

SYNTHESIS & INTEGRATION

Plant functional traits as measures of ecosystem service provision

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Abstract

Despite the relevance of ecosystem services (ES) to society and modern ecological research, current methods of measurement and mapping remain inconsistent and often lack primary data in estimating and modeling ES. A key player in our understanding of ES and their measurements are plant functional traits—chemical and physical aspects of plants—which are often cited as one of the drivers of ecosystem processes and functions. In order to better quantify the ES–plant functional trait indicators, we outline existing evidence of this relationship and identify gaps between the best predicted ES and the most valued ES. This study offers an up-to-date review of plant functional traits’ direct or indirect relationships with ecosystem service provision and discusses the quantitative evidence these traits might hold as indicators. With this review, we seek to (1) offer a current summary of the quantitative evidence on ecosystem service–plant functional trait relationships, (2) identify which traits have been used to successfully indicate ecosystem services, and (3) identify research gaps, and ecosystem services or traits that receive little attention or have weak criteria as indicators. In a comprehensive literature review of the 19 services that were searched for, genetic materials, medicine, and cultural services had no relevant plant functional trait indicators, while the remaining 16 services had a range of traits associated with them. We found that functional traits showed varying relationships to ES, with some depending on the ecosystem type they were found in, while others appeared to remain consistent across ecosystems and conditions. This indicates that there could exist a subset of traits that are “universal” indicators across all ecosystem types, while others are ecosystem dependent. Our review suggests the need for more research on less clearly defined ES (such as cultural, educational, and refugium services) both by more careful definitions to make quantitative measures more applicable, and through increased quantitative and qualitative studies to better understand the nature of ES indicators for these services. This summary shows how plant functional traits can quantitatively and reliably predict and provide details on a subset of ES.

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KEYWORDS

community-weighted averages, ecosystem functions, ecosystem services, indicators, literature review, plant functional traits, service providing units

INTRODUCTION

Ecosystem processes depend on the species and functional composition of an ecosystem, particularly the plant community (Hooper et al., 2005; Lavorel et al., 2007; Lavorel & Garnier, 2002; Suding et al., 2008). Plant species richness and abundances are often used to assess ecosystem health, restoration, external influences (both positive and negative), and other important aspects of ecosystem processes and functions. More recently, the use of plant functional traits—the characteristics of plants that determine responses to and effects on the surrounding environment, other species, and trophic levels (Pérez-Harguindeguy et al., 2016)—has become an efficient and accurate way to investigate the effects of large-scale land and climate change (Díaz & Cabido, 2001; Suding et al., 2008) as well as various disturbance effects (Hooper et al., 2005; Pérez-Harguindeguy et al., 2016). In fact, since they offer both a mechanistic explanation and accurate estimate of multiple ecosystem processes and functions, the use of plant functional traits to explain ecosystem processes has been deemed the “Holy Grail” in ecology (Funk et al., 2017; Lavorel et al., 2007). These functional traits provide accurate measures of many ecosystem processes and responses, directly scaling up from plants (which are often considered the foundation of an ecosystem) to ecosystem-level functions (Kremen, 2005; Suding et al., 2008) since changes in plant traits have a direct and often determinative effect on the ecosystem functions which drive ecosystem processes (Suding et al., 2008). This is particularly relevant, as ecosystem services (ES)—the aspects of ecosystems that directly or indirectly benefit humanity—have also been both theoretically and quantitatively linked to these functional trait responses and measures (see Figure 1; Bardgett et al., 2014; de Bello et al., 2010). These ES can be anything from food and raw materials, benefits of biodiversity, clean air and water, to the regulation of whole systems of water flow, nutrient cycling, and climate regulation (Fisher & Turner, 2008). Given the relevance of ES to society and recent importance in the intersection of conservation and applied ecology, it is essential to have consistent and accurate methods of measurement (Carpenter et al., 2009), particularly with the growing threat of climate change and global land-use change (Imbert et al., 2021; IPBES, 2019; Schlickmann et al., 2020).

