains: less than 0.8% of the
original forest is extant in advanced successional stages, none of which is considered primary forest (Castella and Brittez, 2004). It is a subregion of the Atlantic Forest biome—a global biodiversity hot-spot (Myers et al., 2000)—and hosts 352 known tree species (Leite and Klein, 1999). There are currently 71 taxa classified as threatened (39) and rare (32) (Appendix A), which comprises 20% of all taxa in this ecosystem.

The original extent of the Araucaria forest is an estimated 25,379,300 ha (Ribeiro et al., 2009), yet historic timber exploitation and intensive agriculture has led to large-scale loss of forest habitat. Today the landscape is an environmental agro-mosaic with small patches of edge-affected Araucaria forest remnants <50 ha (Ranta et al., 1998; Gascon et al., 2000; Ribeiro et al., 2009), early-to-late secondary forest patches recovering from cropland or pasture abandonment (Tabarelli et al., 2010), high-yield agriculture (Fonesca et al., 2009), and ecologically-managed monocultures of Pinus and Eucalyptus timber plantations (Carlos et al., 2009) which have been steadily expanding in the last three decades (Fundação, 2001; Baptista and Rudel, 2006).

As the Araucaria forest is comprised of highly fragmented populations, actors must employ active restoration projects with a diverse species composition that promotes successful recruitment and establishment. Evidence of successful legislative high-diversity minimum requirements in Brazil exist: São Paulo state has the exemplary minimum requirement of 80 native species per hectare (Wuehrich, 2007). Unfortunately, the Brazilian states where the Araucaria forest ecosystem is located do not have such requirements. Although restoration projects in this region must legally be comprised of native species, there is no law specifying which or how many species should be used, and consequently a limited selection of approximately 10 to 20 common species are typically found in plantings (Pablo Hoffmann, 2016; pers. comm., 17 December). Silva et al. (2016) reports that most nurseries do not meet their production capacities, which represents a practical and currently missed opportunity to increase the native seed quantity and diversity within inventories.

1.5. Research objectives

In support of the in situ conservation of the Araucaria forest generally and threatened species specifically, targeted high-diversity restoration is essential. Given that commitments to restoration are presently underway, optimal strategies may be identified in order to use available resources for the deliberate protection of a wider number of species. To identify logistical opportunities for less species-biased choices, the present study examines drivers of the species-selection process for nurseries and restoration practitioners.

This study interviewed nurseries and restoration practitioner organizations working in the Araucaria forest to (1) identify a baseline sample of what species are produced and planted in restoration projects; and (2) identify which factors are most important in governing species selection. Nurseries and restoration practitioners will hereafter be referred to as Ns and RPs, respectively.

2. Methods

2.1. Study area

The original extent of the Araucaria forest ranges from 53.95613°W to 48.22327°W (west to east), and from 23.56218°S to 29.74095°S (north to south) throughout Paraná, Santa Catarina, and Rio Grande do Sul states in southern Brazil. Interviews were conducted within the original Araucaria forest extent in Paraná and Santa Catarina (Fig. 1), however due to resource limitations interviews were not conducted in Rio Grande do Sul. According to the AFRP-identified land suitable for restoration (Calmon et al., 2011), Paraná is suitable for the largest area of restoration (2,455,537 ha), followed by Santa Catarina (1,402,183 ha) and Rio Grande do Sul (891,716 ha). Paraná state nurseries are also the main producers for restoration efforts in the Araucaria forest region (Martins et al., 2004), so interviews were prioritized for Paraná and subsequently Santa Catarina.

2.2. Interviews

Ns and RPs were identified from a combination of sources: Diagnosis of the Production of Native Forest Seedlings in Brazil (Silva et al., 2015); Embrapa, an agricultural research institution’s nursery list (Embrapa, 2017); the Brazilian Institute of Forestry nursery list (IBF, 2017); Environmental Institute of Paraná registered nursery list (IAP, 2017); contacts from previous nursery research from The Nature Conservancy; and Internet searches. Participants were selected by stratified random sampling method: nurseries were selected according to municipality and participants within each group were randomly selected and asked via telephone to participate in the study. Those who agreed were scheduled for an in-person interview. The sample represented a gradient of demographic variables such as size and public/private nurseries, and were relatively evenly distributed throughout the study area. RPs were not stratified by location because most had centrally located offices in Curitiba, Paraná’s capital city, although they coordinate plantings throughout the entire study area.

