



Managing forest regeneration and expansion at a time of unprecedented global change

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Forests provide fundamental ecosystem services to mitigate climate change and support biodiversity but they are seriously threatened by local human pressures and the outcomes of global climate change (Trumbore et al., 2015). According to FAO estimates, some 420 million hectares of forest have been lost since 1990, although the rate of deforestation has decreased over the past three decades from 16×10^6 ha/year in the 1990s to 10×10^6 ha/year from 2015 to 2020 (FAO, 2020). There is, however, broad agreement that deforestation still prevails in the tropics, whereas extratropical regions tend to gain in forest cover as rural lands become depopulated, abandoned and recolonized by forest species (Chazdon, 2014; García et al., 2014). Consequently, the proportion of second-growth forests—that is, forest or woodland areas that have re-established after the complete loss of the original tree cover—is rapidly increasing across both hemispheres.

The recent tree cover increment in many regions of the world is partly a result of extensive tree planting programs triggered by ambitious international initiatives to reduce deforestation and forest degradation and to restore forest ecosystem's functions, such as Global Partnership on Forest and Landscape Restoration, REDD + or the Bonn Challenge (Chazdon, Gutierrez, et al., 2020; Corbera & Schroeder, 2011; Laestadius et al., 2015; Leipold et al., 2016). These initiatives have largely focused on low-income countries of the Southern hemisphere, where deforestation rates remain high (Curtis et al., 2018; Song et al., 2018). Notwithstanding, recent programs such as the European Green Deal (European Commission, 2019) similarly pursue to increase the amount and quality of forests for mitigating climate change impacts and restoring ecosystems and biodiversity in the frame of Europe's transition towards

a circular and CO₂ neutral economy. The burgeoning political engagement reflects rapidly growing economic and societal concerns upon the impacts of recent climate change on extant forests (Hanewinkel et al., 2013; Seidl et al., 2014). Forests are increasingly valued as much for their diverse ecological services provided to local communities (Martín-Forés et al., 2020) and their role in mitigating climate change as for the profitable industry generated by wood production (Bastin et al., 2019; Gamfeldt et al., 2013). Strategies to attain healthy, diverse and multifunctional second-growth forests include a diverse array of actions that vary from passive restoration approaches that implement cost-effective interventions to spur autonomous tree regeneration (e.g. Benayas et al., 2008) to active reforestation approaches that can involve extensive surfaces planted with millions of young trees (afforestation).

The high-economic costs of large-scale tree plantation programs, as well as their eventual social and environmental impacts (Bullock et al., 2011; Fagan et al., 2020; Holl & Brancalion, 2020; Lamb et al., 2005) render passive forest restoration as an indispensable management tool in many regions of the world. In addition, the ecological success of restoration actions is commonly higher with approaches based on natural forest regeneration than those using active restoration (Crouzeilles et al., 2017). And although passive restoration initiatives usually develop locally, their upscaled effects can become quite significant (Crouzeilles et al., 2020). Despite all these proven advantages, our practical knowledge of how to use the natural regeneration potential of tree populations and communities for fostering forest restoration remains incomplete (Hampe et al., 2020). For example, long-term empirical studies investigating the

effectiveness of different restoration strategies are scarce and few works have systematically compared the success of alternative restoration approaches in generating truly multifunctional forests (but see Chazdon, Lindenmayer, et al., 2020; Cruz-Alonso et al., 2019).

This Special Feature compiles six review and original research articles with the aim of synthesizing and deepening our understanding of the ecology and functioning of forest recovery in different parts of the world. Three contributions provide empirical evidence on the effectiveness of low-cost and nature-based solutions to enhance forest regeneration and expansion, such as applied nucleation and induced seed dispersal. They highlight the instrumental role of seed dispersal interactions in enhancing tree establishment in neotropical

ecosystems. A further study on a major European forest tree reveals that second-growth forests may rapidly attain high levels of functional diversity while exhibiting increased tree growth as a legacy effect of former land uses. Finally, a Policy Direction paper argues for the need to consider also a number of ecosystem disservices (such as fire hazards or biotic invasions) associated with the expansion of secondary forests while a Commentary paper argues for reconsidering plans for large-scale massive tree planting. Overall, these contributions shed light on important knowledge gaps on the regeneration and restoration of tropical, mediterranean and temperate forests, and provide evidence-based guidelines to design effective forest management plans. These guidelines are articulated around three main topics (Figure 1).