Many frameworks for measuring the demand and flow of ES focus on social variables that influence ES provision (Olander et al., 2018; Quintas-Soriano et al., 2018; Spangenberg et al., 2014) investigate trade-offs between ES and conservation (Chianucci et al., 2018; Lang & Song, 2018; Moein et al., 2018), or categorize the world's ES potential on global, national, and municipal levels (Ala-Hulkko et al., 2019; Milheiras & Mace, 2019). Unfortunately, these methods of measurement and mapping remain inconsistent between studies, often relying on indirect indicators such as land cover (Burkhard et al., 2009) which overlooks significant beta diversity changes and other heterogeneity across a single habitat. Since landscape averages and ecosystem type estimates depend on generic characteristics of an ecosystem to predict provision, rather than recognizing and investigating the dynamics of the ecological or biotic mechanisms of service delivery, these measures do not account for the complexities and influence of multiple environmental and human drivers (Suding et al., 2008). Additionally, the social measures that are a frequent alternative (Sherrouse et al., 2011) are highly subjective (Malherbe et al., 2019; Martínez-Harms & Balvanera, 2012; Olander et al., 2018; Paudyal et al., 2019). These inconsistent and subjective measures remain the norm, despite several calls to develop a standard indicator (Boyd & Banzhaf, 2007; Kremen, 2005; Layke et al., 2012) and to include more primary data in service measures (Eigenbrod et al., 2010; Lavorel, 2013). Using plant functional traits as a standard indicator of ES delivery can reference the mechanism or a deeper understanding of ecological principles which allows for management of ES and prediction of future service availability. With the growing consensus that it is composition and functional effects of individual species, rather than species diversity or richness, that better predicts ecosystem processes (and thus ES), plant functional traits are one option to provide an accurate and holistic explanation of ecosystem services (Chapin III, 2003; Díaz & Cabido, 2001; Manzoor et al., 2019; Shipley et al., 2006).

The idea of functional traits providing measures of ecosystem services is not new. In fact, de Bello et al. (2010), completed a general review outlining the relationships between plant functional traits and ecosystem services, justifying the increasing attention that these traits were receiving as a key factor in how biotic forces influence the ecosystems around them, including ES. In

