

REVIEW

Conservation-oriented restoration – how to make it a success?

Sergei Volis

Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, China

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Plant conservation biology needs a new paradigm to stop ongoing environmental degradation and species loss. This paper provides detailed methodological guidelines for the conceptual integration of conservation biology and restoration ecology through “conservation-oriented restoration” as introduced in a companion paper. Based on the latest theoretical developments in community ecology and vast experience gained by researchers in restoration ecology and conservation biology, this paper provides recommendations, among others, for (i) identification of a reference ecosystem; (ii) making operational species lists for introduction; (iii) choosing optimal restoration in terms of planting design, plant number and density; (iv) collecting, storing and using seeds; and (v) addressing plant–animal interactions.

Keywords: ecosystem restoration; endangered plants; species recovery; plant conservation; conservation strategy; introduction; relocation

Introduction

The unprecedented rate and scale of destruction of original habitats by humans resulted in almost complete disappearance of such habitats in many countries. Consequently, many previously common species became rare and threatened. The remaining populations of threatened plant species often do not regenerate naturally because once-existing environmental conditions and biotic interactions have been altered. Those that do have recruitment usually exhibit a negative growth rate. The future of these populations in fragmented or degraded habitats can be described as “extinction debt”, when declining populations eventually go extinct, but with a time delay of different duration (Tilman et al. 1994). This time delay offers an opportunity to restore the populations’ habitat and thus to safeguard the persistence of species that are otherwise doomed to extinction. On the other hand, introduction into the habitats not only within but also outside the species’ historical range can prevent the species’ global extinction even if the local extinction debt is paid.

A conceptual integration of conservation biology and restoration ecology can be achieved through conservation-oriented restoration (Volis 2016). In this concept, large-scale restoration and assisted colonization are the complementary crucial components of the conservation of biodiversity allowing many threatened species to recover. Restoration ecology focusing on ecosystems, i.e. on

species composition, structure and processes, can help to identify and restore the environmental conditions needed to make a population viable. Assisted colonization – namely, introduction of threatened species into locations within their potential distribution range but with no historical records – can be a part of ecosystem restoration.

A preceding paper of this issue (Volis 2016) presents the concept and the major methodological guidelines. Here, a step-by-step description of these and other guidelines is provided (Table 1).

Use of reference in restoration

Traditionally, ecological restoration uses a reference – a set of conditions under which a restored ecosystem is likely to be functioning and self-sustaining. The reference conditions can be equated to the historical range of variability of natural conditions in ecosystem composition, structure, and function, and can be used for (i) evaluating changes in ecosystems; (ii) working out the management actions to bring the restored sites to the target (reference) state; and (iii) measuring the success of ecological restoration (Kaufmann et al. 1994; Christensen et al. 1996; Egan and Howell 2001; Holl and Cairns 2002; Wortley et al. 2013).

Re-establishing historic plant communities and natural disturbances as an achievable goal of ecological restoration and usage for this purpose of remnant populations

Table 1. Stages of conservation-oriented restoration with corresponding major issues and suitable for solving them methodology.

Stages	Issues	Methodology
(1) Restoration site	Prioritization	Ecological threshold, suitability for threatened species
(2) Reference conditions	Considering past, present and future conditions, search for alternative states	Ecological niche modeling, historical records, fossil data
(3) Choice of species	Number of species and their identity	Species abundance distribution, regional and local species pool, plant functional groups
(4) Material for planting	Seed collecting and storage Obtaining outplants	Restoration seed bank <i>Quasi in situ</i>
(5) Site preparation	Considering biotic interactions	Introduction of animals and facilitating plant species
(6) Planting design	Importance of spatial scale, heterogeneity and local extinction Number of plants introduced and planting density	Small-scale restoration, replicated multi-species experiments Considering Janzen–Connell effect, Allee effect, autotoxicity
(7) Management and observations	Monitoring, interventions	Population viability analysis

and communities as legitimate proxies has been questioned (Harris et al. 2006; Suding 2011), and led to an idea that we should focus instead on creating and managing “novel” ecosystems (Hobbs et al. 2006, 2009, 2013). The reasons include lack of clear picture of the particular historic conditions even in the case when detailed historical records exist (e.g. Chambers et al. 1999), the dynamic nature of these systems rarely having a single equilibrium state and trajectory, widespread introduction of exotic species, disruption of natural processes and many anticipated climate-change impacts (Hobbs and Harris 2001; Harris et al. 2006; Blois et al. 2013). Indeed, many plant communities are dynamic and the current remnants can be quite different from the communities that existed in the recent and more distant past. However, it was recognized a long time ago that “a single reference ecosystem generally is inadequate and inappropriate for evaluating the degree and effectiveness of restoration” with a recommendation to use “multiple reference sites that account for patch dynamics and physical site heterogeneity” (Clewell and Rieger 1997). A shift from the idea of self-replacing communities that reflect stages of succession toward the climax community to the concept of alternative meta-stable states into which a community can develop under the same environmental conditions (Hobbs and Norton 1996) does not negate the need for proxies in restoration programs. Extant, reconstructed from historical data or theoretically predicted reference conditions are vital to restoration as a baseline for recreating ecosystem function, structure and composition. Recognizing that a single solution does not exist or is inappropriate (White and Walker 1997; Holl and Cairns 2002; Balaguer et al. 2014), we should try to identify and target the alternative states as reference conditions (Hobbs and Norton 1996; Temperton et al. 2004) and compare the outcomes. Searching for alternative reference states should be based

on assembly rules theory of theoretical community ecology in which community assembly is deterministic in the composition of trait-based functional groups, but stochastic in terms of species composition. The functional groups fill the available niches created by the particular environmental conditions, while species compositions within functional groups are determined by the order of species arrival (also known as “priority effects”; Connell and Slatyer 1977). As a result, local biotic communities can enter alternative stable states even when they share the same species pool and the same environmental conditions (Connell and Slatyer 1977; Chase 2003; Beisner et al. 2003, Schröder et al. 2005). That assembly is a historically contingent process in which, under given environmental conditions, assemblages converge in species traits but diverge in species identities was demonstrated experimentally by Fukami et al. (2005). Fukami (2015) identified the conditions under which alternative stable states can be expected. They include factors that promote fast local population dynamics (small habitat patch size, low environmental variability and low predation), and a rich regional species pool with a choice of species for each functional type.

In cases where there are no extant habitats that could serve as reference ecosystems, a proxy to once-existing ecosystems may still be possible to find. Long-term data can help defining appropriate reference ecosystems. For example, the natural forests on black marls at the altitudinal belt between 600 and 1200 m do not currently exist in the entire Haute Province, France. However, a regional ecological survey and historical records allowed Vallauri et al. (2002) to identify oak *Quercus pubescens* as the dominant tree species in the pre-existing forests and to propose an appropriate intervention (thinning of introduced Austrian black pine) to promote establishment of native broad-leaf vegetation. Similarly, analysis of fossil

pollen, microscopic and macroscopic charcoal helped to determine the pre-anthropogenic vegetation and the disturbance regime by humans in the Apuseni Natural Park (Romania) during the last 5700 years, and to reveal an anthropogenic cause of a decline in abundance of a regionally endangered *Abies alba* (Feurdean and Willis 2008). Another example are rare and endangered plants of the group of “arctic-alpine” species of the Scottish Highlands, northern England and northern Wales that currently grow only in inaccessible cliff ledges. Pollen data provided evidence that during the Holocene these taxa were growing in an open, herb-rich vegetation at or above the tree limit, and, as a result of anthropogenic impact in the last two centuries, were replaced by grazing-tolerant vegetation and forced into locations inaccessible to sheep herbivory (Birks 1996). These and other examples (Muller et al. 2012; McCarroll et al. 2016; Natlandsmyr and Hjelle 2016) show high utility of paleoecological data for guiding conservation management through their ability to disentangle the roles of climate and human activities in long-term community changes.

