Drivers of native species regeneration in the process of restoring natural forests from mono-specific, even-aged tree plantations: a quantitative review

Klaus N. Kremer1,2,3, Jürgen Bauhus1

A substantial proportion of the existing tree plantations has been established following clearing of native forests. This form of conversion has become widely unacceptable, and there are increasing demands to reverse it through ecological restoration. Yet, there is a lack of integrated knowledge on how best to restore. Here, we reviewed 68 studies to identify the main factors determining establishment success of regeneration of native woody species when restoring natural forests from plantation forests using active and passive approaches, beneath existing canopies, and following their removal. According to the evidence collected, herbivory, within-gap position, soil properties, and ground cover type and structure had limited influence on regeneration, showing significant effects in less than 26% of cases in which their influence was tested. In contrast, spatial landscape configuration, overstorey structure, ground vegetation structure, overstorey composition, and climate and geomorphology had significant effects in 67, 47, 47, 52, and 63% of cases, respectively. Regeneration diversity and abundance increased with proximity to natural vegetation remnants and seed sources. Lower canopy and understorey stocking levels positively influenced regeneration, as did interventions to reduce them. Canopy cover reduction proved especially effective in warmer regions, in stands of broadleaved species, younger ages (<30 years), higher densities (>1,000 trees/ha), and taller canopies (>20 m). Restoration of native forests can be optimized by adopting interventions that prove most effective, and prioritizing more responsive stand types. However, the specific stand attributes and environmental factors described should be further studied to understand the mechanisms underlying their influence on regeneration.

Key words: conversion, environmental factors, forest restoration, monoculture, plantation forest, silviculture

Implications for Practice

- When restoring native forests from plantations, the decision upon a passive or active approach should consider the distance to native forest remnants, as well as the structure of the canopy species and its attractiveness to seed dispersers.
- An integrated management of canopy and understorey layers should be conducted to provide growing space for regeneration.
- Canopy cover reduction to facilitate regeneration is especially effective in tropical and temperate climates. Higher effects are also expected in broadleaved stands, of younger ages (<30 years), higher densities (>1,000 trees/ha), and taller canopies (>20 m).
- Despite functional and structural resemblance among plantation ecosystems, general restoration approaches should incorporate measures to overcome ecosystem-specific limitations for regeneration, such as those imposed by climate or canopy species.

Introduction

Despite their relatively small share of the world’s forested area of approximately 7%, planted forests have a disproportionately large importance in terms of production. Already in 2012, they provided 46.3% of the annual industrial roundwood production globally (Payn et al. 2015; FAO 2020). To meet a growing demand for forest products and services, the area and productivity of planted forests is expected to keep increasing (Payn et al. 2015; FAO 2016). However, most of them are relatively simple in terms of structure and composition (Moore & Allen 1999): today, 45% of the total area of planted forests is represented by plantation forests (i.e. intensively managed planted forests of one or two species, even-aged, and with regular spacing) (FAO 2020). Compared to natural forests, planted
forests have a lower capacity to provide ecosystem services and habitat for native species (Moore & Allen 1999; Baral et al. 2016). For these reasons, clearing of natural forest and woodlands for establishing tree plantations has become widely unacceptable (FSC 2015; Payn et al. 2015; PEFC 2018). Instead, in the context of forest landscape restoration and initiatives such as the Bonn Challenge, the New York Declaration of Forests, and AFR100, among others, the expansion of planted forests is expected to occur on lands of low conservation value, where they can contribute to solve environmental problems (Bastin et al. 2019; Silva et al. 2019). At the same time, focusing wood and fiber production in planted forests is seen as an approach that facilitates setting aside forests of ecological importance for conservation (Payn et al. 2015; Silva et al. 2019). However, the establishment of tree plantations following clearing of native forests has been a common practice in several regions in the world (Schroth et al. 2002; Domec et al. 2015; Hansen & Spiecker 2016; Zhang et al. 2016), largely motivated by the goal to grow more productive species with defined product qualities, in forests that can be managed more efficiently than irregular and diverse forests (Johhan et al. 2004).

This replacement of natural forests through plantations, together with the recognition of the limited capacity of plantations to deliver the goods and services expected from natural forests, has given rise to public policies and private initiatives calling for restoration activities aimed at achieving more natural and species-rich forests (Baumgarten & Von Teuffel 2005; FSC 2015; PEFC 2018; Silva et al. 2019). In addition, there is a growing interest of plantation owners to demonstrate sustainable management practices to comply with certification standards, such as FSC and PEFC, among others. According to these, plantations established directly after clearing of natural forests are not eligible for certification, and their restoration to more natural conditions is encouraged (FSC 2015; PEFC 2018).

The silvicultural activities to change the structure and/or composition of pure, even-aged stands toward mixed, uneven-aged stands are usually grouped under the term conversion (Hasenauer 2004; Fischer & Fischer 2009; Hansen & Spiecker 2016). Alternatives for this range from clearcutting followed by planting the desired species, to promoting natural regeneration below canopies of existing stands (Von Lüpke et al. 2004; O’Hara 2014; Stanturf et al. 2014; Hansen & Spiecker 2016). However, as in any restoration initiative, the choice for a specific approach should be based, among other aspects, on the available evidence on the drivers of transitions toward the target ecosystem state (Hobbs 2007).