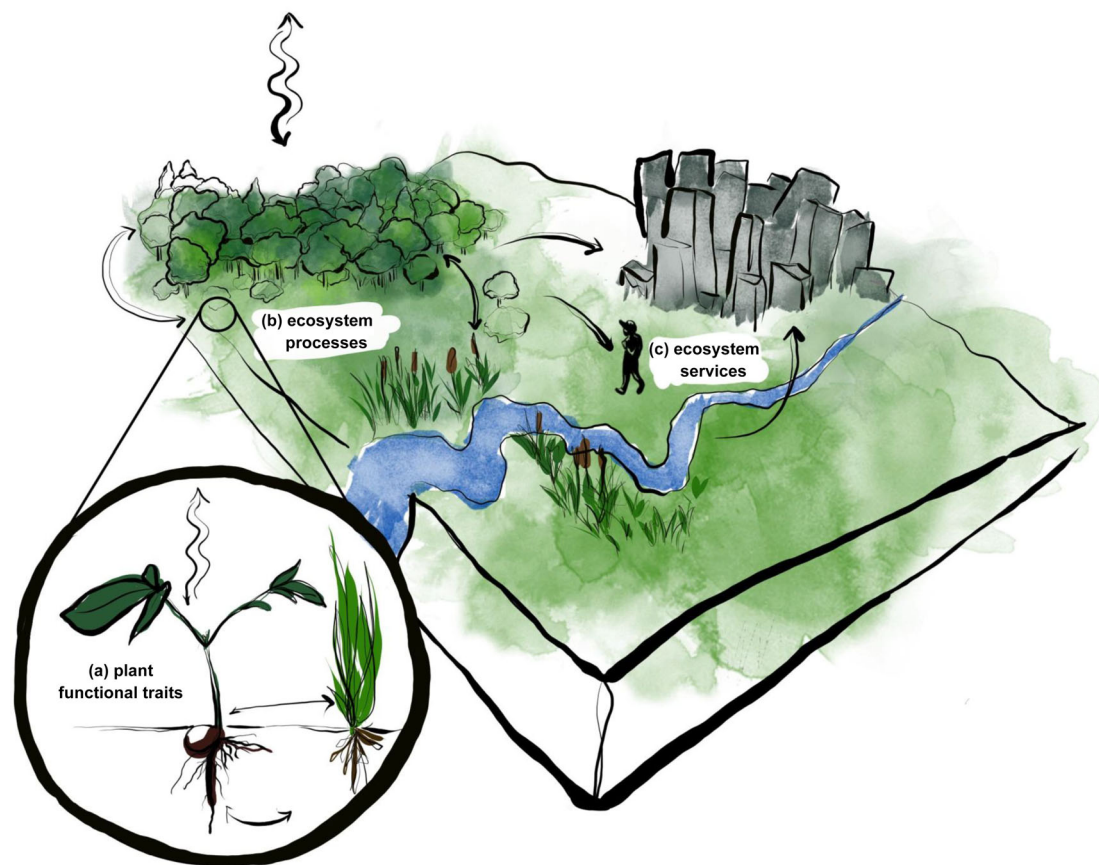


FIGURE 1 The relationship between plant functional traits (shown in the circle), ecosystem functions and processes (shown with double sided arrows), and ecosystem services (with movements shown with a single arrow). (a) Plant functional traits can both determine ecosystem processes (through community averages shaping the way the ecosystem function or be shaped by them (the influence of ecosystem determining how individual plants or communities respond, or filtering which traits are able to survive). Traits of the plant community, as the producers of an ecosystem, form the basis for (b) ecosystem processes or ecosystem functions, which are the flows of nutrients or processes in an ecosystem (e.g., water filtration or carbon sequestration) that occur on an ecosystem-wide scale and keep the ecosystem functioning as whole. Ecosystem processes include how plant communities interact with abiotic factors of the environment such as soil–root interactions. These processes can be complex or simple and although they occur at a large scale, they encompass the traits and characteristics of entire communities across the ecosystem. They occur, whether or not humans are present or benefit unlike (c) ecosystem services, which refers to ecosystem processes that have a direct or indirect benefit to human society or individuals. Ecosystem services refer only to the benefits that society derives from these naturally occurring processes and is thus necessarily anthropocentric in nature

this paper, they listed 247 studies of trait–service relationships between plants and invertebrates, discussed many theoretical mechanisms of how traits lead to ES, and provided a basis for the applicability of these traits to measure and explain ES and trait–service clusters for ES prediction. In the 10 years since its publication, many new papers have continued the investigation of the links between ES and plant functional traits. To better understand the potential that functional traits hold for accurately measuring service delivery, we offer a current review of the literature from 2010 to 2021, investigating the use of plant functional traits as indicators for ES. We outline what plant functional traits specifically have been used to identify relationships with ES provision and discuss the theoretical and quantitative evidence these traits

might hold as indicators. ES are increasingly relevant for both researchers and policymakers alike, and knowledge of functional traits as measures of ES could be incorporated into estimates of natural resources and capital for municipalities (Lam & Conway, 2018; Sang et al., 2021), conservation and restoration (do Vale et al., 2010; Zirbel et al., 2017), and measures of changes in ecosystems due to climate change and urban expansion (Song et al., 2019). The objectives of this paper are to (a) offer a current review of the literature on ecosystem service–plant functional trait relationships, (b) identify which traits have been used to successfully indicate ecosystem services, and which traits have strong theoretical evidence, and (c) identify research gaps, and ecosystem services or traits that receive little attention or have weak criteria as

indicators. In this way, we seek to further the understanding of current trait–service research to provide an updated and thorough summary of the research as well as outline which traits have the potential to act as robust indicators of ecosystem service.