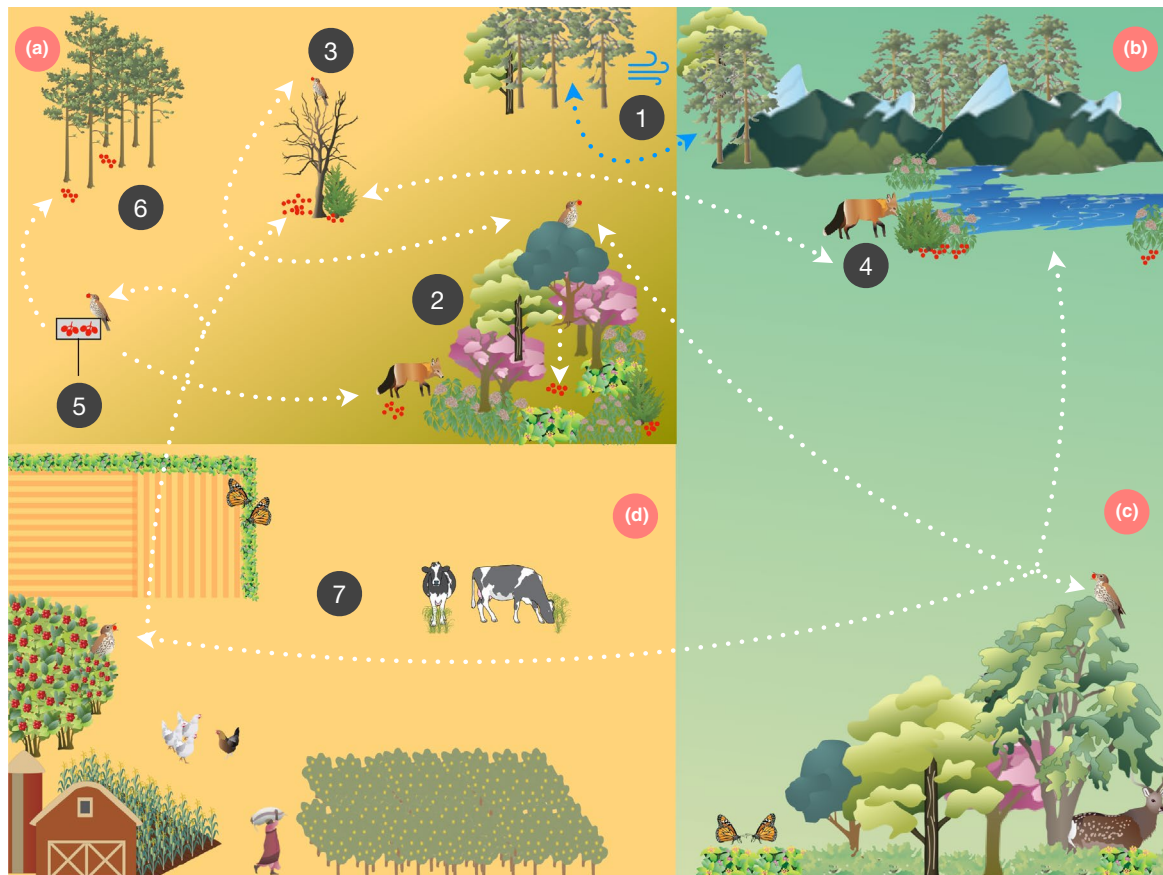


FIGURE 1 Schematic representation depicting restoration alternatives (1–6) that drive forest regeneration and expansion in rural abandoned lands (a) typically surrounded by patches of different types of forests (b and c) and areas of productive agricultural lands with orchards, croplands and hedgerows (d). These restoration and forest recovery alternatives are documented and discussed in this Special Issue. Spontaneous forest regeneration (1–4) might occur from adjacent mature forests (1) when propagules are dispersed by wind (blue arrow) or by frugivorous vertebrates (white arrows; 2–4). Seed dispersal by frugivores fosters forest regeneration locally (2–4), overcoming seed limitation and enhances seed deposition and establishment of multiple animal-dispersed plants. Some landscape structures, such as dead trees where birds typically perch (3) or ponds and lakes that vertebrates visit to drink (4), trigger the arrival of propagules (red dots) that nucleate the formation of new forest patches (2–4). Additionally, feeding stations (5) can induce seed dispersal to effectively overcome seed limitation and exploit the different services provided by frugivores to animal-dispersed plants including enhanced seed germination, seed deposition in suitable sites and dispersal of propagules to remote locations. Where environmental conditions hamper seed arrival and establishment, local artificial afforestation (6) can overcome both limitations. Ultimately, all these cost-effective nature-based solutions can help restore diverse and resilient secondary forests. Biotic processes, such as pollination and seed dispersal link long-established forest (b and c) and secondary forests (1–5), and latter may act as a cost-effective species reservoir for the (re)colonization of long-established and managed forests. This mutual interdependent dynamic is represented in the picture as a double-headed line. At a regional scale, policy initiatives should promote multifunctional farming systems and sustainable forest management to maximize the ratio of ecosystem services versus disservices delivered by secondary forests (7)