2.3. Data collection

2.3.1. Baseline data

Structured interviews (Neuman, 2014) were conducted in Portuguese from April to June 2017. The 36 interviews included 20 Ns (9 public, 11 private) and 16 RPs (11 private consultants, 4 NGOs, 1 government agency). N participants were nursery managers and RP participants were company owners, managers, or high-level staff involved in planning and coordinating restoration projects.

During each N interview, annual inventory lists were collected to ascertain species occurrence, as defined by which species were present/absent in any given nursery. Abundance, defined by the quantity of present species produced annually, was also recorded. The R interviews collected similar data, although occurrence is defined by which species were present/absent in any plantings of the past year, and abundance is defined by the quantity of each species planted annually. Species which were only present on one nursery or planting list were noted but excluded from further analysis, as the majority of species were singly occurring and would have skewed the results to disproportionately represent rarely occurring species as commonly present.

2.3.2. Questionnaires

Separate structured questionnaires were given to Ns (Appendix B) and RPs (Appendix C) to assess the economic, technical, and institutional constraints on species selection. Questionnaires were composed of open-ended, multiple-choice, and Likert-scale response (Likert, 1932) questions. The N questionnaire was composed of 62 questions in the following categories: infrastructure, business objectives, seedling sale, technical knowledge, market and client needs, seed acquisition methods, fluctuations in

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1 This list is adapted from Hoffmann et al. (2015), but this paper advocates for many of the species’ threat statuses to be updated, given their observed rarity in the field. It is likely that in actuality their threat statuses are more severe.
nursery operational activity, regulations, inventory decision-making processes, and incentives for using threatened species. The RP questionnaire was composed of 64 questions in the following categories: project planning, business objectives, nursery selection, species selection, staffing, and the planting process.

3. Results

3.1. Baseline sample

Participant responses provided baseline data on how many species are present in N and RP inventories (Table 1). In total 139 native species were found to occur in two nurseries or more (Appendix D). Only 25 tree species occurred in nine (median occurrence) or more nurseries. In RP lists, 63 tree species occurred in two or more plantings (Appendix E), although only 18 species occurred in six plantings (median occurrence) or more. The mean number of occurring species (richness) is 34 in nurseries and 21.8 in RP planting lists.

Although 20% of Araucaria forest taxa are threatened, less than 20% of recorded occurrence and abundance are comprised of threatened species. Of the Ns and RPs which had high occurrences of threatened species (defined as > median occurrence), their inventories showed a significantly lower proportion of threatened species than one would expect to occur by chance (N: t (138) = 4.19, p < 0.001; RP: t (61) = 2.92, p < 0.005). Of the taxa commonly occurring in N and RP lists (>median frequency), only 4.6% (N) and 4.7% (RP) are threatened.

3.2. Questionnaire responses

3.2.1. Factors governing species selection in nurseries

N responses indicated that although 40% of nurseries purchase seeds and 15% farm seeds, 100% of nurseries participate in wild seed collection. This practice enables nurseries to acquire seeds for free and they are only limited by the resources (fuel, time, and staff labor) required for travel and seed collection. One hundred percent of Ns reported that on seed collection trips they do not target...
certain species but rather collect any seeds they happen across. Ninety percent of nurseries reported adding additional species to their inventory in the last year, the primary reason (55% of responses) being opportunistic: they simply found a new species' seeds in sufficient quantity.

Seedlings most commonly occurring in N inventories were common species easily available for seed collection. When asked which species were most easy and inexpensive to acquire, common species were most frequently reported, with the exception of *Araucaria angustifolia*, which is a flagship species and despite its threatened status is found in every nursery (and therefore is also easy and cheap to acquire). Conversely, when asked what are the most difficult and expensive species to acquire, mostly threatened species were cited (Table 2). “Sporadic seed availability,” “technically advanced seed collection requirements,” and “difficulty to access” were cited as primary reasons for difficulties collecting these species.