METHODS

For this review, we followed the guidelines for systematic review outlined by Pullin and Stewart (2006) to search for papers investigating the relationship between plant functional traits and ecosystem services. A Boolean search was performed in Google Scholar, including the keywords of plant functional traits and the titles of 19 different ES (as outlined by de Groot et al. (2002) and cross-referenced with IPBES, 2019 Science’s more modern interpretation of these classic categories) (see Appendix S1 for full search terms for each service–trait relationship). The 19 ecosystem services that were searched for were as follows: gas regulation, climate regulation, disturbance prevention, water regulation, water supply, soil retention, soil formation, nutrient regulation, waste treatment, pollination, biological controls, refugium, nursery, food, biodiversity, medicinal, raw materials, genetic resources, and ornamental resources. All results were amalgamated, and duplicates were removed resulting in a total of 1427 papers from all searches. The papers were then refined—the abstract and text were skimmed, and only quantitative studies that measured a relationship between one of the ecosystem services listed and at least one plant functional trait were kept, eliminating papers that did not measure specific functional traits or functional diversity. We also eliminated any meta-analysis or literature reviews, books, reports, summaries, as the focus was on discovering published quantitative studies that had investigated trait–service relationship. Finally, papers that investigated functional trait or plant community assembly through management, land-use type, land-use change, or ecosystem type, rather than direct or indirect links between functional traits and ecosystem services were removed. This resulted in a total of 127 papers.

RESULTS

We found a total of 127 relevant studies with primary results showing relationships between plant functional traits and ES or service-related functions (see Appendix S2 for full details). For these papers, there were 84 individual plant functional traits cited as having associations with ecosystem services (see Table 1 and Appendix S2). Specific leaf

area (SLA) was the functional trait that was cited most often, being referred to in 45 papers, and with 18 different ES relationships (Appendix S2) and relating to 11 different ES categories—biodiversity, climate regulation, disturbance prevention, erosion prevention, food/fodder, gas regulation, nutrient cycling, raw materials, refugia, soil fertility, and water provision. SLA was also cited as being related to several subservices. For example, SLA was associated with N content, litter decomposition, and soil carbon all of which are often used as indices of soil fertility (Daou & Shipley, 2019; Partey et al., 2017; Yageta et al., 2019). Plant height was the second most frequent functional trait, along with functional diversity (the diversity of several different traits, dependent on the paper) identified in 29 papers. Plant height was found to be relating to seven different ES—climate regulation, disturbance prevention, pollination, raw materials, soil fertility, and water provision, while functional diversity was related to nine services: climate regulation, disturbance prevention, erosion prevention, gas regulation, multifunctionality, nutrient cycling, pollination, raw materials, and soil fertility (Appendix S2). Functional diversity was tied with plant height for reference used in 29 papers. Leaf dry matter content (LDMC) and leaf nitrogen content (leaf N) were fourth and fifth with 25 and 24 citations, respectively, followed by leaf area (with 18 citations)—the other leaf nutrient contents, such as phosphorus (7) and carbon (7) cited much less frequently (see Table 1 for full list of citations and traits).

Of the 19 services that were searched for, two of them came up with no relevant plant functional trait indicators in our literature review: genetic materials and nursery services. The remaining 16 had a range of traits associated with them, from medicinal resources—which found only two functional traits related—to soil fertility—which had 65 citations (some trait associations were repeated across studies) (see Table 2 and Appendix S2). The second most commonly cited ES (after soil fertility) was climate regulation (cited 63 times), followed by disturbance prevention (56 times), water provision (52 times), raw materials (45 times), and erosion prevention (35 times) (see Table 2 and Appendix S2). Traits were frequently associated with more than one ES and those that were related to multiple services could even be related to different aspects of ecosystem functioning (e.g., both soil and water, or both raw materials and atmospheric regulation, as opposed to soil retention and soil fertility, both of which refer to aspects of the soil). Additionally, there are several service–trait relationships that were repeated in the literature, the most frequent of which was the positive association between plant height and raw materials (seven occurrences) closely followed by the negative association between SLA measures and disturbance prevention (seven occurrences) (see Appendix S2 for all details).