There have been numerous studies worldwide on restoration of natural or semi-natural forests from plantations. Here, we wanted to find out whether there are some common factors influencing early restoration success despite the high variability of settings regarding biomes, plantations, main tree species involved, restoration approaches (active vs. passive), and silvicultural treatments to initiate regeneration (e.g. partial or complete tree canopy removal).

Specifically, we addressed the following question: “What are the main factors that determine the early establishment success of native woody species when restoring natural forests from plantations?” A second aim of this review is to synthesize the current knowledge to provide guidance for the design of efficient approaches for this form of restoration. To address these objectives, we describe the frequency upon which a specific intervention or environmental factor has been reported in peer-reviewed scientific articles to significantly influence regeneration of native woody species in mono-specific, even-aged stands.

### Methods

This review was developed following the PRISMA guidelines (Moher et al. 2009). Due to the open-framed nature of our review question, some of these guidelines were not applicable. However, the approach is still recommended for different types of reviews as a basis for transparent and accountable reporting (Moher et al. 2009).

### Literature Search

We organized our search based on the categories (columns) listed in Table 1. Except for “Context,” each category represents a key concept of the research question. Terms from a same category are either a synonym of the corresponding concept, or a term related to it. Terms from the category “Context” were used to limit the results to the fields of forestry and silviculture. Along the search string, categories were combined using the Boolean operator “AND,” while terms from a same category were linked with “OR.”

On the 17th of November 2018, we conducted analog systematic searches in Web of Science, Science Direct, and CAB Direct. In every database, the terms were searched by title, abstract, and keywords (Table 2).

### Study Selection

After removing repeated records, the studies obtained during the search were screened. By reviewing the title and abstract, studies not addressing the review question were discarded. The remaining studies were subjected to full-text assessment to verify further inclusion criteria: (1) full-text available; (2) peer-reviewed journal article; (3) written in English, French, German, Italian, Portuguese, or Spanish; (4) based on a field study; (5) addressing a relevant population (mono-specific, even-aged forest stands); (6) relevant comparison (stands subjected to different

### Table 1. Search terms used to build the corresponding search strings. The asterisk (*) denotes alternative endings of the corresponding terms.

| Subject       | Intervention | Outcomes  | Context         |
|---------------|--------------|-----------|-----------------|
| Plantation    | Conver*      | Regeneration | Forest          |
| Monoculture   | Restor*      | Establishment | Silvicultur*     |
| Even-aged     | Rehabilitat* | Survival   |                 |
| Uniform       | Facilitat*   | Growth     |                 |
| Conventional  | Underplant*  | Seedling   |                 |
|               | Transform*   | Recruitment |                 |
|               | Transition*  |            |                 |
treatments, or observed under contrasting levels of an environmental variable); (7) results based on statistical analyses; (8) relevant outcome (reporting effects of interventions or of environmental conditions on the early survival, early growth, abundance, and/or diversity of native woody species regeneration). These expressions of the state of regeneration could be accounted for in different ways (e.g., both seedling density and percentage cover of seedlings could stand for regeneration abundance). Seedlings (woody plants of height < 1.3 m), saplings (woody plants of height >1.3 m and dbh [diameter at breast height] <7 cm), and understory vegetation excluding herbs and ferns were regarded as forms of woody regeneration. In tropical forest stands, individuals up to 10 cm dbh were considered saplings, following conventional inventory classification (Guariguata 2009). Both natural and artificial regeneration forms were included, with the latter including sowing and planting. In addition, stands with at least 85% of their basal area or total stocking represented by a single species were regarded as monocultures, while stands with less than 20% variability in age of canopy trees were considered even-aged.

All the articles included after full-text review were assessed for data extraction.

Data Extraction
As stipulated during the study selection, all articles included describe the response of an attribute of regeneration of native woody species (either survival, early growth, abundance, or diversity of seedlings and saplings; i.e., the response variables) to an intervention or to the exposure to an environmental factor (explanatory variables). In most of the studies, these variables were assessed on single species. However, several studies used broader subjects, such as functional groups or size classes. Regardless of the subject addressed, we deemed each effect reported by a study as an observation. Based on the data provided, observations were classified as significant or null, and significant effects were classified as positive or negative. However, in several studies, multiple subjects were addressed to determine the response of an attribute of regeneration to an explanatory variable. In these cases, the response of the regeneration attribute to the corresponding explanatory variable was divided into a number of “sub-observations” equal to the number of subjects reported. The output of each of these sub-observations was given by the response of the corresponding subject, and was weighted by the multiplicative inverse of the number of subjects addressed in the corresponding study. Thus, if one study reported a significant positive effect of canopy openness on the seedling density of species “A,” a significant negative effect on species “B,” and a null effect on species “C” (with species “A,” “B,” and “C” as the different subjects within that study), the data output from that study was 2/3 observations reporting significant effects (species A and B), 1/3 observations reporting significant positive effects (species A), 1/3 observations reporting significant negative effects (species B), and 1/3 observations reporting null effects (species C) of canopy openness on the abundance of woody species regeneration. The purpose of this was to avoid assigning excessive weight to studies with multiple subjects, and therefore with multiple observations for a single relationship between an explanatory and a response variable (there were studies using up to 30 subjects to describe the effect of an explanatory factor on a single regeneration attribute). However, since a single study can report multiple interactions, the total number of observations was in fact larger than the number of studies included.

Aside from this, the specific variables used to account for the different attributes of regeneration varied among studies. Specifically, diversity was reported either as species richness or through diversity indices. When a single study provided results for diversity expressed both as richness and diversity indices, only the latter were included in the analysis (Magurran 2013).