Extant reference sites are often small-sized remnants of a natural habitat usually representing only a sample of its original variation in terms of environment, community composition and successional stage. The fact that available reference sites are just a subset of suitable for the species conditions, and the dynamic nature of many vegetation communities during the last 5000 years revealed by paleobotany, suggest that we should always look for alternative potential reference states for the target species.

The latter considerations justify introduction of the threatened species, as part of community restoration, into locations outside their historical range, especially if the latter is poorly documented or unknown. What particularly suits this purpose is an approach realigning biological communities to present and expected future conditions rather than confining species to their historical ranges (Millar 1998; Millar and Brubaker 2006), and a similar approach is the recently proposed pre-restoration concept (Butterfield et al. 2016). Realignment is based on the idea that compositions, structures and distributions of plant communities constantly shift over long timeframes due to changes in regional and global conditions, resulting in shifting, contracting and expanding historic ranges of species. Thus, by knowing a species’ pre-history and biological requirements, one can predict its suitable range of conditions in the present and future. A good example of how this approach can be used is a conservation assessment of Monterey pine (*Pinus radiata*), as described in Millar and Brubaker (2006). *Pinus radiata* is currently represented by only five small and declining populations that are human-disturbed in California and Mexico. All conservation plans for this species initially focused on rehabilitation of extant populations. However,

paleoclimatic data suggested that the species responds sensitively to fluctuations in climate, and its range shifted many times in response to climatic changes during the Quaternary. The known distribution range of Monterey pine in the past included coastal northern California, which is 600 km from the closest current native population. In this region, Monterey pine has been planted and naturalized widely, spreading into parks and nature reserves where the species is considered an unwanted exotic. Based on paleoecological knowledge, Millar (1998) proposed a realignment restoration strategy for this species to encourage it to persist in areas on the north coast of California, where it has naturalized rather than been removed as an exotic. These locations overlap with the historic range of Monterey pine under similar climates to those experienced at present, as well as resembling floristic associates found in Monterey pine fossil assemblages and which can be considered “neo-native” sites for this species.

A reference is needed not only for choosing the restoration site and designing the interventions, but also for assessing restoration success. Criteria used in judging whether a restoration is successful are numerous (Hobbs and Norton 1996, Ruiz-Jaen and Aide 2005), but in a restoration project having conservation goals the population biology perspective should be a priority, i.e. that the populations of target species are restored to a level allowing their long-term persistence (Montalvo et al. 1997; Guerant and Kaye 2007; Menges 2008). This means that the restored population must possess attributes necessary for successful regeneration and adaptive evolutionary changes, i.e. viable demographic structure evident in the presence of new generations in addition to the founders, and sufficient genetic variation. In addition to evaluating these attributes in the restored site, it is necessary to compare them with values from the reference sites. The variation among reference sites in these attributes can be important for understanding restoration failures; thus, more than one reference site (when available) should be used for estimating restoration success (Hobbs and Norton 1996; Ruiz-Jaen and Aide 2005).

Making species lists for restoration: how many species?

One of the first steps of ecological restoration, after the area for restoration is chosen, is a decision about the number and identity of the species to be introduced as a part of the habitat restoration. There is a relationship between species diversity and a variety of ecosystem functions (Schwartz et al. 2000; Hooper et al. 2005; Vilà et al. 2007; Paquette and Messier 2011; Chisholm et al. 2013; Gamfeldt et al. 2013) which has a very practical application in restoration ecology, namely “how many species are needed to make a functioning ecosystem?” A

complete or nearly complete ecosystem function in most cases can be achieved with a limited number of species given that they represent all the necessary functional groups (Walker 1992; Hooper et al. 2005). However, conservation-oriented restoration has a goal of reinstalling not just functioning but maximum-diversity communities, and desirably providing a home for endangered species.

Based on these considerations, a small number of introduced plant species can hardly be justified in conservation-oriented restoration projects. The only exception would be a situation where the restored habitat still has a high species diversity of late-successional species and the introduction list can be limited to only a few threatened species. This, however, is rarely the case. Although a few studies showed that it was feasible to use as many as 20–30 species (Lamb 2011), and even 60–80 species (Arroyo-Rodríguez et al. 2009; Garcia et al. 2014), restorations traditionally use a limited number of species that are easy to collect and propagate, and with high survival and growth rates. Clearly, threatened species usually do not possess these attributes and therefore currently are not the species of choice in restoration projects.

Under lack of seed flow from neighboring locations, local impoverishment within small patches of restored habitat is highly likely due to the negative demographic and genetic effects of small population size, competition and predation (Shaffer 1987; Montalvo et al. 1997; Kramer et al. 2008), as demonstrated experimentally by Gibson et al. (2013). When restoration starts with a limited subset of the species pool characteristic for the habitat, the above process can only accelerate species loss. To mitigate this loss, restoration must maximize the number of species introduced, and include in the list species with a narrow regeneration niche and limited dispersal ability but that are of high conservation value. Introduction into multiple locations will result in extinction of these species in some but hopefully not all locations (Drayton and Primack 2000).

Species in a given plant community can be ranked by their abundance, reflecting their importance in the community. The shape of the community species-abundance distribution will depend on system productivity (Whittaker 1965; Hubbell 1979), succession stage (Bazzaz 1975) and relative importance of filtering and random assembly (Jabot et al. 2008; Qiao et al. 2015). The information provided by species-abundance distributions, such as dominance order, species richness and evenness, can have important conservation implications (Maina and Howe 2000; Hubbell 2013). Two ways to plot species-abundance distribution in a way useful for decisions about species choice for restoration are rank abundance diagrams and empirical cumulative distribution functions (McGill et al. 2007). A challenge in successful experimental restoration is the choice and number of species and a sufficiently large number of introduced plants to

prevent losses due to their small population sizes. The above diagrams and functions can be compared among the potential restoration and reference sites to determine the number and identity of the species to introduce. Each habitat patch has a small number of dominant abundant species, and a large to very large number of infrequent or rare species. In habitats with relatively short “tails” of rare species, such as boreal forests, a list of species even for large-scale restoration will be short. In contrast, habitats having very long tails of rare species, such as tropical forests, will require making a much longer list of species for reintroduction, and a particular combination of the species that are reintroduced can vary substantially from patch to patch. The reason is that in communities with very skewed species-abundance distributions, the occurrence of rare species varies across patches, often unpredictably, due to patch-colonization dynamics and/or dispersal limitation. Decisions based on species-abundance distributions must take into account that some species can be rare but viable under the given conditions while other species can be accidental or otherwise inviable under the same conditions (Maina and Howe 2000).