1 | APPLIED NUCLEATION AND INDUCED SEED DISPERSAL ARE COST-EFFECTIVE NATURE-BASED SOLUTIONS THAT CAN SPEED UP FOREST RECOVERY AND EXPANSION

The initial stages of forest recovery are often limited by the arrival of propagules (Cramer et al., 2008) and/or stressful environmental conditions that challenge the successful establishment of recruiting plants (Basnou et al., 2016). Applied nucleation is a well-established restoration approach that aims to overcome both limitations by mimicking the natural regeneration process where a patch of (planted) woody vegetation enhances the deposition of seeds and the posterior establishment of other individuals and species (Benayas et al., 2008). Previous research has shown that species composition and ecosystem functioning change through the course of forest recovery and expansion, but long-term datasets remain scarce (Meli et al., 2017). The paper by Holl et al. (2020) summarizes the accumulated impact of applied nucleation, tree planting and passive natural regeneration on the flora, fauna and ecosystem functioning in plots located in abandoned tropical rural lands monitored over a period of 15 years. Notably, both applied nucleation and tree planting favoured seed deposition and the establishment of all floral and faunal taxa surveyed. All metrics of taxonomic diversity and tree cover reached higher values in plots with nucleated and planted trees compared to unaided natural regeneration. Within the nucleation and planting treatments, the effect increased proportionally to the size of the patch restored. Although both applied nucleation and tree planting speeded up forest recovery, the passive restoration approach was 66% less expensive. Interestingly, the authors confirm that the success of applied nucleation relies on the availability of frugivores in the regenerated area. They, hence, conclude that both tree planting and applied nucleation are likely to fail in highly defaunated sites where animal-dispersed trees are deprived of dispersal services (Dirzo et al., 2014). Or, alternatively, in areas with high levels of seed predation and/or herbivory where dispersed propagules are unlikely to become established (McAlpine et al., 2016). Thus, this long-term study reinforces the notion that forest managers should consider both the environmental conditions determining tree recruitment as well as the biological processes that amplify plant fertilization and recruitment dynamics, such as seed dispersal or effective pollination (Farwig & Berens, 2012; Potts et al., 2016).

Animal-mediated seed dispersal during the very initial stage of applied nucleation is in the focus of the following paper by Camargo et al. (2020), who report on a tree planting experiment in a pasture woodland of the Brazilian Atlantic Forest. Comparing plots planted with either a wind-dispersed or one of two bird-dispersed species with contrasting fruits, they observed great differences in the frugivorous bird assemblages and visit rates, as well as in the abundance and species richness of the arriving seed rain. One of the bird-dispersed tree species attracted a more diverse of frugivores than the other. Interestingly, the respective frugivore assemblages of the two

species differed in their functional traits, and in particular the average gape width and wing-load of each frugivore assemblage were related with differences in the seed rain that arrived under each tree species. The study therefore presents solid evidence illustrating how the choice of tree species for applied nucleation initiatives influence the composition and abundance of the seed dispersers it attracts and the resulting seed rain. This knowledge can guide forest managers with selecting the most effective tree species for applied nucleation programs in line with the local disperser assemblages and forest restoration targets.

Still focusing on animal-mediated seed dispersal, the third paper of this Special Issue (Silva et al., 2020) presents a proof of concept and feasibility for a simple and highly cost-efficient technique to reinforce forest expansion into abandoned agriculture lands by the so-called induced seed dispersal. The authors embedded seeds of the target tree species for restoration in the pulp of commercial or native fleshy fruits that they placed in two feeders in former agricultural lands over a period of 2 years. Using camera recordings and seed traps, they could identify a relatively diverse frugivore assemblage dominated by common generalist species that dispersed a noteworthy amount of seeds (>600 seeds per ha and month) of the native pioneer tree *Cecropia hololeuca*. The easy implementation of the presented technique makes it a suitable candidate to overcome seed dispersal limitation issues in small-scale restoration programs. The approach can be of special interest in highly disturbed landscapes where it can take advantage of the generalist frugivores that typically remain in such landscapes (McAlpine et al., 2016).