Data Synthesis
We recorded the frequency of significant, null, positive, negative, and nondirectional effects of each explanatory variable on the response variables (survival, growth, abundance, or diversity of native woody species). For example, for the explanatory variable “canopy openness,” all observations reporting significant effects of this variable on native woody species regeneration either as survival, early growth, abundance, or diversity were added up to calculate their proportion from the total number of observations accounting for this interaction. The same was performed for null, positive, and negative effects, and the process was repeated for each of the response variables individually. The same procedure was applied to all the explanatory variables identified.

The results obtained were sorted by explanatory variable. Owing to their large number, these were grouped into categories based on the functions and structural features they represented to facilitate interpretation. Each category represents a specific attribute of forest stands. Variables accounting for very specific stand attributes were left as single-variable categories. Categories with less than five observations in total were excluded from further analysis, since such small sample sizes would have not allowed meaningful interpretations about their influence on regeneration.

In some cases, the reported effect of an explanatory variable on regeneration applied to other explanatory variables as well. This was the case, e.g., for stand tree density. When this variable was manipulated through a silvicultural treatment, its reported effects on regeneration also applied to basal area. To avoid redundancy of the observation output, the manifold nature of such observations was ignored when evaluating the overall effect of the stand attribute (i.e., the category) to which both explanatory variables belonged (in this case, “overstory structure”). However, when evaluating the effect of a single explanatory variable, all the associated observations were included.
For this reason, the number of observations included to determine the effect of a category could actually be less than the sum of the observations reporting the effect of the explanatory variables that were part of that category.

When observations of a category or variable were sufficiently frequent, comparisons were made between results of stands with differences in structural and climatic conditions that may influence the effect of the corresponding attribute or explanatory variable on regeneration. For comparing plantations of different ages, we considered 30 years to represent an approximate threshold between short- and longer rotation regimes, based on the approximate median values of the stands described in the studies included (Table S1). In addition, thresholds of 1,000 trees/ha and 20 m were selected for tree density and canopy height, respectively.

Results and Discussion

From the 5,181 records retrieved from the different databases, 1,254 were discarded as duplicates. The remaining 3,927 were screened to select 265 for full-text assessment. Following the inclusion criteria during this stage, 68 articles were finally considered for data extraction (Fig. S1; Table S1).

Overview of the Studies Selected

Except for one article published in 1983, all studies included had been published between 1996 and 2018. Despite the large number of studies published in 2016 compared to previous years, there is no clear temporal trend in the number of studies published per year. However, when considering the 265 studies pre-selected for full assessment during the screening (which also address the review question, although under conditions that make them unsuitable for this review), an increasing trend in the research interest from 1990 onwards can be observed (Fig. 1).

From a geographical perspective, the set of 68 publications reviewed shows a strong bias toward the northern hemisphere, where 91% of the studies were carried out (Fig. 2). Two studies were conducted in Africa, and only one in South America. In addition, 54% of the studies were conducted in temperate regions, while 22, 21, and only 3% stem from tropical, cold, and arid regions, respectively, according to the Köppen climatic classification. Most of the studies (81%) were conducted in conifer stands, 16% in broadleaved stands, and 3% in both types. From the 68 studies, 65 were conducted in planted forests, two in simplified secondary forests, and in one case, the stand origin was not reported. More than two thirds (68%) were manipulative experiments, most of which (57%) assessed artificial regeneration. The remaining 32% were observational, only assessing natural regeneration. While most of the studies evaluated regeneration beneath the tree canopy, 3% included clearfelling (>1 ha size) as a treatment, and only one study assessed regeneration exclusively following clearfelling.

Categories of Explanatory Variables

From the 68 studies reviewed, 45 explanatory variables were identified, whose effects on regeneration of native woody species had been evaluated in even-aged, mono-specific stands. Based on the forest stand attributes they represent, the explanatory variables were grouped into 12 categories (Table S2). According to this classification, “overstorey structure” was by far the most frequently studied category with 195 observations. “Ground vegetation structure” was the second most frequently studied attribute, with 20 observations, followed by landscape (“landscape spatial configuration and seed sources”) and climatic and geomorphological factors (“geomorphology and climate”), with 18 observations each. The categories “fire occurrence,” “root competition with canopy species,” and “previous stand management” were excluded from further analyses for having less than five observations (Table S2; Fig. 3).

Drivers of Regeneration

From the nine categories finally included, “landscape spatial configuration and distance to seed sources,” “canopy species,” “geomorphology and climate,” “overstorey structure,” and “ground vegetation structure” had significant effects on the different regeneration variables in more than 47% of the cases in which their influence was evaluated. These categories are
presented below in more detail. At the same time, “herbivory,” the “position within gaps” of the canopy, “soil properties,” and the characteristics of “ground cover” such as litter cover, litter thickness, and woody debris cover significantly affected regeneration in less than 26% of the cases (Fig. 3). Aside from the relatively low number of observations obtained for these categories, their limited influence on regeneration may be related to intrinsic aspects of plantation forests. Their generally

![Image of a world map with data points marked, possibly indicating location of studies included in the review.]

Figure 2. Location of the studies finally included in the review.