Nursery participants were asked to score a list of barriers that prevented them from increasing the number of threatened species in their inventory. The highest mean scores were “seeds too far away” (8/10), “difficult to find seeds” (8/10), and “not enough resources to acquire seeds” (7/10) (Fig. 2a). Customers wanting or not wanting the seeds was not highly scored (5.5/10). When N respondents were asked their reasons for the addition of a new species to their inventory, only 35% cite “customer request” as a reason. Seventy percent of nurseries would be willing to add threatened species to their inventory if clients would pay more, but only 25% believe they would. These scores indicate that nurseries do not consider customer demand as a high priority, and that it is not driving their species selection decision-making process.

### 3.2.2. Factors governing species selection for restoration practitioners

When RPs were asked to cite the greatest barriers to increasing the use of threatened species in their plantings, nurseries simply not carrying those species was the most cited reason (Fig. 2b). When asked to select only one driving reason that would limit their use of threatened species, the majority (62.5% of responses) cited an absence of those species in nursery inventories; the next most cited reason was price (18.75%). Nurseries, regardless of customer demand, are simply not carrying these species, thus eliminating the option for RPs to include them in their plantings.

Another factor which proved important to the decision-making process was willingness of RPs to be flexible with their planting list. Respondents were more likely to adapt their planting list to match what a nursery had on hand than search for another nursery with a more species-diverse stock of seedlings. Of RPs, 81.25% reportedly come to nurseries with pre-defined lists of species, although 75% of RPs were willing to shorten their list if the nurseries did not carry all the species on it. N responses substantiate the RP claims: when a client discusses a species list with a nursery, 30% of Ns report that the clients request specific species, while 70% say their clients are willing to purchase whatever the nursery has in its inventory. Taken together, most RPs are more likely to change their lists than spend time contacting and liaising with multiple nurseries.

### Table 1

Summary of native species occurring in Nursery (N) annual inventories and Restoration Practitioner (RP) annual planting lists. Data collected April—June 2017 in Paraná and Santa Catarina, Brazil.

| Category               | Species                          | Ranking | Threat Status                              |
|------------------------|----------------------------------|---------|-------------------------------------------|
| Easy to Acquire        | *Araucaria angustifolia*         | 1       | Near Threatened<sup>a</sup>, Endangered<sup>b</sup>, Critically Endangered<sup>c</sup> |
| Inexpensive to Acquire | *Psidium cattleianum*            | 2       | –                                          |
| Inexpensive to Acquire | *Eugenia uniflora*               | 3       | –                                          |
| Inexpensive to Acquire | *Eugenia involucrata*            | 2       | Rare<sup>c</sup>                           |
| Inexpensive to Acquire | *Psidium cattleianum*            | 2       | –                                          |
| Difficult to Acquire   | *Ocotea odorifera*               | 1       | Near Threatened<sup>a</sup>, Endangered<sup>d</sup>, Critically Endangered<sup>d</sup> |
| Difficult to Acquire   | *Ocotea porosa*                  | 2       | Near Threatened<sup>d</sup>, Endangered<sup>d</sup>, Vulnerable<sup>d</sup> |
| Difficult to Acquire   | *Caesalpinia echinata*           | 3       | Endangered<sup>d</sup>                     |
| Difficult to Acquire   | *Cedrella fissilis*              | 3       | Endangered<sup>d</sup>                     |
| Expensive to Acquire   | *Ocotea odorifera*               | 1       | Near Threatened<sup>d</sup>, Endangered<sup>d</sup>, Vulnerable<sup>d</sup> |
| Expensive to Acquire   | *Ocotea porosa*                  | 2       | Near Threatened<sup>d</sup>, Endangered<sup>d</sup>, Vulnerable<sup>d</sup> |
| Expensive to Acquire   | *Cedrella fissilis*              | 3       | Endangered<sup>d</sup>                     |
| Expensive to Acquire   | *Jacaranda pubera*               | 3       | –                                          |
| Expensive to Acquire   | *Caesalpinia echinata*           | 3       | Endangered<sup>d</sup>                     |

<sup>a</sup> SEMA (1995).
<sup>b</sup> MMA (2008).
<sup>c</sup> Hoffmann et al. (2015).
<sup>d</sup> IUCN (2013).
Rather than receiving an order with adequate time to grow the requested number of seedlings, nurseries are expected to have large quantities of seedlings in stock at all times, with little or no notice before making a potential sale. The mean advance notice a typical RP gives a nursery prior to transaction is 1.5 days. The mean time RPs plan a planting is 4.1 weeks. As plantings happen relatively quickly, the time it takes participants to find a suitable nursery carrying all the species on their original planting list would consume a considerable amount of their overall planning time, impacting their profit margin.