Making species lists for restoration: which species?

Once the approximate number of the species needed is worked out, the next goal is making an operative list of the species to be introduced as part of the habitat restoration. This list will be a subset of a larger species pool, “a set of species which are potentially capable of coexisting in a certain community” (Eriksson 1993). The species-pool concept has been developed as a theoretical framework for explaining species richness at different spatial scales, and states that species richness on a smaller scale is primarily determined by the availability of “appropriate” species at the next larger scale (Partel et al. 1996, 2011; Zobel 1997). As a result of environmental filtering and dispersal limitations, the local community species pool (the set of species present in the target community) is a subset of the higher-scale (regional) species pool (Partel et al. 1996, 2011; Zobel 1997; Zobel et al. 1998).

The importance of both local and regional processes in structuring natural communities has been recognized by restoration ecology, stressing a role of the regional species pool as a source of the species that might successfully colonize a restored site (Zobel et al. 1998; Brudvig and Mabry 2008). Thus, the regional species pool provides the upper bound for species richness at restored sites and limits the choice of the potentially suitable species. These candidate species must be evaluated for their actual chances to establish in the target community. Zobel et al. (1998) proposed a set of ecological, functional and phyto-sociological approaches as well as an experimental approach based on probability of germination and survival

of the introduced seeds for evaluating species not observed at the restoration site but present in the regional species pool.

A study by Brudvig and Mabry (2008) is an example of how to apply the above concept and produce manageable lists of key species for habitat restoration. To make a species list for the restoration of degraded Midwestern oak savannas in Iowa, USA, the authors first assembled a list of species for the regional pool which was supposed to represent the historic savanna communities in the region. They used three reference lists: (1) a list of species with habitat requirements that match the mixed-light conditions found in Midwestern oak savannas; (2) a list determined by species survival in experimental introductions; and (3) a list of species found at a pristine reference site. Then, they used life-history traits to target species from the regional species pool. After removing exotic species, species from non-savanna habitats and species already present at the restoration sites, they applied a set of filters to select those species most appropriate for restoration. These filters included distance-limiting seed dispersal mode, affinity for intact native habitat and affinity for high-light environment. As a result, they were able to narrow down the regional species pool (900 species) to a manageable species list (111 species).

Compiling species list should utilize both species-centered and functional approaches. The species-centered approach applies to the endangered and rare species, which should be top-listed. Their functional type is secondary, but for the non-threatened candidate species, their functional roles in the ecosystem (i.e. in primary production, nutrient cycling, canopy structure, seed dispersal, pollination service, etc.) are very important. Functional groups are groups of species not necessarily sharing the same niche but having similar effects on ecosystem functions or similarly responding to particular environmental factors (Gitay and Noble 1997; Lavorel and Garnier 2002; Rusch et al. 2003; Franks et al. 2009). The core list of traits considered to be of general importance in the identification of plant functional types can be found in Weiher et al. (1999), with more detailed lists and classifications elsewhere (e.g. Box 1996; Díaz and Cabido 1997). In restoration, the functionally important species must represent functional groups lost during ecosystem degradation and which are necessary for ecosystem functioning. The ideal choice for non-threatened candidate species are functionally important and co-occurring with the introduced threatened and/or keystone species because the co-occurring species are known to have an ecological niche similar to that of the focal species (Halme et al. 2009).

The choice of traits for defining the functional groups will depend on the ecological context. In frequently disturbed ecosystems, the traits should be related to colonization success, e.g. seed bank persistence, germination cues, resprouting ability and longevity (Tozer et al. 2012), or

light tolerance, leaf type and succulence, dispersal and regeneration mode (Gondard et al. 2003). In species-rich communities such as subtropical and tropical forests, the focus should be on the ecosystem's functional diversity, i.e. diverse flower and fruit types, that support diverse pollinator and frugivorous fauna, which in turn enhances the functionality of a plant community (Tucker and Murphy 1997; Martínez-Garza and Howe 2003; McConkey et al. 2012; Garcia et al. 2015). Thus, lists of species for restoration in these environments must include flower types typical for bird, bat, butterfly, moth, bumblebee and bee syndromes, as well as plants producing edible fruits of different size, which may require inclusion of not only trees in the list but also shrubs, sub-shrubs and herbs (Garcia et al. 2015).

Designing a restoration map can start from large spatial units of hundreds of hectares having the same plant community, but then should proceed to delimitation of relatively small working units of few hectares accommodating small-scale patchy spatial distribution for some species and spatial heterogeneity of assemblages.

With the knowledge of the species' environmental requirements, suitable locations for each species within the target area can be identified and mapped using spatial distribution modeling and, after maps are superimposed, the species assemblages can be defined for any spatial scale (see figure 1 in Volis 2016). One example of an application of this approach in restoration is the study by García del Barrio et al. (2013) in which distribution maps for 40 native tree species of Spain were used to identify the species pools for each region within the country and at different scales down to a grid of 1×1 km. Another example is a study of Siles et al. (2010) in which an operative restoration target map with a grid of 100×100 m was worked out based on predicted species assemblages for 23 target species.

Importance of small scale in restoration

Small-scale restoration, i.e. the restoration of small habitat patches, is becoming increasingly popular in the tropics because tropical forests are both species-rich and heterogeneous over space. A mosaic of habitat patches having somewhat different species composition and abundances can provide more opportunities for the survival of rare species by offering these species a wider range of microhabitats, different neighboring vegetation and animal interactions while maintaining a connectivity between the patches even over inhospitable environment through seed and pollen dispersal (Turner and Corlett 1996; Benayas et al. 2008; Arroyo-Rodríguez et al. 2009). In addition, restoration of habitat patches embedded in agricultural habitats will ease succession spreads when the latter lands are abandoned (Benayas et al. 2008).

As populations of many species in small patches will have an extinction debt as a result of destruction of their regeneration niche, restoration of the local habitat must be accompanied by conserving as many patches as possible and decreasing patch isolation by restoring other small and intermediate patches (dos Santos et al. 2007; Arroyo-Rodríguez et al. 2009). Restored connectivity among patches, in addition to improvement of their quality, may restore the ecological processes needed for successful regeneration such as pollination and seed dispersal by animals (Arroyo-Rodríguez et al. 2009). That small patches can be extremely valuable for maintaining regional plant diversity was shown by Arroyo-Rodríguez et al. (2009), who found that in the fragmented rainforest the distribution of most plant species was restricted to a few patches, and each landscape had a set of patches with very distinct communities. At the same time, species diversity in patches as small as 0.1 ha was similar or even higher than in the much larger patches. Although some communities (e.g. grass-dominated prairies) under small-scale restoration are predicted to converge in species composition and species-abundance distributions rather quickly, most communities may retain diversity among the habitat patches indefinitely (Howe and Martínez-Garza 2014). In consideration of the conservation value of small patches, one should keep in mind that in many highly deforested and fragmented regions, preserving and restoring small-sized remnants of the formerly continuous natural habitat has no alternative because nothing else is left.

