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REVIEW ARTICLE

Functional traits and ecosystem services in ecological restoration

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The application of a functional trait-based approach to ecological restoration is receiving growing attention worldwide, but lack of knowledge on functional traits and how they link to ecosystem services imposes a major barrier to operationalize such approach. Synthesizing the existing knowledge on functional trait-based restoration is thus a timely and important challenge. We systematically reviewed the literature to assess how ecosystem services are associated to functional traits across organisms, ecosystem types, and continents. We also assessed the existing trait-based frameworks to target ecosystem services in restoration ecology. Then, we discussed future perspectives for the field, especially the challenges of applying trait-based frameworks in megadiverse tropical ecosystems, which have ambitious restoration commitments. Most papers focused on plants (72%), terrestrial habitats (69%), and non-tropical ecosystems (68%) and monitored ecosystem services and functional traits after restoration started rather than using them as previous targets. Only 12% of the papers targeted the restoration of both services and traits *a priori*, and 3.8% presented a clear trait-based framework to target ecosystem services in restoration. The possibility of selecting alternative subsets of complementary species in their provisioning of ecosystem services should make functional restoration more feasible than traditional approaches in species-rich tropical ecosystems. With this review and our critical insights on the perspectives of applying functional trait-based restoration widely, we hope to assist broad-scale restoration programs to obtain higher levels of benefits for nature and human well-being per unit of area undergoing restoration, going beyond the area-based approach that has dominated restoration commitments.

Key words: ecosystem function, functional diversity, functional restoration, reassembly, restoration target, trait-based restoration

Conceptual Implications

- Using functional traits enables practitioners to select species for delivering target ecosystem services during restoration.
- By using trait-based frameworks, restoration practitioners may select alternative sets of native species delivering similar ecosystem services.
- The flexibility in selecting alternative sets of functionally similar species may enable broad-scale functional restoration, especially in the tropics.

Introduction

Ecological restoration usually focuses on restoring species composition of pre-disturbance communities (Engst et al. 2016) either by reintroducing targeted native species or by favoring their spontaneous recolonization on degraded sites (Rodrigues et al. 2009; Chazdon & Guariguata 2016). Restoration programs usually rely on the premise that the increased abundance of species typically found in reference ecosystems would support the recovery of key ecosystem services such as nutrient cycling, soil protection, and water supply (SER 2004; Wortley et al. 2013; Laughlin 2014; Kollmann et al. 2016). However, recent meta-analyses on restoration success have demonstrated that either species composition or ecosystem services have not been fully recovered (Crouzeilles et al. 2016; Moreno-Mateos et al. 2017; Shimamoto et al. 2018). Incomplete recovery might be explained by a lack of an explicit approach to restore ecosystem services, which are the benefits people obtain from ecosystems, such as provisioning (e.g. fresh water), supporting (e.g. nutrient cycling), regulating (e.g. climate regulation), and cultural services (e.g. recreation) (MEA 2005). Biodiversity drives ecosystem functions that underlie ecosystem service (MEA 2005)

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provisioning by influencing ecosystem processes that directly or indirectly affect energy and material flows (Díaz et al. 2015). Here we consider that every ecosystem function is an ecosystem service by its direct or indirect effects on ecosystem benefits to humans.

If the loss of ecosystem services is a major concern in a world facing severe global changes (MEA 2005; IPBES 2019), services must be explicit targets in restoration programs (Ehrenfeld & Toth 1997; Funk et al. 2008; Montoya et al. 2012; Wortley et al. 2013; Laughlin 2014; Perring et al. 2015; Engst et al. 2016), and not only consequences of interventions guided for achieving other goals. However, a recent literature review found that most (52%) restoration project objectives have not explicitly considered ecosystem services (Kollmann et al. 2016). Although several papers and assessments have emphasized this need (e.g. SER 2004; MEA 2005; Montoya et al. 2012; Brancalion & Holl 2016) and some frameworks linking traits and services have been proposed (Laughlin 2014; Laughlin et al. 2018; Rayome et al. 2019), a clear framework on which services to consider and how to restore them using species traits is still missing (Kollmann et al. 2016), especially for broad-scale restoration. Therefore, the stability of communities over time and the services provided by restored ecosystems to support human well-being, especially under global changes, may be compromised.

Operationalizing ecosystem services as targets for restoration is still a major challenge (Kollmann et al. 2016), and the selection of species to attain target services is not trivial because multiple species may support several ecosystem services (Lavorel & Garnier 2002; Díaz et al. 2007). Knowing which species combination to reintroduce to restore ecosystem services while maintaining a stable restored community is a challenging task (Laughlin 2014; Laughlin et al. 2018). Traditional approaches to consider ecosystem services in restoration programs involve direct measurement of abiotic and biotic components (SER 2004). However, quantifying abiotic features hardly enables a clear association of ecosystem service and species composition, which has led ecologists to look at more meaningful and predictable parameters such as functional traits (Liebsch et al. 2008; Suganuma & Durigan 2015; Laughlin et al. 2017; Brancalion et al. 2018).

A common approach has been to classify species into "functional groups" a priori, and then trust that reintroducing members of each group would restore the targeted ecosystem services (Perring et al. 2012). Nonetheless, a priori grouping of species into "functional groups" has several shortcomings. First, the performance of a species in a given functional group may be context dependent, as the performance of a function may be determined by trait-environment interactions (Brancalion et al. 2019a). Second, a species may belong to more than one functional group, and thereby perform several services in varying degrees (Díaz et al. 2007). Third, the link between species and ecosystem services is mediated by effect traits, that is, those that impact ecosystem processes (Lavorel & Garnier 2002; Violle et al. 2007). Species have multiple effect traits that contribute independently or jointly to ecosystem services (Gamfeldt et al. 2008). Therefore, the effect of multiple species on different ecosystem services is more a multivariate continuum than a scenario with species classified into discrete functional groups. Fourth, by separating species into functional groups a priori, one may at best confirm an arbitrary decision rather than interpret how species relate to functional trait patterns a posteriori, which may provide information on which species contribute more to different ecosystem services. Because of the limitations to operationalize the use of traditional approaches of ecosystem service recovery by ecological restoration, new directions have been proposed in the literature (Funk et al. 2008; Laughlin 2014).