![Image of a bar chart showing categories of factors explaining regeneration performance. The chart includes bar graphs for various categories such as Canopy species, Fire occurrence, Geomorphology and climate, Ground cover, Ground vegetation structure, Herbivory, Landscape spatial configuration and seed sources, Overstory structure, Position within gap, Root competition with canopy species, Soil properties, and Previous stand management.]

Figure 3. Categories of factors explaining regeneration performance. (a) Number of observations per category (black bars); and (b) proportion of observations per category showing significant effects on regeneration (gray bars). The proportion of observations showing significant effects was not calculated for categories with less than five observations (fire occurrence; root competition with canopy species; previous stand management). The complete list of factors included in each category is listed in Table S2.
Continuous canopy cover, for instance, has proven less attractive to ungulate herbivores than open areas, especially when intensive management has occurred, leading to lower carrying capacities (Kuijper et al. 2009). Similarly, insect herbivory has also shown to decrease with increasing overstorey density (Löf et al. 2005). Thus, the levels of herbivory experienced below the canopy of plantations may have generally not been sufficient to create contrasting conditions. In addition, soil properties were in most cases addressed as co-variables as part of complementary analyses, rather than as the main focus of the studies included. Thus, their little effect may be partly a result of the absence of an explicit control to observe regeneration under contrasting soil conditions. Furthermore, low levels of light beneath the canopy of plantations may also mask the effects that changes in soil fertility could cause in regeneration performance (Löf 2000). Thus, to confirm the relatively low influence shown by these attributes on regeneration within plantations, it may be necessary to specifically control for their effects, in interaction with the main drivers mentioned above.

### Table 3. Main categories (>5 observations in total) of attributes of a forest stand, their corresponding explanatory variables, and their effects on regeneration performance. Single explanatory variables with less than five observations are also not shown here. “N,” number of observations; “S,” proportion of observations showing significant effects; “+,” proportion of observations showing significantly positive effects; “−,” proportion of observations showing significantly negative effects; “±,” proportion of observations showing nondirectional significant effects (e.g. when following a nonlinear distribution, or when no specific trend was informed); “0,” proportion of observations showing null effects. The last three columns represent the proportion of observations with positive, negative, and nondirectional effects (“+,” “−,” and “±”), from the total observations showing significant effects of the corresponding explanatory variable. The category “Soil properties” had no variables with more than 5 observations.

| Category | Variable (>5 observations) | N° | Effects on Regeneration (%) | Percentage From “S” (%) |
|----------|-----------------------------|----|----------------------------|------------------------|
|          |                             |    | S  | +  | −  | ±  | 0  | +  | −  | ±  |      |
| 1. Canopy species | –                           | 16 | 62.5 | –  | –  | –  | 37.5 | –  | –  | –  | 0.0 |
| 2. Geomorphology and climate | Altitude | 8 | 59.4 | 34.4 | 25.0 | 0.0 | 40.6 | 57.9 | 42.1 | 0.0 |
| 3. Ground cover | Litter cover (%) | 5 | 14.5 | 10.9 | 3.6 | 0.0 | 85.5 | 75.0 | 25.0 | 0.0 |
| 4. Ground vegetation structure | Understory cover (%) | 17 | 43.5 | 11.2 | 26.5 | 5.9 | 56.5 | 25.7 | 60.8 | 13.5 |
| 5. Herbivory | Insecticide application | 6 | 18.9 | 18.9 | 0.0 | 0.0 | 81.1 | 100.0 | 0.0 | 0.0 |
| 6. Landscape spatial configuration and seed sources | Distance to remnants | 13 | 58.3 | 0.0 | 58.3 | 0.0 | 41.7 | 0.0 | 100.0 | 0.0 |
| 7. Overstorey structure | Basal area | 45 | 54.8 | 1.6 | 50.7 | 2.5 | 45.2 | 2.9 | 92.4 | 4.6 |
| | Canopy openness | 33 | 61.2 | 42.0 | 4.0 | 15.2 | 38.8 | 68.7 | 6.6 | 24.7 |
| | Reduction in canopy cover | 73 | 55.6 | 48.7 | 2.7 | 4.1 | 44.4 | 87.7 | 4.9 | 7.4 |
| | Harvesting method (spatial pattern of harvested trees) | 11 | 41.8 | – | – | – | 58.2 | – | – | – |
| | Intensity of reduction in canopy cover | 49 | 27.7 | 19.6 | 0.0 | 8.2 | 72.3 | 70.6 | 0.0 | 29.4 |
| | Stand age and size of trees | 12 | 51.6 | 33.9 | 17.7 | 0.0 | 48.4 | 65.8 | 34.2 | 0.0 |
| | Time after canopy disturbance | 6 | 67.2 | 53.3 | 0.0 | 13.9 | 32.8 | 79.3 | 0.0 | 20.7 |
| | Tree density | 47 | 57.3 | 3.7 | 50.3 | 3.3 | 42.7 | 6.4 | 87.9 | 5.7 |
| 8. Position within gap | – | 5 | 21.7 | – | – | – | 78.3 | – | – | – |
| 9. Soil properties | – | 5 | 21.7 | – | – | – | 78.3 | – | – | – |

### Landscape Configuration and Distance to Seed Sources.
This category comprises all variables related to the landscape structure that may influence native woody species regeneration in even-aged, mono-specific stands (Table S2). Our results suggest that the landscape component is the most decisive attribute for regeneration, with 67% of the 18 observations showing significant effects (Fig. 3). With 13 observations, proximity of plantations to natural forest and seed sources was the most frequently studied factor in this group, and had only positive effects on regeneration diversity and abundance (Table 3; Fig. 4), most likely due to a higher availability of propagules in the proximity of seed sources (García et al. 2016). Although this trend is well known for forests and fragmented landscapes in general (Collinge 2009; Peel 2010), the simple structure of plantations, which renders them less attractive for animal dispersers compared to native forests (Nájera & Simonetti 2009), may cause weaker responses of regeneration. However, the evidence collected here confirms previous findings that proximity to native forest remnants or seed sources facilitates passive restoration, which reduces operational costs (Holl & Aide 2011). The number of observations in this category facilitated a comparison between stands younger and older than 30 years. Yet, no clear differences were found in the proportion of observations reporting significant effects (Table 4), suggesting the landscape setting has constant effects across ages.