Various restoration planting methods have been developed to reforest degraded lands (e.g. Knowles and Parrotta 1995; Lamb et al. 1997; Miyawaki 1999; FORRU 2005) and existing approaches cover a range of species, density and configuration of planting (reviewed in Stanturf et al. 2014). Several strategies recognizing the importance of the small-scale planting deserve particular attention.

The “woodland islets” (Benayas et al. 2008) and “nucleation” (Corbin and Holl 2012) strategies, proposed as low-cost alternatives to continuous plantation-style restorations (Benayas et al. 2008; Corbin and Holl 2012; Corbin et al. 2016), suit conservation-oriented restoration because the proposed planting in patches or islands creates areas (nuclei) where establishment of planted material is followed by dispersal and establishment of new recruits, and expansion of the nuclei (Albornoz et al. 2013; Zahawi et al. 2013; Peterson et al. 2014; Piironen et al. 2015). The planted nuclei are also expected to attract birds and other animals that may introduce and disperse seeds of species for which they are the dispersal vectors (Cole et al. 2010; Corbin and Holl 2012; de la Peña-Domene et al. 2014). Thus, nucleation planting can improve the recruitment of resident populations by attracting the pollinators and seed dispersers needed to restore regeneration, and facilitate the recruitment of other species through enhanced seed dispersal and improved

establishment conditions. It is not only forest remnants, groups of trees or scattered trees embedded in the deforested or degraded landscape that can serve as nuclei (Guevara et al. 1986; Toh et al. 1999; Slocum 2001; Carrière et al. 2002a, 2002b; Schlawin and Zahawi 2008; Holl et al. 2011), but also the small remaining populations of endangered species. Supplementation of the latter nuclei with planted conspecifics can boost regeneration and lead to population growth and expansion. Alternatively, the planted clusters of endangered tree or shrub species can serve as nuclei in sites where the species does not have extant populations. Gradual spatial expansion of nuclei will eventually coalesce into species-rich and highly heterogeneous compositions of species across the contiguous forest landscape (Corbin and Holl 2012). There is a minimum critical island size below which islands do not enhance seed rain and tree recruitment (Cole et al. 2011), which for tropical forests appears to be about 100 m² (Zahawi and Augspurger 2006; Zahawi et al. 2013).

Another useful approach for conservation-oriented restoration is “systemic experimental restoration”, which is the establishment of mosaics of replicated treatments within mosaics of habitats (Howe and Martínez-Garza 2014). This approach is an alternative to the commonly applied “best-available practice” of establishing a single combination of a limited number of commonly used plant species. Created in this way, plant communities are expected to differ in species composition at the small scale, mostly in presence and abundance of rare species, but their populations must be able to serve as sources of colonization for each other. The idea of doing restoration as numerous experimental introductions replicated at a small spatial scale is highly relevant to the restoration whose goal is to rehabilitate existing habitats or create new habitats of threatened species because introductions of such species in general have a low chance of success (Maunder 1992; Seddon et al. 2007; Godefroid et al. 2011; Dalrymple et al. 2012). Thus, broadening the list of reintroduced/translocated species as much as possible with endangered and rare plants and introducing them in different combinations and treatments is a way to succeed.

Importance of restoring regeneration niche

Spatial heterogeneity in environmental conditions can act as a filter, causing non-random germination, survival and growth of individuals that differentially affect plant species (Harper 1977). Niche-based models recognize abiotic (e.g. topography and soil) and biotic (e.g. competition and facilitation) filters as important determinants of community assembly (Keddy 1992; Weiher and Keddy 1999; Chase and Leibold 2003). Habitat specialization of coexisting species serves as a framework for explaining the spatial distribution of plant species (reviewed in Rees et al. 2001; Wright 2002), although neutral processes

based on dispersal limitation leading to local species sorting can also be important (Bell 2001; Hubbell 2001). Environmental filtering is the predominant driver of species assembling in temperate forests, whereas in the tropics dispersal limitation becomes equally or even more important (Myers et al. 2013). However, although the contribution of neutral processes to shaping biodiversity patterns can be significant at intermediate and small geographic scales (Webb and Peart 2000; Harms et al. 2001; Condit et al. 2002; Baraloto and Goldberg 2004; Laliberte et al. 2009), from an ecosystem restoration perspective, environmental filtering is more important (regardless of its proportional contribution) because it is more constraining. When ecologically similar species are likely to coexist, this is because their similarities are primarily related to ecological traits that make them fit this environment (Leibold and McPeck 2006). If seed limitation is removed but the habitat conditions are not met, the species will not establish.

Although habitat specialization is predicted to operate throughout plant ontogeny, it became recognized, after a seminal paper by Grubb (1977), that the crucial life stage that defines the species niche and to large extent creates niche separation among species is the period from germination to establishment. Particular sets of conditions favoring seedlings of different species thus function as regeneration niches that promote species coexistence (Grubb 1977, Huston 1994).

Adults of many species have a broader niche than one in which they can successfully recruit. Recruitment failure can be due to lack of pollinators, low seed production, seed predation, low seed viability, lack of germination cues, altered/unfavorable canopy and unfavorable substrate conditions. However, establishment limitations – namely soil conditions (moisture, pH, litter thickness), light, temperature and biotic interactions limiting seed germination and seedling survival – are among the strongest filters on recruitment for many taxa (Clark et al. 1998; Kobe 1999; Fine et al. 2004; Engelbrecht et al. 2007; Baldeck et al. 2013). The limiting role of these factors varies among species and can have either a synergetic or interacting effect (Denslow et al. 1998; Coomes and Grubb 2000; Beckage et al. 2000; Beckage and Clark 2003). Suitable soil conditions may require the presence of specific biota (microbes, fungi and arthropods) (Haselwandter 1997; Turnau and Haselwandter 2002; Fahsel 2007). Leaf litter can be an important recruitment filter, inhibiting or enforcing seed germination through its effect on local humidity and infestation/predation rate (Facelli 1994; Schupp 1988; Molofsky and Augspurger 1992; Santos and Válio 2002), and enhancing early seedling survival (Ibáñez and Schupp 2002). The favorable microhabitat providing necessary regeneration conditions can also be one created through facilitation, e.g. by shrubs acting as “nurse plants” for the seedlings (Maschinski

et al. 2004; Gómez-Aparicio et al. 2005; Kunstler et al. 2006; Garrido et al. 2007; Torroba-Balmori et al. 2015; Tones and Renison 2016). For example, in areas with stressful environmental conditions, e.g. in those experiencing seasonal drought, planting seedlings beneath the shrubs’ canopy reduces the irradiance/drought impacts that otherwise would require expensive manipulations such as construction of water catchments around each plant, use of water-retention gels in the root zone or individual tree shelters (Castro et al. 2002, 2004). Some threatened species, such as the yew *Taxus baccata*, critically depend on the presence of prickly shrubs that protect the yew recruits against ungulate herbivores (García and Obeso 2003).

Beside topography and soil, local heterogeneity generated by canopy openings creating much higher light intensities than in the understorey can also be related to the regeneration niche. Seedlings of many species, including non-pioneers, are heavily dependent on gaps and are termed “gap specialists” (Denslow 1987). However, in tropical forests, the spatial patterns of tree diversity are better explained by seed limitation than by canopy-gap availability (Hubbell et al. 1999; Curran and Webb 2000). Although gaps promote regeneration by creating opportunities for seedling recruitment, local seed pools determine which species will establish in a given gap (Hubbell et al. 1999; Curran and Webb 2000). The seed limitation applies first and foremost to the species with large gravity- or animal-dispersed seeds and to the sites where species occur at low densities (McEuen and Curran 2004).