The claim for a new paradigm on ecological restoration demands a comparison on the advantages and disadvantages relative to the traditional paradigm (Table 1). Although restoration ecology studies have increasingly considered ecosystem services, on-the-ground restoration programs often experience difficulty applying biodiversity and ecosystem service theory in concert with the traditional restoration approach (Aerts & Honnay 2011; Kollmann et al. 2016; Naeem 2016). An alternative would be to use species effect traits clearly related to ecosystem services (Lavorel & Garnier 2002; Funk et al. 2008). An advantage of trait-based approaches is that they enable the assessment of the relationship between community assembly and ecosystem functioning (Laughlin 2014). This advantage exists because functional traits are two-sided coins in which "function" can be related either to response to community assembly processes mediated by abiotic and biotic interactions or to effect on ecosystem services (Lavorel & Garnier 2002; Violle et al. 2007; Suding et al. 2008).

Functional traits may be classified into "soft traits," that is, those that are easy and quick to measure, and "hard traits," that is, those that are harder to measure (Hodgson et al. 1999). Hard traits are usually more closely linked to mechanistic processes, but as they are hard to measure for a great number of species, they are usually replaced by soft traits that might be relevant to such processes. For instance, seed mass is a soft trait because it is relatively easy to collect and process seeds to get dry mass values, and at the same time represents correlated functions harder to measure, such as competition versus colonization abilities at initial stages of development (Turnbull et al. 1999). Functional traits may be related to mechanisms of community assembly such as competitive hierarchies (Keddy & Shipley 1989), limiting similarity (MacArthur & Levins 1967) and environmental filtering (Kraft et al. 2015). They can also relate to processes explaining how dominance of traits (i.e. mass ratio hypothesis, Grime 1998; and priority effects, Weidlich et al. 2018) or diversity of traits (i.e. niche complementarity, Tilman et al. 1997) influences ecosystem functioning. While the information on how traits affect ecosystem services relates to the biotic and abiotic components at an ecosystem-level framework, approaching how traits mediate community assembly mechanisms may provide information on community stability and resistance to environmental changes (Laughlin 2014).

The advantages of the trait-based approach for restoration rely, however, on the availability of information on functional traits for the species used in restoration projects (Table 1). Such shortcoming makes the use of a trait-based restoration especially

Table 1. The traditional approach for ecological restoration is based on species composition of the original community, often informed by reference ecosystems, and does not use species traits, while the trait-based approach relies upon theories of community assembly and biodiversity and ecosystem functioning, using functional traits that inform about species coexistence and species contribution to ecosystem services.

	Traditional Approach	*Trait-Based Approach*	*References*
Aim	Recover species composition of the original ecosystem and, consequently, ecosystem services	Recover ecosystem services of the original ecosystem based on functional traits	Funk et al. 2008; Montoya et al. 2012; Laughlin 2014; Engst et al. 2016
Advantages	(1) Seeks to restore the original ecosystem that was lost; (2) Once species have been reintroduced or regenerated naturally, ecosystem service recovery is expected	(1) Closely linked to ecological theory on community assembly and biodiversity and ecosystem functioning; (2) Enables targeting one or multiple ecosystem services based on functional traits	SER 2004; Laughlin 2014; Silva et al. 2015; Viani et al. 2017; Wainwright et al. 2018
Disadvantages	(1) Limited to local species pools; (2) Hard in ecosystems missing information on original communities; (3) Reintroduction of native species does not assure species composition will be similar to the original ecosystem	(1) The restored ecosystem may present a species composition that is different from the original community; (2) May be hard in megadiverse ecosystems lacking functional trait information for many species	Aerts & Honnay 2011; Laughlin 2014; Ostertag et al. 2015; Laughlin et al. 2017
Feasibility of applying in tropical ecosystems	Moderate, because the main objective is original species composition recovery, which involves difficulty and high costs in obtaining a high number of native species in nurseries	High (once traits are available), because a species unavailable for reintroduction may be replaced by a functional equivalent native species available in local nurseries	Funk et al. 2008; Aerts & Honnay 2011; Laughlin 2014

challenging for species-rich tropical ecosystems, because the existing knowledge on functional traits is still concentrated in temperate species (Hortal et al. 2015). Moreover, in tropical regions, there are many taxonomic uncertainties due to high species richness, lack of surveys, and overall low scientific development (Karlsson et al. 2007; Hortal et al. 2015; Wilson et al. 2016). Consequently, there is a lack of basic taxonomic, ecological, and physiological information for a great number of native species in the tropics, making it hard to recompose species composition of originally mega-diverse tropical communities. This knowledge gap is an important barrier for the ambitious restoration programs planned for the upcoming years, which have a clear focus on supporting human well-being through the recovery of ecosystem services in degraded landscapes worldwide, but especially in the tropics (Brancalion et al. 2019b). Synthesizing the existing knowledge on functional trait-based ecological restoration is imperative to transform the potential of this conceptual approach into more successful on-the-ground projects, fostering research to new directions that may better match the demands of restoration practitioners.