TABLE 1 Functional traits found to have statistical evidence of relationship to ecosystem services

Plant trait	Functional trait	No. references	Citation number
Diversity measures	Plant functional identity	18	[2,4,10,22,25,44,49,50,55,67,77,83,86,120]
	Functional diversity (aspects see papers)	29	[11,15,21,23,28,32,41,42,51,52,57,58,59,61,64,65,68,76,81,84,88,102,123]
	Functional evenness	3	[41,61,87]
	Functional divergence	3	[46,103]
	Functional dispersion	1	[56]
	Functional variation	3	[84,114]
	Functional richness	3	[87,112]
	Functional variance	10	[14,33,115]
Whole plant	Plant functional identity	18	[2,4,10,22,25,44,49,50,55,67,77,83,86,120]
	Plant height	29	[1,12,14,18,24,27,32,34,35,46,52,53,58,60,66,84,85,94,98,100,115,119,121,122]
	Aboveground biomass	3	[4,16,35]
	Basal area	2	[24,35]
	Wood density	6	[27,33,48,84,93,119]
	Legumes	6	[32,55,77,96,109,123]
	Leaf/stem biomass	1	[37]
	Xylem vulnerability	1	[38]
	Shoot mass	3	[40]
	Root : shoot ratio	2	[40]
	Plant tensile strength	1	[61]
	dbh	1	[62]
	Shoot biomass	1	[75]
	Shoot length	2	[75,125]
	Growth rate	2	[78,94]
	Wood specific gravity	1	[87]
	Canopy density	2	[92,122]
	Bark thickness	2	[100,127]
	Wood P content	1	[105]
Flowers	Floristic status	1	[123]
	Nectar availability	2	[52,124]
	Pollen tubes	1	[52]
	Flower size	1	[52]
	Flower color	2	[52,124]
	Seed mass	3	[27,39,90]
Leaf	SLA	45	[3,6,12,13,14,18,20,22,23,27,31,34,35,36,40,41,53,54,58,60,69,71,74,75,76,78,85,93,96,99,101,109,111,113,115,123,127]
	Leaf length	1	[4]
	Leaf width	4	[4,40]
	Lignin content	2	[5]
	Leaf area/surface area/leaf area density	18	[7,18,23,27,30,31,60,62,70,78,89,92,98,104,109,117]
	Leaf N content	24	[7,18,19,20,34,48,54,55,58,60,66,69,72,85,91,105,107,111,115,125]
	Leaf C:N ratio	6	[7,20,73,74,120]

(Continues)

TABLE 1 (Continued)

Plant trait	Functional trait	No. references	Citation number
	LDMC	25	[8,18,20,23,36,39,48,58,60,71,79,82,85,96,101,113,115]
	Leaf thickness	9	[9,13,31,36,39,101,108,109]
	Stem density	5	[10,47,60]
	Leaf toughness	2	[13,54]
	LAI	3	[17,22,122]
	Leaf mass per area	1	[19]
	Leaf weight ratio	1	[19]
	Leaf K content	2	[19,73]
	Leaf cover	2	[24]
	Leaf biomass	1	[30]
	Photosynthetic rate	1	[36]
	Leaf P content	7	[36,72,105,107]
	Leaf turgor loss	1	[38]
	Leaf force to tear	1	[41]
	Leaf chlorophyll	2	[43]
	Leaf density	4	[47,89,101]
	Leaf C content	7	[58,85,107,115]
	Leaf N:P ratio	5	[60,72,107]
	Leaf pubescence	2	[70,104]
	Leaf Ca content	1	[73]
	Stomatal density	1	[73]
	Leaf surface area: volume ratio	1	[99]
	Leaf bulk density	1	[99]
Root	Root depth/shallow root allocation	8	[12,26,32,40,58,98,119]
	root thickness	1	[26]
	root density (deep root density, root tissue density, root mass density)	7	[26,45,47,53,58,115,116]
	SRL	3	[26,63,78]
	Root chemistry	2	[29]
	Root biomass	2	[37]
	Fine root proportion	4	[37,58,95]
	Coarse root proportion	1	[37]
	Root mass	4	[40,80,126]
	Root surface area	1	[41]
	Root diameter	6	[41,63,95,103,109]
	Root aerenchyma	1	[53]
	RDMC	1	[53]
	SRA/surface area	3	[58,109]
	Root length density	1	[79]
	Root N content	1	[91]
	Fine root density/fine root length density	3	[91,126]

(Continues)

TABLE 1 (Continued)

Plant trait	Functional trait	No. references	Citation number
	Root tensile strength	1	[103]
	Root C content	2	[106,109]
	No. Tillers	1	[110]
	Tiller density	1	[110]
	Root length	5	[108,110,116,118,126]

Notes: The traits are divided by plant trait type (whether it is a leaf, root, whole plant, etc.). The citation numbers correspond to the paper citation in Appendix S2. The number of references might be higher than the number of citations as some papers reference multiple trait–services per study. See Appendix S2 for details of the trait–service relationship.