### Canopy Species.
The studies addressing this component evaluated whether different dominant plantation tree species can have a different potential for facilitating regeneration. From the 16 observations gathered, 63% yielded significant effects.
of canopy species identity (Fig. 3), suggesting a considerable influence of this factor on regeneration. Most of these observations represent results on abundance and diversity of native woody species advanced regeneration. Although none of the studies experimentally addressed the specific patterns through which the canopy species affected regeneration, contrasts between species suggest that crown architecture may be an important driver (Fimbel & Fimbel 1996; Powers et al. 1997; Otsamo 2000), thus, adding importance to the factors related to the overstorey structure. Species with less dense crowns that cast intermediate shade and are more attractive to potential seed dispersers showed a higher potential for promoting advanced regeneration (Fimbel & Fimbel 1996; Powers et al. 1997; Otsamo 2000), which may also facilitate passive restoration approaches. The geographical provenance of the canopy species (native/exotic) does not seem to make a difference in regeneration performance (Thijs et al. 2014; Wolfe et al. 2015). However, canopy species with invasive potential can indeed have a lower potential for restoration, owing to an eventually dense conspecific regeneration (Thijs et al. 2014). In addition, canopy trees appear to negatively affect the survival of seedlings of phylogenetically closer understory species, possibly owing to higher abundances of host-specific shared pests and pathogens (Janzen 1970; Schweizer et al. 2013).

However, our findings may not necessarily be representative of even-aged monocultures overall. With only one exception, all observations from this category came from studies in tropical regions, where higher functional diversity and species turnover can promote a higher adaptability of understory assemblages to conditions imposed by the canopy species. Understoreys in temperate or boreal forests, in contrast, characterized by a lower overall diversity and adaptability (Chazdon & Arroyo 2013), could eventually be even more affected by traits of the canopy species.

**Geomorphology and Climate.** In this category, macroclimatic and geomorphological variables affecting microclimatic conditions were included, with geomorphological variables including altitude, aspect, slope, and position along the slope (Table S2). From the 18 observations, 52% yielded significant effects (Fig. 3). Altitude, the only explanatory variable in this category with more than 5 observations (8 in total), showed significant effects in 59% of cases, 58% of which were positive and 42% negative (Table 3; Fig. 4). However, altitude represents several other variables, such as temperature, precipitation, or soil properties, which may directly affect regeneration (Sharma et al. 2018). The relevance of this category stresses the importance of ecosystem- and site-specific approaches for the design of restoration plans. Within large plantation estates covering regions with different types of native forest and varying climatic and geomorphological conditions, the different limitations that these conditions impose on regeneration need to be considered.

![Figure 4. Trends in the influence of the most frequently studied quantitative explanatory variables (≥5 observations) from the most influential categories (those with >47% significant effects). Bars represent the proportion of observations yielding either positive (right) or negative (left) significant effects on regeneration. Nondirectional significant effects are not represented here.](image-url)

| Stand age   | N  | s    | o    |
|-------------|----|------|------|
| <30 years old | 8  | 79.2 | 20.8 |
| >30 years old | 10 | 67.5 | 32.5 |

**Table 4.** Effects of landscape factors on regeneration, grouped by stand age. “N:” number of observations; “s,” proportion of observations showing significant effects; “o,” proportion of observations showing null effects.
Still suggest that canopy structure is a relevant feature for regeneration, a highly reliable outcome given the large sample size.

| Climate            | Tropical | Cold | Temperate | Cold+temperate | Conifer | Broadleaved | Density <1,000 trees/ha | >1,000 trees/ha | Age <30 years old | >30 years old | Canopy height <20 m | >20 m |
|--------------------|----------|------|-----------|----------------|---------|-------------|------------------------|-----------------|-----------------|---------------|------------------|--------|
| N                  | 14       | 27   | 30        | 57             | 67      | 9           | 29                     | 24              | 30              | 39            | 33               | 9      |
| S                  | 71.4     | 41.4 | 61.4      | 49.6           | 53.1    | 83.3        | 47.2                   | 57.9            | 65.6            | 49.8          | 46.7             | 77.8   |
| “+” (%)            | 71.4     | 37.7 | 48.0      | 42.5           | 45.6    | 83.3        | 40.3                   | 57.9            | 58.9            | 42.1          | 43.7             | 66.7   |
| “−” (%)            | 0.0      | 0.0  | 6.7       | 1.8            | 3.0     | 0.0         | 0.0                    | 0.0             | 0.0             | 5.1           | 3.0              | 0.0    |
| “±” (%)            | 0.0      | 3.7  | 6.7       | 5.3            | 4.5     | 0.0         | 6.9                    | 0.0             | 6.7             | 2.6           | 0.0              | 11.1   |
| 0 (%)              | 28.6     | 58.6 | 38.6      | 46.9           | 46.9    | 16.7        | 52.8                   | 42.1            | 34.4            | 50.2          | 53.3             | 22.2   |
| Effects on Regeneration (%) | 100.0 | 91.0 | 78.3      | 85.8           | 85.9    | 100.0       | 85.4                   | 100.0           | 89.8            | 84.5          | 93.5             | 85.7   |