Reliable determination of the species regeneration niche is not easy. When the factors determining species distribution are inferred from seedling, sapling or adult spatial distributions, the observed patterns in many cases can be equally well explained by topographic–edaphic variables or space-limited seed dispersal. Observational and experimental evidence suggest that in both tropical and temperate forests there are often more safe sites than the seeds reach (e.g. Turnbull et al. 2000; Zobel et al. 2000; Foster and Tilman 2003; McEuen and Curran 2004).

Because we almost never know whether lack of seeds limits recruitment or seed germination/seedling survival failure, in restoration we should use some general and easy-to-follow guidelines. Our base assumption should be that seed limitation is the only reason why the species does not grow in an otherwise suitable environment. To make this assumption reasonable, for each planted species, the choice of planting location must be based on good knowledge of its ecology and preferred environmental conditions at both large (altitude, vegetation community, soil type, rainfall, temperature) and small spatial scales (slope exposition, rock cover). The former information will be useful for species distribution modeling and the latter for spatial design of experimental trials within

the chosen location. As plant community structure and composition often predictably vary across topographic micro-habitats, the regeneration of a particular species along the topographic gradients in some cases can be reliably predicted (e.g. Tang and Ohsawa 2002). Knowledge of the species' ecology is also essential – whether it is a late-successional (slowly growing and long living) or pioneer species (aggressive stump sprouting and juvenile competitive), light requirements (shade-tolerant or not) and effect of shading on juvenile survival. To enhance seedling survival and growth, some interventions may be necessary before planting, such as decreasing tree density by systematic thinning or the creation of gap openings (Qian et al. 2016). When combined, all the above information can serve as a reliable basis for making a detailed multi-species restoration map.

Planting in restoration: importance of number and density

Restoration in essence is introduction accompanied by some interventions (e.g. the removal of exotics or thinning) if necessary. Therefore, the introduction guidelines developed by plant conservation biology apply here, and the reasons of success vs. failure of many reintroduction and translocation projects must be carefully learned.

There is a constantly growing number of studies showing that rare species can persist when placed into suitable habitat not only within (Bell et al. 2003; Kirchner et al. 2006; Maschinski and Duquesnel 2006; Aguraiuja 2011; Abeli et al. 2016; Fenu et al. 2016) but also outside of their known range (Jusaitis et al. 2004; Maschinski and Wright 2006; Van der Veken et al. 2007, 2012; Colas et al. 2008; Wendelberger et al. 2008; Pico et al. 2009; Marsico and Hellmann 2009; Reckinger et al. 2010; Roncal et al. 2012; Maschinski et al. 2012; Bontrager et al. 2014; Munt et al. 2016). However, the long-term success of reintroductions and translocations in general is low (reviewed in Seddon et al. 2007; Godefroid et al. 2011; Dalrymple et al. 2011, 2012, but see Guerrant 2012) and can be even lower considering publication bias towards successful reintroductions (Menges 2008; Miller et al. 2014). The most probable causes of failure in unsuccessful projects include the use of seeds rather than seedlings/saplings, inadequate or absent post-introduction monitoring and management, an inability to identify *a priori* the factors determining introduction success, too few families, too small population sizes and improper planting density (Guerrant and Kaye 2007; Godefroid et al. 2011; Dalrymple et al. 2011, 2012).

In many reintroduction projects, populations originated from a very small number of founder individuals (even a single founder individual in 7% of the reported experiments; Godefroid et al. 2011), which is likely to lead to inbreeding and loss of genetic variation in

subsequent generations. Godefroid et al. (2011) also showed that in 25% of the analyzed reintroduction projects the number of reintroduced individuals was less than 50 individuals, and in 43% of the cases it was less than 100 individuals, which apparently is substantially lower than the minimum viable population size, especially given that mortality of seedlings in the first year after introduction is usually high.

Considering the effects of density in plant introductions, we must take into account that the density of conspecifics can have both negative and positive effects on plant performance (Rathcke 1983). In general, there is a negative effect of conspecific seedling and adult neighbors (Harms et al. 2000; Comita and Hubbell 2009), apparently through density-dependent effects of host-specific natural enemies, which at the early seedling stage frequently are soil pathogens (Mangan et al. 2010). At the later developmental stages both pathogens and insects can cause density-dependent mortality in established seedlings and saplings (Wong et al. 1990; Gilbert et al. 2001). For example, Wong et al. (1990) showed that juveniles distant from adults may have higher survival rates than juveniles close to adults due to higher susceptibility to insect outbreaks. In tropical forests, seedlings of species less common as adults in the forest community appear to suffer from the presence of conspecific neighbors more than seedlings of common species (Comita et al. 2010; Mangan et al. 2010; Johnson et al. 2012; Zhu et al. 2015).

A negative density-dependent effect can also arise from autotoxicity effects (Li and Romane 1997; Cavieres et al. 2007). For example, experiments with endangered *Nyssa yunnanensis* revealed the inhibitory effect of root extract on seed germination and seedling growth (Zhang et al. 2015).

There is a decline in the strength of conspecific negative density-dependence across life stages: from strong negative effects at early life stages to a weak positive effects for adult trees (Zhu et al. 2015). However, because individuals can spend decades in the seedling bank, weak neighborhood effects may accumulate over time (Comita and Hubbell 2009). This implies that seedlings of rare and endangered species must be planted at a distance from each other and from the adult trees, preventing negative density effects, but this does not negate various positive density effects which become evident at later stages of the life cycle.

A positive density dependence in population growth rate at low densities is known as an Allee effect (Allee 1931). This can be caused by various genetic, demographic and ecological factors, e.g. by increased levels of inbreeding depression, skewed sex ratios and reduced availability of mates. In plants, the latter phenomenon is apparently widespread in small and fragmented populations of species that require animal pollination (Aizen and Feinsinger 1994; Agren 1996; Xia et al. 2013). Pollinators

usually exhibit frequency-dependent foraging behavior when they forage more in dense patches in order to reduce the inter-patch travel time. Thus, plants growing at low densities may experience reproductive decline or failure due to difficulties in attracting pollinators (Allison 1990; Feinsinger et al. 1991; House 1992; Kunin 1992, 1993; Lamont et al. 1993; Agren 1996; Roll et al. 1997; Ghazoul et al. 1998; Bosch and Waser 2001; Forsyth 2003; Le Cadre et al. 2008). Genetic effects can also be significant as the outcrossing rates of wind-pollinated conifers (Perry and Knowles 1990; Boyle et al. 1991) and animal-pollinated trees (Murawski and Hamrick 1991; Hall et al. 1994; Boshier et al. 1995) correlate with the density of flowering individuals.

Another process contributing to an Allee effect is the lack of improved habitat that otherwise would be induced by the presence of sufficiently large number of conspecific individuals. An example is the hemlock *Tsuga heterophylla*, which can acidify soil and sequester water in the upper soil only at sufficiently high density (Ferson and Burgman 1990).