When asked to rate on a 1–10 scale the different considerations involved in selecting which nursery to purchase seedlings from, "timely delivery" and "price" were rated the most important reasons. When asked to choose one primary reason driving nursery selection, the majority of RPs selected price as the primary factor (43.75%). On average RPs rated 9.77/10 level of interest in increasing their use of threatened species, however because price and time are limiting factors, one can infer that despite a strong reported interest their decisions are ultimately governed by minimizing costs.

The mean number of species RPs used in plantings was 20.73, which is notable given in another question RPs reported a mean number of 30.1 species as "sufficient for a quality planting," and 73.5 species as an "ideal number for any quality planting." RPs, given their priorities of price and time, are on average knowingly planting fewer species than they consider sufficient or ideal for a quality planting (which supports the difficulties outlined by other authors (Rodrigues et al., 2009)).

4. Discussion

4.1. Seed availability

The Southeast region of Brazil has the greatest number of nurseries and produces the largest quantities of seedlings compared to other regions in Brazil, yet has the smallest variation in the number of species produced between nurseries (Silva et al., 2015). While nurseries across the region vary greatly in their capacity to produce a diverse range of native seedlings (Silva et al., 2016), the present study demonstrates that nurseries in the Araucaria forest region focus on a disproportionally low number of threatened species in occurrence (17.9% occurring in two nurseries, 5% occurring in 7 or more) and abundance (comprising 13.8% of total abundance). RPs have lower species occurrences in their plantings than the ideal recommended amount (80–90), instead planting on average 21 species, supporting previous findings which draw the same conclusions (Volis, 2016b; Aronson et al., 2011).

Although consumer demand did not emerge as a crucial driver of species selection for Ns, opportunities for seed acquisition were found to be extremely important. Ns cannot acquire more species without expending considerably more of their resources on accessing new seeds and cultivating them in large enough quantities for an RP to immediately purchase. RPs are unwilling to spend additional back-and-forth time with nurseries in order to request and secure a more species-rich planting, which in turn makes nurseries less likely to carry a wider variety of species in the future.

In both public and private nurseries, the two most highly reported factors impeding the increased use of threatened species are lack of resources and opportunity for seed acquisition. This is a common difficulty in other regions of Brazil (Branclillon et al., 2011) and countries in Europe (Bishoff et al., 2008). If nurseries, therefore, could acquire additional species’ seeds at no or minimal extra cost, which would not then be passed on to practitioners, one of the substantial hurdles would be eliminated which could spur increased adoption of threatened species for both N and RP actors.

4.2. Short-term actionable recommendations

As the existing restoration framework currently does not provide incentives to increase the number of species for Ns and RPs, actionable steps must be outlined to preferentially improve access to currently under-represented and threatened taxa. Results suggest that increasing seed availability is a most crucial factor governing the species selection decision-making process, and is...
therefore the first step toward increasing diversity in nurseries and subsequent restoration plantings. The following recommendations mirror similar recommendations put forth by other researchers in this field (Silva et al., 2016; Jalonen et al., 2017), and are geared toward increasing seed availability and improving the conditions which would enable actors to broaden the focus of seed collection and restoration efforts to include more (including threatened) species.

4.2.1. Comprehensive species list
The creation of a comprehensive list of species is crucial if restoration actors are to know what variety of species are available to them and appropriate for their site. Paraná-based NGO Sociedade Chaus provides such lists, grouped by region (http://www.societadechaus.org/floraparana). They include identifying photos and cultivation information for public use. Comprehensive lists such as these could also provide assessments of the state of wild seed supply for collection, information which would be useful to all nurseries who participate in wild seed collection.

4.2.2. Foster knowledge-sharing  
Adequate information about each species on a comprehensive list is necessary for actors to successfully use these species. Insufficient knowledge of threatened species’ reproductive biology, and lack of efficient propagation and planting methods are primary barriers for their use in restoration projects (Volis, 2016a). Some Araucaria forest species exhibit seasonal fluctuations in phenology, have low levels of fruit production, or produce a high proportion of non-viable seeds (due to maturation and predation complications), hence the timing and ease of seed collection remains a constant challenge (Hoffmann et al., 2015).