**Table 5.** Effects of reduction in canopy cover, grouped by stand characteristics. “N,” number of observations; “S,” proportion of observations showing significant effects; “+,” proportion of observations showing positive significant effects; “−,” proportion of observations showing negative significant effects; “±,” proportion of observations showing nondirectional significant effects; “0,” proportion of observations showing null effects. The last three columns represent the proportion of observations with positive, negative, and nondirectional effects (“+,” “−,” and “±”), from the number of observations showing significant effects.

**Overstorey Structure.** This category contains all the structural features related to the canopy layer, including interventions carried out to manipulate it (Table S2). Despite many observations, overstorey structure did not show the highest influence among the different stand components analyzed: from the 195 observations gathered, 47% yielded significant effects (Fig. 3). Yet, these results still suggest that canopy structure is a relevant feature for regeneration, a highly reliable outcome given the large sample size.

**Stocking level and canopy openness**

The influence of stocking level was mainly reported as tree density and basal area, with 47 and 45 observations, respectively. Both factors showed similar results, with 57 and 55% of the corresponding observations indicating significant effects on regeneration. When significant, the effects of basal area were essentially negative (92%), and only in few cases positive (2.9%). Meanwhile, the significant effects of density were 88% negative, and 6.4% positive. The few positive effects were recorded in studies conducted on steep mountain slopes and/or highly degraded lands, where denser canopies may have sheltered tolerant species from adverse site conditions (Forbes et al. 2019). Similarly, 61% of 33 observations reporting effects of canopy openness showed significant effects, of which 69% were positive, and only 6.6% negative (Table 3; Fig. 4). The lower frequency of positive significant effects of canopy openness compared to the frequency of the negative significant effects of density and basal area suggests that stocking level does not only affect regeneration through light and/or rainfall interception, but eventually also through competition for belowground resources (Gerhardt 1996).

**Reduction in canopy cover and time after release**

Reduction in canopy cover (e.g. through thinning or gap creation) was the most frequently studied factor in this category (73 observations). In addition to increasing levels of light at the forest floor, canopy openings can favor regeneration by reducing belowground competition from canopy trees (Gerhardt 1996), and by enhancing habitat heterogeneity and suitability for animal dispersers (de la Montaña et al. 2006). Accordingly, 56% of the observations addressing this variable yielded significant effects. In accordance with the mainly negative effects of the stocking level and with the mainly positive effects of canopy openness, 88% of the significant effects of reductions in canopy cover were positive, and only 4.9% were negative (Table 3; Fig. 4). The negative effects stemmed from a single study, and according to its authors, they were likely explained by the depletion of soil seed banks through intensive grazing prior to thinning (Igarashi & Masaki 2018).

When grouping these observations based on features of forest stands, the type of climate, canopy height, and type of canopy species (broadleaves vs. conifers) revealed a sharp influence on the effect of canopy cover reductions (Table 5). Stands in tropical climates had a higher rate of significant effects (71%) than stands in temperate (61%) and cold climates (41%). In addition, the height of dominant trees seemed to increase the effect of reductions in canopy cover. Stands with canopies taller than 20 m showed significant effects in 78% of cases, compared to 47% of stands with lower canopies. Stands with broadleaved canopy species showed 83% significant effects in canopy cover reductions, against 52% in conifer-dominated stands. Factors such as stand age and tree density had a relatively small influence on the effect of canopy cover reductions. The effect was higher in (1) stands younger than 30 years (66 vs. 50% significant effects) and (2) stands with densities above 1,000 trees/ha (58 vs. 47% significant effects) (Table 5).

The lower frequency of significant effects of canopy cover reductions in colder climates may be explained by the generally less species-diverse communities and the slow-growing regeneration in forests in such regions, probably less capable of a quick response to openings (Körner 2012; Skaret & Rosvall 2013). In contrast, communities in tropical forests should generally be able to respond more vigorously to releases in growing space, owing to a higher functional diversity, higher
Restoration of native forests from plantations

growth rates, and a higher adaptability. A similar response, but to a lesser degree, should be expected in temperate forests (Perry et al. 2008; Chazdon & Arroyo 2013).

Growth form and crown architecture of canopy trees may explain the higher effects of canopy cover reduction in broadleaved stands, since broadleaves usually develop wider crowns than conifers for the same stem diameter (Oliver & Larson 1996; Poorter et al. 2012). Thus, for a given proportion of the stocking removed, relatively higher increases in light may be achieved in broadleaved stands, from which regeneration would benefit. In addition, some plantations of broadleaved species with decurrent growth form are established at high densities to control stem quality (Fujimori 2001). Especially in such cases, highly suppressed seedlings and saplings could benefit from openings.