TABLE 2 Ecosystem services found to have statistical evidence of relationship to plant functional traits

Ecosystem service	No. references	Study number (see Appendix S2)
Raw material	45	[1,14,21,32,34,46,58,60,64,66,90,119,123,125]
Nutrient cycling	27	[2,5,20,29,62,72,76,82,86,91,115]
Disturbance prevention	56	[3,4,11,15,17,26,31,37,38,53,63,78,99,100,101,102,108,109,118,121,123]
Soil fertility	65	[6,8,9,10,13,19,23,24,27,29,43,47,48,50,62,66,67,72,74,75,76,81,91,94,105,112,113,115,126]
Water provision	52	[6,7,18,22,30,35,36,39,43,47,59,65,73,74,75,79,83,94,98,101,126]
Climate regulation	63	[8,12,14,16,18,33,40,46,50,55,56,74,80,84,85,87,93,106,107,111,114,115]
Waste regulation	8	[9,44,104,117,120]
Nursery	1	[10]
Gas regulation	5	[14,50,81]
Food/fodder	15	[24,25,54,69,71,77,96]
Habitat provision	1	[24]
Multifunctionality	2	[28,97]
Erosion prevention	35	[40,41,42,45,57,61,70,89,92,95,103,110,116,122]
Biodiversity	6	[40]
Pollination	13	[49,51,52,68,88,102,124]
Refugia	2	[127]

Notes: The citation numbers correspond to the paper citation in Appendix S2. The number of references might be higher than the number of citations as some papers reference multiple trait–services per study. See Appendix S2 for details of the trait–service relationship.

DISCUSSION

Plant functional traits offer some of the clearest potential to measure ES and provide a scientifically defensible and comparable quantification method, with both inter- and intra-specific traits being strong indicators of environmental conditions and change (Cadotte, 2017; Pérez-Harguindeguy et al., 2016). As the ecological community continues to scale up the implications of plant functional traits to larger ecosystem-level processes and effects (Suding et al., 2008), we must not overlook the potential to use these traits to measure the changes in ES provision (Chapin III, 2003; Hooper et al., 2005; Shipley et al., 2006). Our review reveals 127 research articles with

statistical evidence of the potential of functional traits as indicators or co-indicators of ES. This is fewer papers than de Bello's 247 papers, a fact most likely due to de Bello et al.'s search for multiple trophic levels (including the functional traits of birds, invertebrates, microbes, and vertebrates as well as vegetation), and inclusion of theoretical relationships, while our review focused only on quantitative evidence. In keeping with de Bello et al., the majority of our searches found functional indicators for ES which had clear definitions (e.g., food/fodder, water regulation) compared to more loosely defined services often directly tied to human use (e.g., cultural and medicinal services). The only two services that seemed to differ in frequency between our results and those of de Bello

were disturbance prevention and soil retention (first and sixth most commonly studied services, respectively, and which were not clearly outlined in de Bello et al.'s paper). This is likely due to the increase in the rampancy of invasive species and the recent push from ecologists and stakeholders alike for preventing invasive species takeover both natural areas and urban sites (Lishawa et al., 2019; Molloy et al., 2017). This could also relate to the increase in disturbance phenomena (i.e., flooding, forest fires, runoff, etc.) in the past decade and an effort to use knowledge of ecological processes to mitigate their negative effects (Abatzoglou & Williams, 2016; Arnell & Gosling, 2016).