The major consequence of an Allee effect, either genetic, pollinator-mediated or environment-facilitative, is the existence of a density threshold below which the aggregation unit (population) is likely to go extinct. As introductions of rare and endangered species usually use small to intermediate propagule sizes, the possible Allee effect on the introduction success must be considered (Forsyth 2003; Deredec and Courchamp 2007; York et al. 2013; Abeli et al. 2016). The mechanisms underlying Allee effects suggest that population persistence is dependent on population size and the spatial distribution of flowering plants. The probability of reintroduction success is positively related to the number of introduced individuals (Abeli et al. 2016). In flowering plants, sufficiently large numbers of individuals spaced not too far from each other are needed to insure high pollinator visitation rate (Groom 1998; Colas et al. 2001; Hackney and McGraw 2001; Le Cadre et al. 2008; Dauber et al. 2010), and the density appears to be more important than the population size for attracting pollinators (Kunin 1997).

The above considerations plus results of long-term planting density experiments (if they exist) (e.g. York et al. 2013) must serve as the basis for decisions about number and density of planted individuals.

Importance of biotic interactions

Restoration focusing only on focal species introduction has a high chance of failure if it does not consider re-establishment of the integrity of disrupted interactions crucial for ecosystem functioning. To restore seed dispersal, pollination, nutrient cycling and the food web, one may need to introduce or control a suite of interacting species such as soil biota, herbivores, seed predators and

frugivorous vertebrates (e.g. Bond and Slingsby 1984; Brown and Heske 1990; Vander Wall 1994; Chapman and Onderdonk 1998; Traveset and Riera 2005; Beyer et al. 2007; Kaiser-Bunbury et al. 2010; Traveset et al. 2012; Taillefer and Wheeler 2013; Anderson et al. 2014) and environmental engineers (McColley et al. 2012; Zysk-Gorczyńska et al. 2015). Moreover, for re-establishing a viable ecosystem, one may consider the introduction of top predators or environmental modifications needed for vertebrates, such as availability of perches or structural complexity of the vegetation (Beyer et al. 2007; Seddon et al. 2014; Fraser et al. 2015). The establishment success of introduced plants may require treating seedlings with natural mycorrhizas and soil bacteria (Barroetavena et al. 1998; Fisher and Jayachandran 2002; Gemma et al. 2002; Zandavalli et al. 2004; Zubek et al. 2009; Shen and Wang 2011; Ferrazzano and Williamson 2013; Fajardo et al. 2014).

Disruption of pollination services is a common problem of degraded and altered ecosystems and restoration plans must include re-establishing pollination processes and vectors that underpin the plant reproductive continuity of a restored ecosystem (Dixon 2009; Menz et al. 2011). Loss of specialist and especially generalist pollinators, and changes in pollinator assemblages servicing a species, may have detrimental consequences such as low or zero seed set, and even coextinction (Dixon 2009).

Pollinator colonization and persistence in restored sites can be achieved only by satisfying the pollinators' needs essential for the completion of their life cycle either within the restoration site or within the pollinators' foraging distance. For example, solitary bees strongly depend on the availability of nest sites (Gathmann and Tscharrnke 2002; Steffan-Dewenter and Schiele 2008) and butterflies on the availability of both larval host plants and nectar resources as adults (Dennis et al. 2003). Thus, the presence of habitat patches with pollinator-rich communities in proximity to restoration sites will facilitate re-establishment of pollinator activities there. Establishing restoration sites in a highly fragmented landscape as stepping stones should enhance the connectivity among the habitat patches and facilitate dispersal of pollinators. In restoration sites embedded within an ecologically hostile matrix, wide-ranging generalists such as bumblebees and the honey bee, may succeed as colonizers, while non-flying or restricted-range pollinators, such as cursorial mammals, lizards and many invertebrates, will stand little chance of colonizing these sites by themselves. Knowledge of degree of specialization, colonization capability and minimum habitat area requirements of the crucial pollinator groups is essential. In general, in species-rich plant communities, plants are more likely to exhibit higher levels of pollinator specialization. Such ecosystems with highly specialized pollinator associations present the greatest challenges for restoration and will require detailed

knowledge of the ecological requirements for both plants and their pollinators.

Re-establishing pollination service in the restored site may require introduction of facilitating plant species serving one of the following roles: framework species (species that provide a major nectar or pollen source); bridging species (plants that provide resources over resource-limited times); and magnet species (plants with attractive flowers associated with species with unattractive or small flowers) (Dixon 2009). Once the candidate framework, bridging and magnet plants are identified, the best choice will be those species supporting the greatest local abundance and diversity of pollinators.

Because pollinators contribute ecological functions that are critical to the ecosystems, the exact identities of these species are less important than their functional role. Thus, if the crucial native pollinators are extinct, substitution by extant species can be a viable option. For example, the extinct bird pollinator of *Freycinetia aborea* from Hawaii was replaced by an introduced bird (Cox 1983).

The functioning of many ecosystems is impossible without another plant–animal mutualism such as frugivory. Many plants have evolved edible seed coverings or appendages to attract frugivores who will ingest the seeds together with the flesh, and then regurgitate or defecate the viable seeds. Seed consumption followed by their release after passage through the gut can have two advantages for the plant: dissemination of the seeds away from the conspecifics and enhancement of seed germination.

Animal seed dispersal is a predominant form of dispersal in the tropics, with over 70% of tree, shrub and vine species in tropical and subtropical rainforests having seeds enclosed in fleshy fruit (Howe and Swallower 1982). Seed dispersal may be necessary for successful recruitment at different spatial scales by enabling seeds and seedlings to escape high mortality that occurs in proximity to parent plants (i.e. the Janzen–Connell effect) (Gilbert et al. 1994; Packer and Clay 2000; Mangan et al. 2010), to colonize new sites and maintain gene flow between populations. In the absence of dispersers, the seeds and seedlings may remain near parents and die due to competition with the adults and higher susceptibility to enemies when at high density.

The second positive effect of seed consumption by vertebrates can happen through increase in germination percentage or rate as a result of gut treatment. This can be due to mechanical and/or chemical scarification of the seed coat, separation of seeds from pulp, and the effect on germination and/or future seedling growth that results from fecal material surrounding the seeds (Traveset 1998). Two reviews of seed passage through the digestive tract of vertebrate frugivores in more than 200 plant species revealed a predominant enhancement effect, with ingested seeds germinating in greater numbers and more rapidly than uningested seeds (Traveset 1998; Traveset

and Verdu 2002). Although no experimental evidence of this exists, germination failure in some species can be a result of local or global extinction of the associated frugivores.

Some frugivores, such as many small-sized birds and mammals called pulp feeders, consume the fruit pulp but not the seeds, thus leaving them in the vicinity of the parents. Nonetheless, by consuming part or most of the fruit pulp, such pulp thieves can provide an essential service to the plants by releasing seeds from the pericarp's inhibitory effect (Robertson et al. 2006). Fedriani et al. (2012) experimentally showed, studying an interaction between *Pyrus bourgaeana* and its pulp feeders, that pericarp removal had a consistent strong and long-lasting positive effect on seed performance (e.g. lower rotting and higher germination percentages) and seedling fate (greater emergence, growth, and survival to two years old). In this study, the cumulative probability of establishment for depulped seeds was 4–25 times higher than for seeds in intact ripe fruits (Fedriani et al. 2012).