There might be several reasons for the higher effect of reductions in canopy cover on regeneration in taller stands. In addition to being more attractive to seed dispersers, stands with taller trees are presumably older, thus, having more time to accumulate advance regeneration, which in turn may respond more readily to openings (Lemenih & Bongers 2010). Increasing ages also carry a decrease in the crowding levels, leaf area index, and growth and transpiration rates (Delzon & Loustau 2005), all of which contribute to reduced competition with the understory (Ashfaq et al. 2019). Nevertheless, as mentioned above, the effect of canopy cover reductions was less pronounced in older stands (>30 years). This apparently contradictory outcome may be due to other factors related to increasing age that could dampen a release effect on regeneration. A weak response of regeneration to reductions in canopy cover in older stands, for instance, may be a consequence of sustained suppression of advance regeneration, which after long periods under shade may not be able to respond to releases (Coban et al. 2016), or of a higher accumulation of leaf litter, which can inhibit germination and/or seedling establishment (Loydi et al. 2013).

Finally, the higher effect of reductions in canopy cover on regeneration in stands of higher tree density may be explained by a higher relative increase in the access to resources following releases (Rodríguez-Calcerrada et al. 2008).

Time after a canopy opening also showed a positive influence on regeneration. This variable was addressed in 6 observations, for up to 11 years after release. Of these, 67% yielded significant results, all of which were positive (Fig. 4; Table 3). This would speak in favor of opening sizes and patterns that delay canopy re-closure, increasing the chances of colonization by woody species that can benefit from the increased resources (Lemenih & Bongers 2010). In line with this, the spatial pattern of the harvested trees (11 observations) showed significant effects on regeneration in 42% of the cases (Table 3). When differences between harvesting patterns arose, generally wider openings in the form of row fellings showed better performances.

Intensity of reduction in canopy cover

Some of the studies assessing the effects of canopy cover reduction also assessed the influence of the intensity of this reduction on regeneration. This was reported in 49 observations, of which 28% showed significant effects. Of these, 71% were positive, and none was negative (Table 3; Fig. 4). The average minimum and maximum remaining basal areas per study were 34 and 67%. Meanwhile, when gaps were created, their average minimum and maximum sizes per study were 546 and 1,714 m². The limited influence of the removal intensity suggests that the magnitude of openings is not decisive, and that even small interventions may create significant improvements for regeneration. However, this result may also be a consequence of the limited variation in the removal intensity across studies, given that the lowest mean gap size may be enough for intolerant species to establish. Although the effects of openings on total irradiance are mediated by the canopy height and by the gap form and orientation, previous studies have shown that rectangular openings of a width equivalent to the canopy height (equivalent to 491 m² round gaps in a stand with a 25 m tall canopy) can raise irradiance up to 97% of full light at their center, which would already be suitable for the establishment of intolerant species (Berry 1964; Figueroa & Lusk 2001). At the same time, the mean maximum size of the openings per study may not be enough to represent fully exposed conditions that would eventually hinder the establishment of sensitive species (e.g. frost intolerant), such as those created by large-scale clearcuts (Keenan & Kimmings 1993).

Stand age and size of dominant trees

Stand age and the size of dominant trees were grouped as a single variable, under the assumption that in mono-specific, even-aged stands, both variables would be generally correlated. From the 12 observations gathered, 52% yielded significant results, of which 66% indicated higher performance of native woody regeneration in stands of higher age or with bigger trees, while 34% indicated negative effects (Table 3; Fig. 4). The presence of both positive and negative effects of age among studies suggests that there are different factors at work, such as the ones described above regarding the influence of canopy height on the effect of canopy openings. However, the number of observations yielding significant effects may also be too limited to identify clear trends in the influence of age and size of trees, especially considering the variety of stands assessed and their differences in dynamics, management approaches, and life spans.

Ground Vegetation Structure. This category comprises all structural aspects of the herb and shrub layers that may affect regeneration (Table S2). Its influence was reported through 20 observations, of which 47% yielded significant effects (Fig. 3). The most frequently addressed explanatory variables were the relative cover of shrub and herb layers (17 observations), and their removal by either mechanical or chemical methods (10 observations). The percentage cover of shrub and herb layers had significant effects on regeneration in 44% of the cases, most of which were negative (61%), while removal had significant effects in 37% of the cases. As indicated by previous studies, herb or shrub layers can further reduce below-canopy light to levels exceeding the shade-tolerance of seedlings (Forbes et al. 2016). However, a dense understory may also negatively affect tree regeneration through rainfall interception and belowground competition (Padilla & Pugnaire 2006), and indirectly through sheltering higher herbivore
abundances (Caccia et al. 2009). In these cases, ground vegetation control would be especially helpful to foster regeneration. Accordingly, the significant effects of ground vegetation removal were predominantly positive (95%). Nevertheless, most studies addressing this factor investigated the control of invasive species, which may have a higher chance of hindering tree regeneration. Therefore, these results should not necessarily be extrapolated to other understorey types.

**Overview and Implications for Management**

The purpose of this review was to identify attributes of forest stands that should be considered in efforts to restore natural or semi-natural forests from plantation forests through regeneration of native tree species. According to our results, the landscape setting of the plantation is the most important feature on which to focus, if a passive restoration approach is to be adopted. Provided that proximity to natural forest stands increases the abundance and diversity of propagules, sites adjacent or closer to remnants should be prioritized to increase colonization by native species, which would allow reducing regeneration cost (Fig. 5). From a landscape perspective, this would also help increase the size of existing patches of natural forests, or increase the surrounding area of natural forest by creating new patches, thus enhancing landscape connectivity and capacity to sustain forest-dwelling species (Collinge 2009).