2 | PASSIVE FOREST REGENERATION RESULTS IN SECONDARY FORESTS WITH ENHANCED GROWTH AND RESILIENCE TO CLIMATE CHANGE

An overwhelming number of studies show that secondary forests can provide relevant ecosystems services such as the regulation of nutrients and hydrological cycling, and particularly carbon sequestration (Pugh et al., 2019). These results have been related to positive effects of land use legacies on soil characteristics such as higher nutrient availability, mineralization rates and microbial activity, that ultimately result in higher tree growth (Vilà-Cabrera et al., 2017). Yet, we largely ignore whether long-established and secondary forests also differ in their resilience to climate change-mediated disturbances (Alfaro-Sánchez et al., 2019; Elias et al., 2020). Comparing secondary and long-established broadleaf forests in NE Spain, Espelta et al. (2020) show that secondary forests tend to exhibit higher tree species diversity, tree growth and reduced insect herbivory while they do not differ from long-established forests in their sensitivity to drought. These results highlight that forest managers should consider promoting tree diversity in temperate forests as a tool for simultaneously enhancing provisioning ecosystem services (ES) such as wood production, by means of enhanced tree growth, and forest resistance to biotic disturbances (e.g. insect pests) with

no effects on their response to drought. Moreover, the higher diversity observed in unmanaged secondary forests points to them as a cost-effective species reservoir for the (re)colonization of less diverse long-established forests, suggesting that planning their inclusion at the landscape level could be a helpful strategy to increase forest landscape resilience (Messier et al., 2019).

3 | POLICYMAKERS SHOULD CONSIDER EVIDENCE-BASED STRATEGIES THAT INCLUDE PILOT STUDIES, LONG-TERM MONITORING AND THE POSSIBILITY OF ECOSYSTEM DISSERVICES

While the provision of ES delivered by secondary forests has been extensively acknowledged, the potential existence of ecosystem disservices (EDS) has been less investigated. Yet forest expansion may also promote landscape homogenization, increase the spreading of biotic (e.g. pests) and abiotic (e.g. wildfires) disturbances and reduce water runoff (Castro-Díez et al., 2019). In addition, the change from a cultivated landscape towards abandoned land is perceived as a 'loss of territory' and regarded as a problem by some local stakeholders (Frei et al., 2020). These negative outcomes from secondary forests may be particularly relevant in regions such as the northern rim of the Mediterranean Basin where extensive forest expansion is occurring largely as a result of rural abandonment. In their Policy Directions article, Varela et al. (2020) summarize the main ES and EDS linked to the establishment of secondary forest in the Euro-Mediterranean region, and make policy recommendations to reduce environmental and economic uncertainties and maximize the ES/EDS ratio of secondary forests expansion. These recommendations include: (a) favouring a climate-smart policy leading to fire-resistant landscapes developed after enhancing value chains that stimulate active forest management; (b) adopting a territorial perspective beyond forest- and farm-based measures and payments; and (c) redirecting the focus and direct payments of the Common Agricultural Policy (CAP) to multifunctional farming systems and sustainable forest management. This Policy Directions article shows that programs supporting conservation require evidence-based and informed policies to avoid conflicting outcomes among stakeholders. For example, the rise in the demand of forest services and products, as natural climate solution initially designed to achieve climate neutrality by 2050, has increased forest harvest area (49%) across Europe since 2015 compromising the goals of attaining sustainable forest management (Ceccherini et al., 2020).

To offset long-term deforestation world-wide, there are at least three ongoing initiatives aiming to ensure the environmental societal well-being of the planet by planting 1 trillion trees (Brancalion & Holl, 2020). These initiatives should be long-term commitments to restore forest cover, ES and biodiversity but frequently their success is merely evaluated as the number of planted trees. Brancalion and Holl (2020) advocate for evidence-based, mixed and multifaceted strategies to achieve socio-economic and environmental targets, namely: (a) first

and foremost, addressing the drivers of deforestation; (b) integrating decision-making across spatial scales; (c) applying adaptive management across a long timeframe; (d) adopting a holistic view of the ecosystem to be restored to avoid a tree-focused approach and consider alternative solutions for non-forested environments; and (e) involving stakeholders at all stages of the program, including initial planning and the coordination of different land uses. They advocate that, ultimately tree planting initiatives should take into account the impact of climate change on forest regeneration dynamics and the ability of planted trees to thrive under new environmental conditions. The authors point out that recent experiments and previous foiled tree planting initiatives teach us that mixed strategies should be strongly considered according to the local needs and targets. Therefore, a large-scale recovery plan, authors state, should combine tree planting (Brancalion & Holl, 2020), passive reforestation (Chazdon, 2014), applied nucleation (Holl et al., 2020) and more bold actions such as assisted migration, if required (Pedlar et al., 2012). Altogether, this forward-thinking guidance should assist in planning, designing, implementing and monitoring tree planting strategies and more broadly forest restoration plans. Robust and integrative forecast modelling efforts would ultimately assist in prioritizing most effective interventions by evaluating the spatial, temporal and economic efforts required to achieve forest regeneration locally and at global scales under different socio-economic and environmental scenarios (Montoya et al., 2020).

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AUTHORS' CONTRIBUTIONS

C.R., J.M.E. and A.H. equally contributed to outline, write and review this editorial.

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