Thus, frugivores can have a variety of positive effects on the plants they feed on. A spectrum of the fruit consumers can be roughly predicted from the fruit type: the species bearing fruits with one or several large seeds are visited by a few large frugivores, while those producing small or large soft fruits with many small seeds are visited by a wide spectrum of frugivores (Corlett 1998; Kitamura et al. 2002). An overlap between diets of different groups of large frugivores is usually small, especially between bird and mammal groups (Kitamura et al. 2002), and even frugivores having similar diets differ in dispersal methods, distances they travel and microhabitats into which they disperse seeds. For example, gibbons disperse seeds via defecation while macaques disperse seeds via their cheek pouches (Kitamura et al. 2002), and small passerine birds disperse most seeds over short distances and into covered microhabitats, while mammals and medium-sized birds disperse seeds over long distances and mostly into open microhabitats (Jordano et al. 2007). The latter differences increase the chance for a seed to be disseminated into a favorable habitat which locations are distributed randomly over space. Thus, if one frugivore group disappears its loss cannot be compensated by another group.

Rainforest clearing and fragmentation on one hand and poaching and bushmeat harvest on the other have resulted in the dramatic decrease in abundance or extirpation of many frugivorous vertebrates over the world. The disappearance of large fruit-eating birds and animals altered seedling banks by favoring seeds dispersed by bats, small birds and wind (Wright et al. 2007; Terborgh et al. 2008; Brodie et al. 2009), and reduced recruitment in species dependent on large frugivores (Cordeiro and Howe 2003; Nunez-Iturri et al. 2008; Terborgh et al. 2008; Sethi and Howe 2009; Wotton and Kelly 2011; Effiom et al. 2013; Pérez-Méndez et al. 2015).

Defaunation has been recognized as a very significant conservation problem for both animals and plants (Redford 1992; Peres and Palacios 2007; Terborgh et al. 2008; Beaune et al. 2013; Harrison et al. 2013) and must be addressed in restoration actions directly or indirectly (Brodie and Aslan 2012; McConkey et al. 2012). Without restoring once-existing but disrupted plant–animal interactions by protecting, attracting or reintroducing frugivore populations, the habitat will never become the one it used to be. When information on fruit–frugivore interactions for a given community does not exist, a priority for conservation and reintroduction in the majority of cases should be the large-bodied, large-gaped and wide-ranging frugivorous taxa (McConkey et al. 2012), because these animals and birds usually have the largest impact on ecosystem functioning (Donatti et al. 2011) but disappear first due to the highest hunting pressure.

The maintenance of the network of plant–animal interactions must be recognized as a cornerstone of conservation policy (Montoya et al. 2008). Practical recommendations, for the areas where functionally important animals (e.g. seed dispersers or grazers) have become extinct, are to reintroduce these species from other regions, or, when this is not feasible because the species went globally extinct or critically declined in number, to use substitutes from the local or regional fauna that are functionally equivalent at the community level (McConkey et al. 2012). For example, introduced tortoises proved to be efficient extant substitutes for extinct beaked grazers/browsers in many island contexts (Gibbs et al. 2008; Griffiths et al. 2011; Pedrono et al. 2013; Burney and Burney 2016).

Legislation and protection categories

A restoration project having conservation goals can succeed only if the restored site has legal protection status as a guarantee that no anthropogenic disturbance will take place afterwards. On the other hand, the conservation status of the target site must allow for the necessary interventions. Thus, a restoration site must have a proper protected area category, allowing management but forbidding any other human activities.

Since 1994, the International Union for the Conservation of Nature (IUCN) has recognized, based on management objectives, approaches and regulations, six different protected area categories ranging from sites where human access is banned to landscapes with settled human communities and permitted extraction of natural resources (Dudley 2008). These categories are used for purposes of planning, setting regulations, and negotiating land and water uses, and reflect a complexity of situations in which decisions about planning and management must be made. Thus far, assignment of a category depended more on how the management authority intended to resolve an

inevitably present conflict between nature and local or visiting human populations rather than on the other criteria. The interventions other than those induced by undesirable human activities are not relevant for most of the existing six categories. For example, categories Ia and Ib specify that the sites are strictly protected from human influence, with category Ib being less restrictive for tourist visits. These areas, by definition, “do not require substantial and ongoing intervention to achieve the conservation objectives” (Ia), and allow for only “low-impact minimally invasive educational and scientific research activities, when such activities cannot be conducted outside the wilderness area” (Ib) (Dudley 2008). The areas in the latter category can include “somewhat disturbed areas that are capable of restoration to a wilderness state, and smaller areas that might be expanded or could play an important role in a larger wilderness protection strategy as part of a system of protected areas that includes wilderness, if the management objectives for those somewhat disturbed or smaller areas are otherwise consistent with the objectives set out above”. Although not stated explicitly, this definition assumes that “restoration to a wilderness state” will occur naturally, as a result of halted human-caused disturbance. Categories II and III emphasize the role of protection against human activity to preserve an ecosystem (II) or some natural features (III), with visitation and recreation usually being encouraged. Categories V and VI assume continuous human interaction with nature by some form of land use. The only category allowing and promoting active conservation management is category IV, which has the aim of protecting particular species or habitats with “management reflecting this priority”, and “many category IV protected areas will need regular, active interventions to address the requirements of particular species or to maintain habitats”. This is the only category that suits conservation-oriented restoration although, by definition, it “provides a management approach used in areas that have already undergone substantial modification, necessitating protection of remaining fragments, with or without intervention”. This definition somewhat limits use of the category IV to cases when the target areas are either small fragments of natural habitats surrounded by hostile environment or which are degraded to some degree. However, active management can be necessary for the last remaining populations of endangered species or threatened habitats located in intact or almost intact natural areas. Moreover, these target sites can be within already strictly protected areas having status Ia or Ib. The latter protected areas are not usually considered suitable for “restoration through time-limited interventions to undo past damage” such as “reintroduction of extirpated species; replanting to hasten forest regeneration; seedling selection; thinning; removal of invasive species” (Dudley 2008, p. 67). In my view, recategorization of a protected area should be allowed not only from

the category IV to categories Ia or Ib after successful restoration, but also from categories Ia and Ib to IV to make restoration possible. When a protected area designated for conservation-oriented restoration is embedded in a larger protected area, the latter should be redesigned to incorporate category IV.

What else is needed for efficient restoration?

The success of restoration projects requires identification of the mother plants as a reliable source of high-quality seeds, because the quality of seeds is directly related to the germination and survival of seedlings and the genetic diversity of populations (Zahawi and Holl 2014). A study by Hoffmann et al. (2015) illustrates how the first stage of restoration using threatened species (selection of the species and sites, identification of mother plants, seed collection) must be done. In the study of Hoffmann et al. (2015), after a list of 39 threatened and 32 rare target species for seed collection was compiled, the potential forest restoration sites were chosen based on the occurrence of at least one target species. The final site selection was based on floristic associations, sufficiently late successional stage, minimum size of 100 ha and active protection. Each selected site was surveyed intensively for mother trees as seed sources. The criteria for selection of mother trees were good health (no signs of damage, disease or infestation) and full reproductive maturity (presence of old fruits, seeds or seedlings under the tree). To collect sufficient genetic variation, at least 12 trees per population > 50 m apart from at least three populations per species were selected. When this was not possible, at least 20 trees per species in the whole study area were selected. The selected mother trees were mapped, tagged and measured for various parameters including diameter at breast height, and monitored for onset and duration of flowering and fruiting. The latter data were used to develop a seed collection calendar.