The shift in frequency of specific trait–service relationships could indicate an evolution of research in ES and is likely connected to whatever services are currently at most risk or have the greatest potential to mitigate negative natural phenomena. (Droste et al., 2018). For example, there were a high number of studies investigating disturbance prevention and erosion prevention, two services the benefits of which are increasingly noticed and valued in both agricultural and development sectors. Erosion prevention not only saves topsoil but can save both money and resources (Alam, 2018) in both industrial and small-scale farming operations—important benefits given concerns over global food security (Rhodes, 2014; Wuepper et al., 2020). Disturbance prevention, especially fire resistance and recovery, is of particular interest as climate projections often suggest an increase in fire frequency and severity due to climate change (Halofsky et al., 2020). The same is true of flooding resistance and recovery, which is also likely to become increasingly necessary in coming years (Hirabayashi et al., 2013). While papers dealing with remediation were not usually included in the results, as they focused on progression of ecosystems rather than service provision, there were quite a few papers returned in the search that used functional traits to measure recovery and restoration goals, another indicator of increased restoration ecology (do Vale et al., 2010; Winfrey et al., 2018).

Several papers from our search discussed trait change due to climate warming, urban expansion, and/or resistance invasion (Schlickmann et al., 2020; Song et al., 2019). These studies were not included in our final table, as they measured changes in traits rather than ES delivery. However, these studies along with those on restoration ecology do indicate that traits are being leveraged to provide insight into current climate and ecological issues. There were also discussions of the development of planting and restoration regimes based on functional trait effects—using trait–service relationships to design systems via known plant functional trait effects that provide the greatest probability of desired ES given a particular ecological risk. For example, the mitigation of

flooding through planning of high soil retaining species or plans to increase resistance to/recovery after forest fires through planting of fire-resistant species (Feagin et al., 2015; Pickering & Barros, 2015).

Three of the ecosystem services searched for—genetic resources, medicinal resources, and cultural services—did not have any functional trait associations. The lack of information on these services is likely due to a two-pronged—difficulty in defining them, and the already established standards of measure. Sources throughout the past decade had difficulty measuring mainly refugium and nursery function, as well as establishing proper measurements for cultural services (de Bello et al., 2010). For nursery services (only one relationship found), there is little information, and it does not serve a concrete and easily measurable benefit to society, being a provisioning service (de Bello et al., 2010). This could also be the case for the less cited services such as refugium (another provisioning service, with only a single study found), or for medicinal services (no studies found), which do not provide a great observable benefit to nearby society (de Groot et al., 2002). This inconsistency in measurement standard also makes it difficult to provide conventional measures of these services, let alone to connect them to functional traits.

The opposite is true of biodiversity (which had only one relationship found) and genetic materials. These services have accepted measures, with species diversity and abundance along with phylogenetic diversity for genetic resources typically acting as measures for these services (Avolio et al., 2012; Mace et al., 2012). However, their benefits to society are much more abstracted. Biodiversity and genetic resources are regulating services—those functions and processes which allow for the provision of life-sustaining ecosystems to continue—while refugium and nursery services are considered habitat services—the provision of habitat and resources for living organisms to live (de Groot et al., 2002; de Groot et al., 2012). Although these services are perhaps the most important (as they act as the foundation for all the other services considered), they possess a minimal market value and are often estimated in indirect costs when their value is estimated in dollars (de Groot et al., 2012). The reason we see few studies investigating new and more accurate ways to quantitatively measure ES for these regulating services could simply be that there is no demand or interest in them from a conservation or management perspective, as they are too abstract (Ruckelshaus et al., 2015).

Along with variation in the number of service studies, there was also a great deal of variation in the number of plant functional traits that were found to have statistically significant relationships to ecosystem services (ranging from zero for some, to 28 for disturbance prevention) (see Table 1). This could be due to the varying complexity

of the ES in question. Some of the ES have little variation, for example, medicinal ES, referring to whether or not plants are used as medicine for human beings, essentially a binary trait. On the other hand, services such as nutrient cycling are far more complex processes with a multitude of different nutrients (e.g., nitrogen, carbon, potassium) being cycled through both plants and soils, each of which could account for some of the variation in this service (Hobbie, 2015; Schröder et al., 2016). As the complexity of the service provided increases, it follows that the number of indicators for this function/service might also increase. One service with multiple iterations and functional trait measures was also observed the case for disturbance prevention, the most frequently cited ES. While it is only a single ES, this trait was found to have multiple types of disturbance prevention, from fire to floods, to drought and exotic species invasion. Floods and fires, both disturbances, are extremely different phenomenon with different functional traits that may prevent or resist them (e.g., deep roots and a high percentage of fine roots aid in flood resistance while thick bark and fast growth rate aid in fire resilience).