Figure 5. Some of the main drivers of regeneration of native species in mono-specific, even-aged stands, such as the landscape configuration, the overstorey structure, and the ground vegetation structure. (A) Highly isolated plantation stands of *Picea sitchensis* in Scotland (left) vs. a *Pinus radiata* plantation stand in Chile, contiguous to stands of natural forest (right); (B) *Pinus radiata* plantation in Chile, with a highly stocked overstorey and absence of woody regeneration (left) vs. a plantation of *Pinus sylvestris* in Germany, with lower overstorey stocking and abundant below-canopy regeneration of *Acer pseudoplatanus* (right); (C) the dense shrub layer of *Chusquea quila* in the understorey of a *Pinus radiata* plantation in Chile (left) vs. regeneration of *Fagus sylvatica* in the absence of shrub cover, in the understorey of a *Picea stichensis* plantation in Ireland (right). Pictures: Jürgen Bauhus, Martin Kohler, Klaus Kremer.
The decision upon a passive or active restoration approach should also attend the limitations imposed by the canopy species. Stands dominated by species that are more attractive for dispersers should have a higher potential for natural regeneration, in which case passive restoration approaches may be more feasible. On the contrary, stands dominated by species less attractive for dispersers may require artificial regeneration. In this case, species with shade tolerances suitable to the crown structure of the canopy trees and their associated light transmission should be used. In addition, species phylogenetically distant to the canopy species should be preferred to prevent the negative effects of eventually higher abundances of conspecific pests and pathogens.

In even-aged, mono-specific stands, regeneration is promoted by lower stocking of both the canopy and the ground vegetation layers, which should be managed simultaneously to ensure enough access to the resources required for regeneration establishment and growth (Fig. 5). Reduction in canopy cover appears to be especially effective in warmer climates. In addition, canopy openings appear to be more effective in younger and denser stands with tall canopies (<30 years; >1,000 trees/ha; >20 m) and in broadleaved plantations, where regeneration shows the best responses.

Owing to the generally positive effect of time after reductions in canopy cover, harvesting methods tending to prolong the conditions achieved through openings should be prioritized. Although the size and pattern of the openings should be partly determined based on the species to establish and the financial returns expected, larger openings may help to achieve this. However, canopy openings may pose various hazards that need to be considered beforehand. One of these is windthrow risk, which may be particularly severe in taller stands with narrow initial spacings (Cremer & Borough 1982). In addition, wide canopy openings may trigger vigorous growth of understorey vegetation, which could eventually outcompete tree regeneration. Therefore, the design of the openings and the residual stocking should be determined based on a careful assessment of these risks (Cremer & Borough 1982; Dodson & Fiedler 2009).

In addition to common trends in the responses of regeneration to interventions in plantations, we identified a relevant influence of climatic and species-specific features, which may pose particular restrictions on regeneration. In drier regions, e.g. seedlings and saplings may profit less from large canopy openings than under humid conditions, due to a higher risk of desiccation in the open (Holmgren et al. 1997). Similarly, stands dominated by more wind-firm species may allow stronger canopy reductions without increasing the risk of wind damage too much (Cremer & Borough 1982). Therefore, while considering the common responses of even-aged, mono-specific stands, restoration approaches should simultaneously attend the ecosystem-specific limitations for recruitment and growth of woody species (Hobbs & Harris 2001).

Additional Considerations and Future Research

The approach used in this review allowed us to integrate the evidence from a broad variety of studies that address regeneration of native woody species from diverse perspectives, with sometimes diverging criteria and definitions. The evidence presented here, rather than suggesting absolute patterns, indicates trends derived from a confined sample of studies, selected through specific, objective criteria. In addition, due to the broad scope of this study and the variety of aspects addressed by the studies included, the sub-samples describing the effect of certain factors on regeneration were sometimes insufficient, or inevitably biased toward specific regions or forest types. Therefore, the conclusions drawn from these results should be regarded with caution, acknowledging the limitations of our methodology.

To improve the information further, individual studies may be conducted to analyze the specific influence of stand attributes and environmental factors on regeneration, e.g. through targeted closed-framed review questions (possibly using meta-analysis approaches). This may help confirming or discarding the trends observed and understanding the mechanisms underlying their influence on regeneration. This is especially the case for those attributes for which the limited number of observations or the restriction to certain climates or regions did not allow robust conclusions on the nature of their effect on regeneration.

It is also relevant to highlight the possibility that several other attributes of mono-specific, even-aged stands not covered here might also have a consistent influence on regeneration during the early stages of restoration to natural or semi-natural forests. Reasons for their absence here may be inherent to the search and inclusion criteria adopted, or it may simply reflect the lack of studies in those specific areas.

Acknowledgments

Klaus Kremer received a DAAD-CONICYT scholarship, which supported his doctoral studies at the Faculty of Environment and Natural Resources, University of Freiburg. In addition, we are thankful to the reviewers of this manuscript for their thorough review and helpful comments.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Overview of the selected studies.
Table S2. List of categories of stand attributes and the associated explanatory factors whose effects on regeneration were assessed in the studies selected.
Figure S1. Flow diagram of the study selection process (adapted from Moher et al. 2009).

Coordinating Editor: Pedro Brancalion

Received: 29 April, 2020; First decision: 25 June, 2020; Revised: 15 July, 2020; Accepted: 16 July, 2020