The central goal of this article is to assess the progress made in ecosystem service- and trait-based restoration. For this, we systematically reviewed the literature on restoration ecology (2007–2017). Although we did this review for all kinds of ecosystems, we had a special focus in tropical ecosystems, which have the most pressing needs to advance with the inclusion of a trait-based approach to guide restoration. Specifically, we answered: (1) is there an increasing trend of published studies on ecological restoration which evaluate ecosystem services and functional traits? (2) how often have ecosystem services and functional traits been used as targets for ecological restoration in general and across continents? (3) are there biases related to target organism, ecosystem type, and geography in the literature towards some ecosystem service type and functional trait? (4) what are the most common approaches of using ecosystem services and functional traits in restoration: a priori or a posteriori? (5) which functional traits are used to evaluate different ecosystem services in ecological restoration? (6) what are the existing trait-based frameworks to target ecosystem services in restoration? After answering these questions, we summarized possible connections between simple-to-measure plant functional traits and ecosystem services and discussed the feasibility of applying trait-based frameworks widely in the tropics, considering both the basic limitations such as the lack of trait information or species in nurseries and the concentration of the >140 million hectares of restoration committed to as part of the Bonn Challenge and the New York Declaration on Forests in tropical countries.

Methods

We systematically reviewed the ISI Web of Science database for papers published between 2007 and 2017. We chose 2007 as a start because a widely accepted concept of functional traits had been published that year (Violle et al. 2007). We followed the PRISMA protocol (http://www.prisma-statement.org/) for paper search and data collection standardization (Supplement S1). We looked for articles and reviews within the categories "Ecology," "Biodiversity conservation," and "Forestry."

We made a general search of papers for obtaining overall patterns within the restoration ecology field. We used the following keywords related to ecological restoration in the title of the papers: *restor** OR *reforest** OR *recover** OR *regenerat** OR *reintroduc** OR *refaunat**. The general search resulted in

7,362 papers potentially on restoration. We obtained the information on the number of papers on ecosystem service and functional trait per country by using ISI Web of Science summarizing tools. In order to map the general trend of publication on functional restoration across continents, we refined this general search by using the following sets of keywords related to services or traits in the topic of papers (title, abstract, and keywords): *function** OR *service** OR *guild** and *trait** OR *attribute**. We used each set of keywords at a time to filter only studies on services or traits, and together to obtain studies that evaluated both subjects simultaneously (by connecting keywords sets with an "AND"). This last refined search (i.e. resulting from searching service-related AND trait-related keywords within the general search) resulted in 337 papers, which were used in the following steps of the methods for obtaining more detailed information (hereafter, "specific search").

We obtained the full text of 334 out of the 337 papers from the specific search: 327 in English, 4 in Portuguese, and 3 in Spanish. We evaluated these 334 papers to identify those about restoration, that is, those with the aim of reestablishing, by means of re-introduction or natural recovery of native species, a pre-existing community entirely or partially lost due to anthropogenic causes. We consider as anthropogenic causes of a native community entire or partial loss phenomena (e.g. land use change, biological invasions). We did not include papers that studied the reintroduction of only one species with no focus on native species regeneration; assessed the recovery of a community after a natural disturbance (e.g. hurricane); aimed to assess restoration success by interviewing local human populations; aimed to spatially prioritize areas for restoration; or did not evaluate biological parameters.

We identified 265 papers on restoration (Supplement S2), which we screened to check: whether the study discussed or analyzed ecosystem services, and if the use of services was a priori (services used as targets in restoration) or a posteriori (services monitored in restored communities); whether the study discussed or analyzed functional traits, and if the use of traits was a priori (traits used to target services in restoration) or a posteriori (traits used to monitor restored communities); what ecosystem services were assessed; what functional traits were assessed; whether the study was carried in the tropics or elsewhere; the country of the study ecosystem; whether the focus ecosystem was terrestrial or aquatic; what was the specific terrestrial ecosystem type (Olson et al. 2001); what organism was used in restoration or was assessed during natural recovery; and whether the study proposed explicit and generalizable trait-based framework to select species for targeting ecosystem services in restoration (i.e. a framework that might be applied in different ecosystems).

Ecosystem services followed the classification by MEA (2005). We considered functional traits sensu Violle et al. (2007), that is, morphological, physiological, or phenological characteristics of organisms that impact species fitness and ecosystem processes and expanded on that definition by also considering life history and performance traits. Plant functional traits were classified into leaf economics spectrum, stem, root (including P and N acquisition strategy), flower (including pollination syndrome), diaspore (including dispersal syndrome, dispersal ability), whole-plant (maximum height, crown architecture), life history (life form, lifespan, carnivory), and performance traits (survival rate, growth rate, reproduction rate, physiological rate, competitive ability, stress tolerance, disturbance resistance/resilience, Grime's competitive/stress-tolerant/ruderal ecological strategies, total/aboveground/belowground biomass, vegetation strata, shade tolerance). We did not consider as functional traits general grouping of species based on habitat use (e.g. pioneer vs. non-pioneer) or mixtures of life forms with phylogeny (e.g. graminoids). For additional information screened from papers, see Supplement S3.

In order to test whether the rate of accumulated number of all papers on restoration (from general search; $n = 7{,}362$) differed from the rate of accumulated number of papers on restoration that also evaluated ecosystem services, functional traits, and both (from the specific search) as $n_{\mathrm{Service}} = 135$, $n_{\mathrm{Trait}} = 169$, and $n_{\mathrm{S+T}} = 76$, respectively, along time, we fitted generalized linear models (GLMs) using function "glm" of the software R (R Core Team 2019). We considered number of papers in each category as the response and year of publication as the predictor variable. We also fitted generalized nonlinear models (GNMs) with an exponential mathematical function using the "gnm" function of R package "gnm," but the linear models presented best fitting as shown by the Akaike information criterion: $\mathrm{GLM_{All}} = 872.6$, $\mathrm{GNM_{All}} = 1882.4$; $\mathrm{GLM_{Service}} = 92.5$, $\mathrm{GNM_{Service}} = 122.9$; $\mathrm{GLM_{Trait}} = 96.2$, $\mathrm{GNM_{Trait}} = 129.7$; $\mathrm{GLM_{S+T}} = 73.8$, $\mathrm{GNM_{S+T}} = 93.9$. We used Poisson distribution (in GLM and GNM) because response variables consisted of count data.