In addition to further empirical research on less-studied species, expanding and strengthening a network of stakeholders in public and private forums can provide opportunities for exchange of cultivation and planting knowledge. Policy regulations alone are not sufficient to meet restoration goals (Silva et al., 2016); they must be simultaneously approached from the stakeholder perspective as a sustainable and feasible economic activity (Brancalion et al., 2012). When stakeholders can develop their knowledge base and exchange success stories, confidence and perceived feasibility of adopting a wider variety of species increases. The stronger the network and exchange of knowledge, the more these networks can produce flexible approaches, increased competency of practitioners, and less risk in implementing new strategies (Nyoka et al., 2015).

4.2.3. Seed sharing program
A seed exchange program is an organized group of seed harvesters with training and coordination for native seed production which could distribute seeds throughout a network of nurseries interested in growing a wider range of threatened species. This solution has been piloted elsewhere in the Atlantic forest (São Paulo state), has proven to be an effective support of high-diversity reforestation initiatives (Brancalion et al., 2011), and such decentralization of seedling production has been recommended by leaders in community- and industry-based restoration communities (Merritt and Dixon, 2011; Nevill et al., 2016; Silva et al., 2016). Programs with collaborative participation between independent seed collectors, community-based organizations, and local seed exchange programs have been shown to yield increased restoration diversity—measured by number of species and seed lots—compared to relying on any one strategy alone (Brancalion et al., 2011).

Seed sharing programs which span over 100 km (long-distance germplasm exchange) are particularly advantageous, given that distance still falls within a species’ native range. Although local germplasm sourcing is important to maximize local adaptations in plant traits and avoid outbreeding depression (Mijnsbrugge et al., 2010; Edmands, 2006), doing so in highly fragmented landscapes produces poor restoration outcomes, so on balance actors should prioritize high quality and highly diverse seeds (Broadhurst et al., 2008; Bischoff et al., 2008). Mixing provenances of germplasm increases the genetic diversity of seed in addition to enhancing taxonomic diversity. Seeds of mixed provenances within a participating network result in enhanced seed quality (Brancalion et al., 2011) which is critical to successful restoration efforts. Enhanced seed quality reduces germination and cultivation risk for Ns, and reduces risk for RPs who have a vested interest in a high survival rate in their plantings. High seed quality also provides resilience of restored areas to climate change, now an important consideration in any restoration project (Jalonen et al., 2017). Moreover, seed sharing networks will positively feedback on comprehensive species lists, associated collective knowledge, and seed sources of local tree species.

4.2.4. Increased coordination of plantings
Increasingly linked stakeholder networks can also produce more coordinated plantings within the RP community. As Ns are encouraged to increase the variety of species available in their nurseries, RPs can likewise improve the degree to which they link their plantings to other plantings in the region. Three quarters of RPs reported mean planting areas of 5 ha or less, while three RPs reported plantings of 115, 200, and 300 ha, raising the mean planting area to 41.87 ha. Even the largest reported plantings (mean 268.9 ha) are still considered small in terms of forest fragments in the Atlantic forest, which are defined by Oliveira et al. (2008) as <300 ha and Ribeiro et al. (2009) as <100 ha. Given that restoration plantings in this region are at best restoring fragments, it is crucial to maximize restoration impact by coordinating plantings occurring in neighboring areas, ideally serving to link and bolster populations of newly added species.

Coordinated restoration efforts across the entire North American Great Lakes region have been shown to be nine times more cost-effective than individual local-scale planning (Neeson et al., 2015). Coordinated efforts also work in direct opposition to habitat fragmentation, one of the leading causes of declining biodiversity and ecosystem services (Fahrig, 2004). Although coordinated plantings at a landscape level have historically been a major challenge for this region (Rodrigues et al., 2009), they are critical to restoring land on a large enough scale to promote a diverse, healthy, ecologically functional ecosystem (Lopes et al., 2009).

Currently RP projects act in isolation of one another and are planting mostly common species which have reliable establishment success rates. Instead of asking individual RPs to add a large quantity of new species (high risk), RPs can coordinate their planting lists to each add a small quantity of new species (low risk), which cumulatively expands the richness of planted species in a given region. Coordination between RPs will serve as a decision-support tool for species selection (Beier et al., 2011), and will help actors identify linkage opportunities, which is currently not possible.