Large-scale restoration requires efficient collection, handling and use of large quantities of viable seed. Unfortunately, existing seed banks of wild species were designed to store a large number of species but not large numbers of seeds per species. A need for modified-for-restoration seed banks, called “restoration seed banks” has been recognized (Merritt and Dixon 2011, 2014). Restoration seed banks are the facilities to collect, store and propagate germplasm to be used in restoration projects (Merritt and Dixon 2011). These facilities should be based on the same scientific principles of germplasm storage as wild species seed banks, but be able to store much larger quantities of seeds per species than traditional seed banks. An example is the Seed Warehouse of the Utah Division of Wildlife Resources, with a storage capacity of 340 tons of seeds. Efficient management of the restoration seed bank requires knowledge on the phenology of seed

maturation summarized in a seed collection calendar (Hoffmann et al. 2015) and control of the quality and viability of collected seeds (Godefroid et al. 2010; Ferrando-Pardo et al. 2016).

Although most angiosperms produce orthodox seeds (i.e. those surviving drying and storage at -20°C), numerous plant species produce non-orthodox recalcitrant and “intermediate” seeds that can be stored in the seed banks only through cryopreservation (Pammenter and Berjak 1999; Berjak and Pammenter 2013). The recalcitrant seeds in addition require dissecting out the embryonic axis and germinating it *in vitro* prior to storage (Walters et al. 2013). This seriously limits the number of seeds that can be stored for a long time. Space limitations of the traditional seed banks, problems with storing non-orthodox seeds and negative impacts of seed harvesting on local population dynamics (Broadhurst et al. 2008) call for an intermediate stage of seed propagation through *quasi in situ* living collections (Volis and Blecher 2010; Volis 2015). The *quasi in situ* concept provides detailed guidelines on choice of material, planting and management of the living collections. The plants maintained in these collections can be a reliable source of seeds for restoration projects. Obtaining a sufficient number of seedlings from these seeds will greatly benefit from using the latest technological developments in overcoming dormancy, promoting germination and reducing pathogen attack (Turner et al. 2013; Madsen et al. 2012, 2014).

The restoration seed bank concept in conjunction with a systems approach combining population demography, ecological processes and management (James et al. 2013) gives a conceptual link between seed collection, storage and germination to establishment and maturation of the young plant at restoration sites (Figure 1). Population demography, central to the conservation and management of rare and endangered species (Schemske et al. 1994), must be integrated into conservation-oriented restoration projects. First, detailed characterization in terms of population size and demographic structure across the distribution range of an endangered species is needed to provide an accurate picture of its current conservation status. Second, studying the dynamics of populations prior to restoration actions is necessary to assess the threats and devise an appropriate management strategy. Third, assessment of the restoration success is impossible without demographic monitoring of the introduced populations. On top of this, monitoring of introduced populations and comparison with natural populations can help to optimize the management of the introduced populations. For example, demographic comparisons of the rare *Centaurea corymbosa* showed that reintroduced populations had higher survival but lower fecundity than natural populations, with a management recommendation to increase plant density to improve mate availability for self-incompatible flowering individuals (Colas et al. 2008).

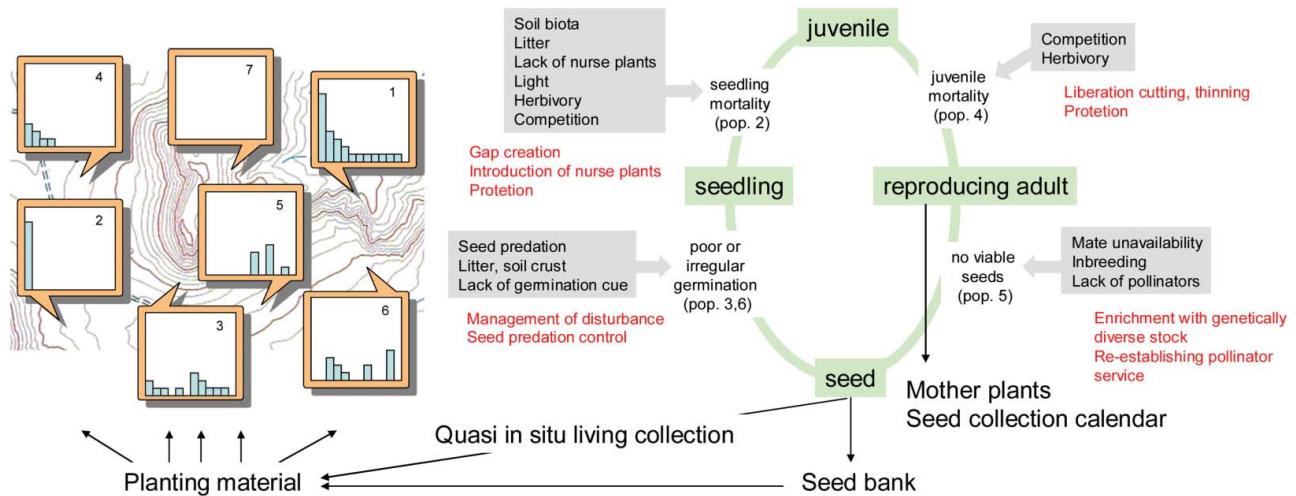


Figure 1. Systems approach in restoration (*sensu* James et al. 2013) linking population demography with restoration actions. Left: populations with size class distributions showing: 1, viable structure; 2, no transition to saplings; 3, poor germination; 4, high juvenile mortality; 5, no viable seeds produced; 6, irregular germination; 7, not occupied suitable environment. In size-class distribution histograms the x and y axes are size classes (the first two are seeds and seedlings) and plant density per unit area, respectively. Right: the transitions between stages of life cycle, possible demographic problems (evident from the population size class distributions), their causes and suggested *in situ* actions.

To summarize, for the success of a restoration project with conservation goals, it is crucial that (i) the environmental conditions at the introduction site satisfy the known species requirements; (ii) the material for introduction has a suitable origin and sufficiently high genetic variation; (iii) the number of introduced individuals is above the minimum founder population size demarked by an extinction boundary; (iv) interspecific interactions are addressed and incorporated into restoration planning; and (v) there is a long-term monitoring with necessary interventions if needed.

Conclusions

Because ecological restoration encompasses ecological processes involving abiotic factors and multi-species assemblages and emphasizes community structure, function and resilience, this discipline can help to identify and restore the conditions under which the threatened species can maintain viable populations. Therefore, ecological restoration with conservation goals can, and should, incorporate threatened plant species into their designs and management plans. However, to be successful, utilization of threatened plants species must be based on an appropriate methodology. The methodological considerations described in this paper should serve as a first approximation to the conservation-oriented restoration guidelines useful for practitioners.

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