We used *t* tests to compare GLM slopes, considering the slopes are part of a Gaussian population of slopes of every possible hypothetical models. The *t* tests compared the slope of the GLM on the number of papers per each category of the specific search and the GLM on all papers, as follows: All versus Service; All versus Traits; and All versus Service + Trait. For computing the *t* tests, we used the estimate and the standard error of the estimate of the slope from the GLM.

We used Pearson's chi-square with Monte Carlo randomization tests (R function "χ^2 test") to check for dependency of relative proportion of studies about services, traits, or both on ecosystem type; services on ecosystem type and geography (tropical or not); and plant traits on ecosystem service categories. We also used chi-square tests to check for the prevalence of a priori versus a posteriori approaches in studies on services or traits.

Results

There was an increasing trend of publication of papers on restoration (specific search; $n = 265$) that assessed ecosystem services, functional traits, or both across the time period analyzed ($n = 228$), which accompanied the trend for the whole area of restoration (general search; $n = 7{,}362$) (Fig. 1). The rates of increase in these specific subjects (GLM slopes $b_{\mathrm{Service}} = 0.26$, $b_{\mathrm{Trait}} = 0.27$, $b_{\mathrm{Service+Trait}} = 0.31$) did not differ from the

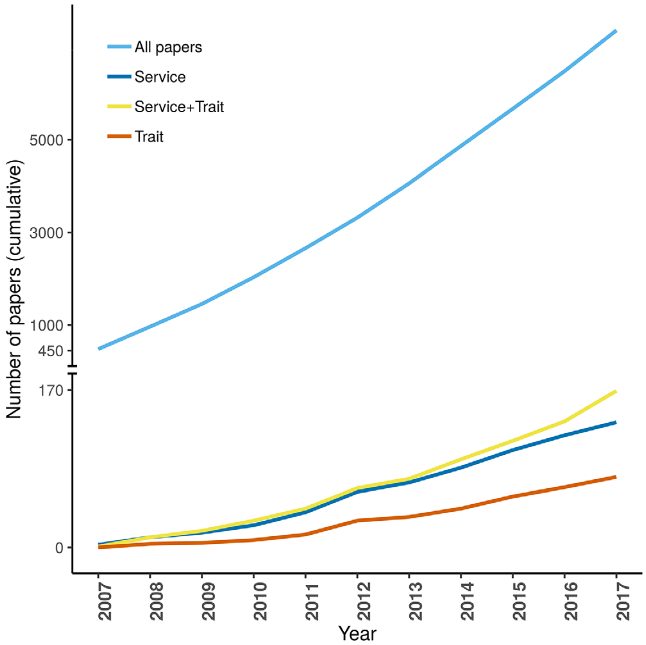

Figure 1. Cumulative trends of the general (All papers; $n = 7{,}362$) and specific searches (Service, Service + Trait, Trait; $n = 228$) in the functional restoration literature (2007–2017). A break was added to the y-axis to reveal trends between the specific subjects.

increase in the publication of papers on the whole ecological restoration field ($b_{All} = 0.21$) as shown by t tests: $t_{All\ vs.\ Service} = -0.95$, $df = 18$, $p = 0.36$; $t_{All\ vs.\ Trait} = -1.31$, $df = 18$, $p = 0.21$; $t_{All\ vs.\ Service\ +\ Trait} = -1.3$, $df = 18$, $p = 0.21$.

Most of the 7,362 papers (from the general search) were published by authors in North America and Europe, indicating the major role of developed countries on the ecological restoration literature (Fig. 2). Among the 7,362 studies, the proportion of papers that mentioned services, traits, or both was nearly constant across continents (Fig. 2).

We identified 228 out of 265 papers (from the specific search) that evaluated either ecosystem services, functional traits, or both. More than half of these papers focused on ecosystem services, whereas two-thirds evaluated functional traits (Table 2).

Most studies involved plants (72%), while 23% studied animals and only 3% micro-organisms, fungi, or algae. Most papers focused on non-tropical ecosystems (68%), terrestrial habitats (69%), and had forests or woodlands as the target habitat (43%). Only 26% targeted open vegetation such as grasslands and savannas, 16% freshwater ecosystems (rivers, streams, lakes, or wetlands), and 7% marine ecosystems (oceans zones, coral reefs, estuaries, and salt marshes).

The relative proportion of studies (from the specific search) on ecosystem services, functional traits, or both depended on the ecosystem type (Fig. 3). Temperate forests and temperate open vegetation were the most common terrestrial ecosystem types in studies that assessed ecosystem services and functional traits, respectively, while tropical forests (dry and moist) were relatively common in studies using functional traits (Fig. 3). Studies integrating both services and traits were more evenly distributed across ecosystem types, being especially common in temperate open vegetation and tropical rainforests (Fig. 3).

Supporting and regulating were the most common ecosystem services evaluated (Fig. 4). All categories of services (supporting, regulating, provisioning, and cultural) were found in both aquatic and terrestrial ecosystems in non-tropical ecosystems, but no papers assessing provisioning or cultural services were found in the tropics (Fig. 4).

Most studies (from the specific search) that focused on ecosystem services assessed them a posteriori ($\chi^2 = 62.59$, $p < 0.001$), that is, they assessed services after rather than before the beginning of the restoration (Table 2). Similarly, most studies on functional traits assessed them after rather than before the restoration began ($\chi^2 = 112.51$, $p < 0.001$). Overall, more studies assessed functional traits (64%) than ecosystem services (51%), especially a posteriori (72% and 61%, respectively). One-third of the studies assessed both ecosystem services and functional traits. Only 31 studies (11.7%) evaluated both a priori, thereby using traits to target services before the start of restoration.