4.3. Long-term strategies
Wild seed collection requires ethical and genetic considerations, particularly when collecting threatened and rare species (Broadhurst et al., 2016). Seed collection of threatened species should be targeted and limited, where the fewest sufficient number of seeds should be collected under strict ecological criteria, in order to prevent
decimating any given population’s ability to sustain itself naturally. Extremely rare species or those having small isolated populations require expert and targeted intervention organized by appropriate conservation organizations, meeting minimum collection requirements before removing any seeds from the wild (Jalonen et al., 2017). The global assessment of forest genetic resources adopted by the FAO (2013) calls for policymakers to reinforce national seed programs to provide sufficient quantities of genetically appropriate seeds for restoration so as not to exhaust wild populations. Hence ex situ seed farming programs are an essential long-term component to the conservation of threatened species, as current and future demand for seeds exceed the volume that can be practically and economically sourced from the wild (Neill et al., 2016).

Intermediate approaches which combine and bridge in- and ex situ strategies exist as long-term methods that can be used for increasing species richness in restoration efforts (Volis, 2017). While botanical gardens and arboreta host small ex situ living collections, opportunities for inter-situ collections exist in areas such as abandoned agricultural lands. These designated areas can exist outside of the current species range but within the past range of a species (Burney and Burney, 2007), and can host a wider range of species in larger numbers than are typically possible in strictly ex situ situations (Volis, 2017). Inter-situ collections can be planted to simultaneously reintroduce a large number of threatened species and restore degraded lands, an ideal conservation solution for highly fragmented regions.

Quasi in situ (Volis and Blecher, 2010) collections are another solution appropriate for a highly fragmented region such as the Araucaria forest, defined as “living collections in protected areas under natural or semi-natural conditions, where site selection accounts for local adaptation, and focuses on preservation and production of plant material.” Planting threatened species outside their current natural range can be advantageous in light of anticipated range shifts due to climate change (Vitt et al., 2016; Butterfield et al., 2016), particularly when there are few alternatives as extant populations are so rare and isolated. This method would produce a large quantity of plant material, relieving pressure on nurseries to access and collect rare and threatened samples from the wilds.

Complementing the inter-situ method, the quasi in situ method focuses on preserving locally-adapted genetic variation and producing large quantities of seeds of species that present the greatest challenge in regional restoration projects. In Belgium, seed orchards propagating locally sourced planting stock have successfully demonstrated the ability to preserve local adaptations and a diverse range of native plants in highly fragmented areas (Vander Mijnbrugge, 2014). Even in extreme cases of critically endangered species of as few as 30 remaining individuals, seed orchards outside a species’ current natural range have been demonstrated to increase genetic diversity of future generations, while also creating more planting material ex situ without detracting from the existing population (Ducci, 2014). These newly emerging, adaptive methods are recommended as long-term strategies to increase the use of threatened species in restoration plantings in the Araucaria forest region.

4.4. Conclusion

Although this study is not exhaustive in sample size or potential decision-making factors to investigate, it provides a baseline sample of what species are commonly used in the restoration industry, and baseline information on N and RP attitudes over a large study area in the Araucaria forest. It provides evidence that some factors such as seed acquisition and financial risk are more important drivers of species selection than others, such as customer demand. Overcoming limitations at various stages of the restoration process will improve the likelihood of increased species use, including threatened species. A multifaceted approach would maximize the ability for restoration actors to increase species richness: (1) seed acquisition support enabling nurseries to carry more species in adequate quantities on hand; (2) increased knowledge of threatened species so restoration practitioners can make informed decisions on which species they can confidently add without depressing status quo survival rates; (3) increasing opportunities for Ns and RPs to create stakeholder networks where knowledge, seeds, and landscape-level plans can be shared between actors; and (4) use of long-term inter-situ and quasi in situ conservation strategies, which simultaneously provide long-term preservation of genetic diversity and increase seed production of target species. With a balance of practical considerations, it is possible for restoration plantings in the Araucaria forest region to be species-rich, representing an increased number of functional groups and targeted for the conservation of threatened species at risk of extinction.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.pld.2018.08.002.

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