All categories of plant functional traits were found in papers (from the specific search) that evaluated regulating or supporting ecosystem services, while only performance and diaspore-related traits were evaluated together with cultural or provisioning services (Fig. 5). Whole-plant, diaspore, and performance

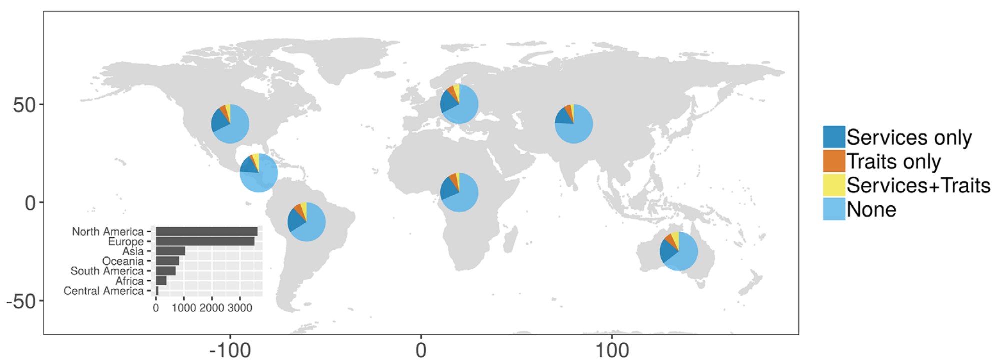

Figure 2. Geographical distribution of studies on ecological restoration (2007–2017) that mentioned the words ecosystem service, functional trait, both (and their derivatives), or none of them ($n = 7{,}362$).

Table 2. Number of papers on ecological restoration (2007–2017) that assessed ecosystem services and functional traits ($n = 228$ out of 265 screened papers; see details on the specific search in the Methods section). Note that all the papers on ecosystem services are under the category "ecosystem services," not only those that studied exclusively services. The same applies for the category "functional traits," and for "a priori" versus "a posteriori" comparisons. Moreover, the category "Ecosystem services + functional traits" represents the intersection (not the union) of studies on services and traits. Therefore, summing up values of the table does not result in 100%.

	Total		*A priori*		*A posteriori*	
	n	%	n	%	n	%
Ecosystem services	135	50.9	53	39.3	82	60.7
Functional traits	169	63.8	47	27.8	122	72.2
Ecosystem services + functional traits	76	28.7	31	40.8	43	56.6

traits were the most common plant traits studied (Fig. 5). Nutrient cycling and food web and community dynamics were the most common supporting services evaluated, while climate regulation, erosion regulation, and water cycling were the most common regulating services (Fig. S1). The different categories of functional traits were well distributed in terrestrial and aquatic ecosystems outside and in the tropics (Figs. S2 & S3).

Only 10 out of 265 screened papers (3.8%) presented a clear trait-based framework to target ecosystem services in restoration (Table 3).

We provided a summary of well-established linkages between plant functional traits and target ecosystem services to guide restoration practitioners (Table 4).

See the number of papers per country and journal in Tables S1 and S2.

Discussion

General Trends and Biases in Functional Restoration Literature

Our review elucidates that restoration studies taking into account ecosystem services and functional traits have been growing in number at a similar pace to the whole field of restoration. However, we found a series of biases in functional restoration research. If someone were to randomly pick a study from a pool of restoration studies, the selected study would be most likely about restoration of plants in forests outside the tropics in a developed country. Furthermore, there would be a good chance that the study evaluated functional traits, but most likely it would merely monitor trait variation along time with no clear relation to ecosystem services or to prior specific restoration targets. Ecosystem services were more rarely evaluated, and mainly in terrestrial, non-tropical ecosystems.

Although many international restoration commitments have been made by tropical developing countries harboring species-rich ecosystems, these countries lack restoration ecology studies considering functional traits, and, especially, ecosystem services. Our findings corroborate the observation made by recent studies about the lack of biodiversity studies in tropical ecosystems in developing countries (Wilson et al. 2016; Clarke et al. 2017). Our results indicate that the most concerning region is Africa, with a large area, high biodiversity, serious threats to native ecosystems, high demand on ecosystem services, and few studies.

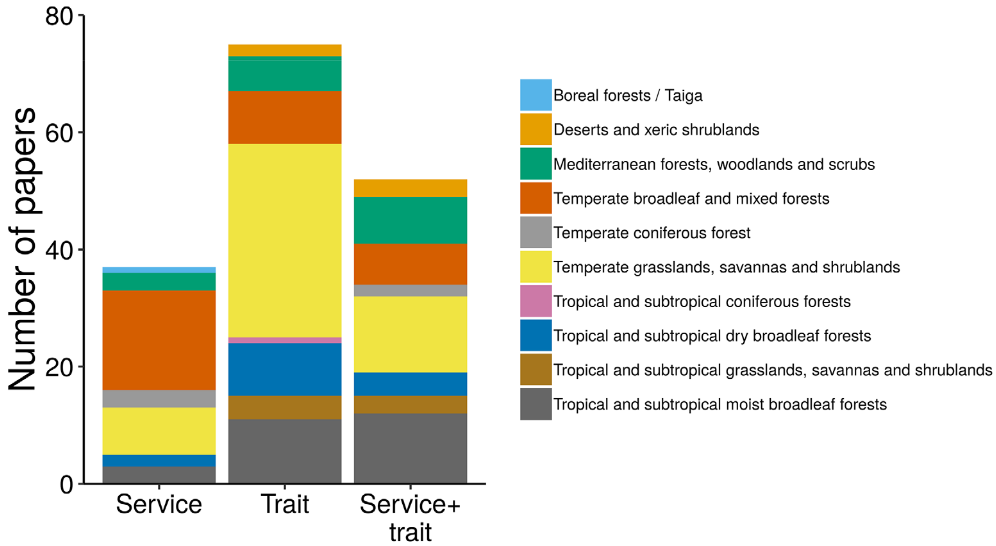

Figure 3. Distribution of terrestrial ecosystem types across 164 papers (2007–2017) evaluating ecosystem services, functional traits, or both. Relative proportions of papers on services, traits, and both depended on the ecosystem type: $\chi^2 = 42.07$, $p < 0.001$. It was not possible to ascribe an ecosystem type to all papers on services, traits, or both ($n = 228$).

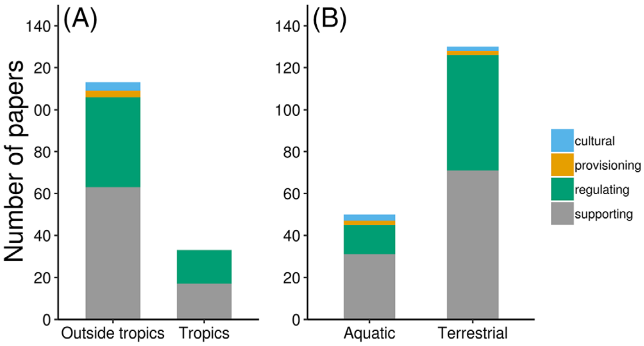

Figure 4. Number of papers considering supporting, regulating, provisioning, and cultural ecosystem services across 135 restoration ecology papers on ecosystem services (2007–2017) that focused on the tropics or elsewhere (A) and on aquatic or terrestrial ecosystems (B). Relative proportions of ecosystem service classes were independent of either geography or ecosystem category: tropics versus outside tropics, $\chi^2 = 2.82$, $p = 0.43$; terrestrial versus aquatic, $\chi^2 = 5.85$, $p = 0.10$.

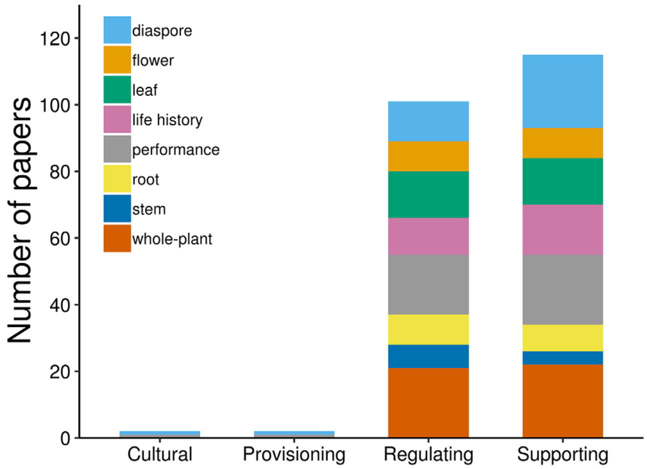

Figure 5. Number of papers (2007–2017) assessing different classes of plant traits and associated ecosystem service class. Relative proportions of plant trait classes were independent of ecosystem service classes: $\chi^2 = 11.38$, $p = 0.98$.

More specifically, our results indicate that, while the number of studies differ substantially, the proportion of studies that consider services, traits, or both is similar between developed (North America, Europe, Australia) and developing regions (South America, Africa). Despite this relative consistency across continents, studies evaluating services were more common in temperate forests, while those assessing traits were more common in temperate grasslands and relatively common in tropical forests. Our results suggest we need more functional restoration studies in the tropics, especially in tropical and subtropical grasslands, savannas, and coniferous forests, but also in tropical forests. These studies should include functional traits, and whenever possible, ecosystem services. As we found no studies evaluating cultural or provisioning services in the tropics, it would be interesting that future studies attempt to assess these kinds of services.

Our finding that most studies used services and traits a posteriori indicates monitoring of services and traits after restoration started is still much more common than their use before the beginning of restoration projects. The use of traits to target services before the start of restoration should be encouraged as a way to pursue the recovery of services in restored ecosystems (Laughlin 2014). Moreover, several of the studies did not evaluate trait functionality properly; they merely used traits as a separate dimension from taxonomic or phylogenetic dimensions of biodiversity without a clear mention to what the function meant. In order to ensure scientific rigor and higher predictability on the success of ecosystem service recovery, it is important that the relation of traits to ecosystem functioning and services be clear upfront in restoration projects.

What Are the Existing Trait-Based Frameworks to Target Ecosystem Services in Restoration?

A common approach among the trait-based frameworks for targeting ecosystem services in restoration was to use the classic theories of community assembly (Brudvig & Mabry 2008; Bochet & García-Fayos 2015), biodiversity and ecosystem functioning (Perring et al. 2012; Mahaney et al. 2015; Ostertag et al. 2015), or both together (Funk et al. 2008; Laughlin 2014). Funk et al. (2008) proposed to select native species with traits similar to traits from invaders for biological control of invaders. Laughlin (2014) proposed a quantitative model to use trait values for targeting ecosystem services in restoration. For instance, species with dense woods and low specific leaf area might be selected to provide the restored community with resistance to future dry conditions; functional trait diversity might also be prioritized. Laughlin's approach was the only to enable the adjustment of species abundances to functional goals of restoration. An important point that only four papers explicitly addressed was the trait-based selection of species from regional and habitat species pool (Brudvig & Mabry 2008; Laughlin 2014; Bochet & García-Fayos 2015; Ostertag et al. 2015). Assessing the functional structure of the habitat species pool at a regional scale may provide alternative candidate species that are functionally similar. Other frameworks focused on selecting species based on functional traits to restore functional redundancy and complementarity in plant-pollinator networks (Devoto et al. 2012), assure primary succession and phytostabilization on soils degraded by mining (Ilunga et al. 2015), and promote natural regeneration under semiarid conditions using nurse species traits (Navarro-Cano et al. 2016).

More recently (beyond our systematic review time frame), novel quantitative trait-based approaches for restoration of ecosystem services have been published. Laughlin et al. (2018) proposed a framework that enables selecting species for restoration to achieve convergent trait value targets and simultaneously maximize functional trait diversity. Rayome et al. (2019) proposed a framework and computer program to select species from regional pools based on the interpretation of multivariate trait patterns, which should enable practitioners selecting functionally redundant or complementary species based on restoration goals. Tsujii et al. (2020) developed a framework that enables selecting species for restoration from species pools to maximize

Table 3. Papers on ecological restoration (2007–2017) that presented a clear trait-based framework to select species for targeting ecosystem services in restoration.

Paper	*General Aim of the Framework*	*Ecological Theory*	*Target Ecosystem Service*	*Functional Ecology Method*	*Regional or Local Habitat Species Pool Is Considered?*	*Species Abundance Is Prescribed?*
Brudvig and Mabry (2008)	To select species from species pool for restoration based on functional traits	Community assembly from species pool	Fire resistance	Functional trait filtering from species pool; functional trait distribution in degraded and reference habitats	Yes (explicitly)	No
Funk et al. (2008)	To use community assembly theory to strengthen resistance to invasion in restored communities	Community assembly from species pool; Biodiversity and ecosystem functioning; Invasion biology	Invasion resistance	Analysis of species overlap in multivariate trait space; Functional diversity	Yes (implicitly)	No
Perring et al. (2012)	To select species for restoration based on functional traits for the provisioning of multiple ecosystem services	Biodiversity and ecosystem functioning; Novel ecosystems	Carbon storage; Soil erosion control; Invasion resistance; Nutrient cycling; Pollination	Functional richness (i.e. number of functional groups)	No	No
Devoto et al. (2012)	To restore functional redundancy and complementarity in plant-pollinator networks	Interaction networks	Pollination	Functional complementarity and functional redundancy in interactions	Yes (implicitly)	No
Laughlin (2014)	To generate ranges of species abundances to define which traits, trait values, and species assemblages should be used in restoration to achieve ecosystem services	Community assembly from species pool; Biodiversity and ecosystem functioning; Invasion biology	Drought resistance; Invasion resistance	Uni- and multimodal trait-based models; Multivariate trait spaces; Community-weighted trait means; Alpha functional diversity indices	Yes (explicitly)	Yes
Bochet and García-Fayos (2015)	To select species for restoration of semiarid ecosystem based on functional traits	Community assembly from species pool	Drought resistance; Soil erosion control	Generalized linear models of colonization success as a function of species traits	Yes (explicitly)	No
Ilunga et al. (2015)	To select species for restoration of degraded soil based on functional traits	Ecological succession	Phytostabilization (reduction of heavy metals in the soil)	Analysis of multivariate trait space (ordination)	Yes (implicitly)	No
Mahaney et al. (2015)	To select species for restoration based on functional traits to recover soil properties and achieve invasion resistance	Biodiversity and ecosystem functioning	Invasion resistance; Nutrient cycling	Analysis of multivariate trait space (ordination)	No	No
Ostertag et al. (2015)	To select species for restoration based on functional traits	Biodiversity and ecosystem functioning	Invasion resistance; Carbon storage	Analysis of multivariate trait space (ordination)	Yes (explicitly)	No
Navarro-Cano et al. (2016)	To select species for restoration based on functional traits of nurse species to improve natural regeneration	Facilitation	Erosion control	Functional diversity index	No	No

Table 4. A summary of plant functional traits that can be used as surrogates to target ecosystem services (MEA 2005) in ecological restoration.

Target Ecosystem Service	*Ecosystem Service Category*	*Associated Ecosystem Function*	*Associated Functional Trait*	*Trait Definition*	*Links Between Trait and Function*	*References*
Nutrient cycling (nitrogen)	Supporting	Soil fertility	Specific leaf area (SLA)	SLA is the one-sided fresh leaf area divided by leaf dry mass	Communities with high mean SLA have high decomposition rate, fast nitrogen cycling, and more fertile soils	Allison & Vitousek 2004; de Bello et al. 2010
Nutrient cycling (carbon)	Supporting	Carbon storage	Wood density (WD)	WD (often stem-specific density) is the dry mass of a wood segment divided by its volume	WD is related to carbon accumulation in lignin molecules. The higher WD among plants in the community, the higher the carbon storage of the ecosystem	Chave et al. 2009
Soil formation and retention	Supporting	Soil erosion control (including protection of river banks)	Foliage density	Foliage density (or canopy density) can be measured as plant dry mass per unit volume of plant	Canopy density of shrub and tree juveniles was correlated with sediment trapping ability in a flow erosion experiment. Denser canopies better protect the soil against flow erosion	Burylo et al. 2012
Pollination	Regulating	Pollination	Flower shape	Flower shapes may be classified as follows: dish to bowl, bell to funnel, head to brush, gullet, flag, tubular, or inconspicuous	Flower shape influences the identity of flower visitors. Accessibility to pollen and nectar is defined by flower morphology and interacts with visitor's morphology and behavior. High diversity of flower shapes might attract high diversity of pollinators	Fontaine et al. 2005; Olesen et al. 2007; Garcia et al. 2015
Seed dispersal	Regulating	Seed dispersal	Dispersal syndrome	Plant species may be classified into the following dispersal syndromes: zoochory, anemochory, hydrochory, autochory	Fruits and seeds show morphological adaptations to different abiotic and biotic dispersal agents. Restoration targeting high diversity of animal seed dispersers might focus on high functional diversity of diaspore-related traits (e.g. seed size, diaspore color)	van der Pijl 1982; Pilon & Durigan 2013
Invasion resistance	Regulating	Control of invasive plant species	Canopy cover	Canopy cover can be measured as the crown area of a tree individual	The larger the canopy cover of trees used in restoration, the highest is the probability of controlling invasive grasses through competitive exclusion	Brancalion et al. 2016; Viani et al. 2017
Natural hazard protection	Regulating	Fire resistance	Bark thickness	Bark thickness is the thickness of the part of the stem external to the wood	Thick barks confer tolerance to fire by protecting living tissues such as meristems and buds	Pérez-Harguindeguy et al. 2013
Climate regulation	Regulating	Climatic change resistance (drought)	Wood density (WD)	See above	High WD offers mechanical resistance against implosion by negative pressure in the xylem. Drought-tolerant plants usually support highly negative xylem pressures without cavitation. In regions where climate will change towards frequent droughts, high WD can be a target trait in restoration	Hacke et al. 2001; Laughlin 2014
Food	Provisioning	Food production	Fruit/seed edibility	Whether a fruit or seed is edible for humans	Edibility of fruits and seeds may be related to fruit/seed size and nutrients such as carbohydrates and oils	van der Pijl 1982; Cámara-Leret et al. 2017
Aesthetic values	Cultural	Leisure	Ornamental character	Whether a given plant is ornamental	Ornamental plants usually have colors or shapes aesthetically appreciated by humans (e.g. large and abundant flowers)	Kendal et al. 2012

functional richness and redundancy simultaneously as proxies for multiple ecosystem services and resilience with the minimal possible set of species. These recent trait-based frameworks permit the choice between functionally similar species from a previously known (regional or habitat) species pool, which may facilitate practitioners to use species that are available in the market, while assuring that certain ecosystem services will be provided in the restored ecosystem. Nevertheless, we consider we still miss a unified approach that simultaneously enables the trait-based selection of species from regional/habitat species pools and the definition of relative abundances of the selected species to achieve the provisioning of target ecosystem services.

Challenges to Put Trait-Based Frameworks for Restoration in Practice at Broad Scales

A major challenge for a trait-based restoration in the tropics (and elsewhere) is the lack of knowledge on functional traits of native species (Aerts & Honnay 2011). Establishing linkages between traits and services is still a major challenge in the ecological literature as a whole and has important implications to restoration ecology. We showed some patterns on how traits and ecosystem services are related in the restoration literature, which might help prioritize future studies. For instance, food provisioning might be targeted in tropical forest restoration, and the edibility of fruits or seeds might be used as a trait to achieve the delivery of this service in the restored ecosystem. In order to help practitioners put in practice a trait-based restoration to recover ecosystem services, we provided a summary of linkages between plant functional traits and target ecosystem services that are more consolidated in the literature.

Ideally, functional traits might be available for the whole regional species pool relative to the sites to be restored. Some functional traits, like performance, whole-plant, and diaspore traits, are relatively well studied in the tropics, while others are less studied. In a major compilation of trait data, Petisco-Souza et al. (2020) found major gaps of information for key functional traits of 2,236 tree species of the Brazilian Atlantic Forest after searching in global plant trait databases, specialized books, regional datasets, and digitized plant specimens: 88% for seed mass; 85% for specific leaf area; 53% for wood density; and 16% for maximum height. These findings emphasize the importance of more funding for basic biodiversity research in the tropics both to fill biodiversity knowledge shortfalls and to advance scientific understanding on ecosystem functioning.

Taxonomic and functional information needs also to be constantly reviewed and updated to accomplish the goals of functional restoration. A good example of broad-scale standardization of taxonomic nomenclature exists for Brazil: the database of the Brazilian Flora 2020 project (Forzza et al. 2012). This database compiles the accepted scientific names and basic biological information of more than 46,000 species of plants, algae, and fungi and is frequently updated by more than 400 experts (http://ipt.jbrj.gov.br/jbrj; accessed 24 Aug 2020). Considerable effort has already been made in research groups working in tropical countries for gathering functional traits as well, and data have been made available in major databases such as TRY Plant Trait Database (Kattge et al. 2020) and Botanical Information and Ecology Network (Maitner et al. 2018), besides several regional databases.

Ecosystem services and functional traits are increasingly being used in ecological restoration, although too few studies have considered them for ecological restoration in the tropics. Trait-based frameworks are useful for broad-scale restoration in the tropics because they may help circumvent common limitations of restoration in developing megadiverse countries (e.g. lack of saplings or trait information) by enabling considering alternative sets of species of the regional pool leading to similar resolutions of target services. While funding for tropical research is impaired and more complete datasets are not available, we advocate the use of the best existing ecological theory and available data in trait-based models to select species sets that will enable the restoration of ecosystem services.

We advocate that next steps towards a broad-scale functional trait-based restoration in the tropics are to: (1) define priority target ecosystem services for ecological restoration; (2) focus on measuring key functional traits linked to priority ecosystem services based on up-to-date scientific evidence; (3) test whether current restoration programs are reaching the functional composition and structure of reference ecosystems (Rosenfield & Müller 2017); and (4) run trait-based quantitative frameworks to select sets of native species and their abundances for areas that will be subject to restoration.

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Supporting Information

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

Supplement S1. Steps followed during the systematic review.
Supplement S2. Papers on ecological restoration (2007–2017) retrieved from the systematic review.
Supplement S3. Additional information screened from papers on ecological restoration (2007–2017).
Table S1. Rank of countries where studies on ecological restoration (2007–2017) were carried out.
Table S2. Rank of journals that published papers on ecological restoration (2007–2017).
Figure S1. Number of papers evaluating different ecosystem services in terrestrial or aquatic ecosystems.
Figure S2. Number of papers of different classes of plant traits in the tropics and elsewhere among ecological restoration studies.
Figure S3. Number of papers assessing different classes of plant traits in terrestrial or aquatic ecosystems.

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