It should be noted that the lack of results for functional trait linkages with services such as biodiversity, genetic, and cultural resources in this search does not mean that no functional trait indicators exist, nor, even, that none have been used. The nature of our search—focused on plant functional traits and specific services—was limited to statistical research with specific criteria and thus was not comprehensive of all possible trait–functional relationships. For example, there were several papers on the subject of cultural services, aesthetic services that referenced functional traits, and using functional traits as an evaluation technique, but did not specifically investigate quantitative ties between traits and services and were thus not included (Goodness et al., 2016; Sautkin & Rogova, 2018). The lack of quantitative study in the papers found indicates the likelihood that there are fewer and less well-read papers on these subjects. Thus, further research on these services and possible functional trait indicators is needed.

As research in the area continues to develop, and new trait–service relationships are studied, functional traits such as SLA, LDMC, and leaf nitrogen hold potential as economic measures of ES proxies (see Appendix S2). Multiple services have been associated these traits, and thus, measures of just one of these traits for a community could offer rough estimates or proxies for several services. This is contrasted with more specific and targeted traits such as leaf tensile strength, number of root tillers, and photosynthetic rate which have much more limited application and would be best suited for a targeted study of a specific desired service in a limited area. We found that

these traits have only been used in association with a single service and would suit a focused investigation rather than a general comparison of functional assembly or multiple service provision. This is where a database of standardized methods would prove particularly useful, allowing general service provision measures with minimal traits or specific traits that target a service but are more labor-intensive and focused. Such a database would allow for selection of traits/indicators to isolate and measure for the services that is most desired by stakeholders. This would ensure comparability and quantifiable measures of service, allow for the customization of testing for ES, and still provide comparable measures, something that is very much in demand as research into ecosystem services continues. Specific indicators would be especially important for such broad and diverse categories as “disturbance prevention.” For services like this, subservices in a database would allow for the specific functional trait associations (i.e., whether, fire resilience or flood prevention that are most desired) could be accurately measured with a minimal amount of resource expenditure. A list of all known and measured trait–service relationships could provide for designing monitoring programs, restoration, and ES measurement as it is unlikely that there exists a catch-all trait—a functional trait that indicates measures of most ES or that measure consistently between diverse ecosystems. Such a database would also ensure that a suitably diverse measure of traits could be used to provide a more accurate measure of ecosystem service provision, as no single trait, no matter how many services it is associated with, can account for all the services and functions required in an ecosystem (Damour et al., 2014).

Including habitat type and other abiotic factors may also prove an important aspect of such a database. We found within this review, 11 papers reported differences in trait–service relationships depending on the habitat type, season or other abiotic differences between plant communities (Kozlov et al., 2015; Linstädter et al., 2014; Ruiz-Jaen & Potvin, 2011). This suggests that subsets of plant functional traits could indicate optimal ES for different ecosystem types/circumstances and that traits could have different, sometimes even opposite relationships dependent on these factors. Certain functional traits or groups of traits act as indicators of improved or ideal ecosystem service delivery for a specific ecosystem (Kozlov et al., 2015; Linstädter et al., 2014), while others show that they might remain constant across ecosystem types (He et al., 2010). These are described as soft traits—those that change depending on the circumstances—and hard traits—those that remain consistent (Belluau & Shipley, 2018). Other plant functional trait–ES relationships are habitat dependent (Sfair et al., 2016), and even season dependent (Hou, Lu, et al., 2020; Hou, Zhu, et al., 2020), rather than

universal. Since trait–service relationships are often dependent upon the service and the habitat which they are found in (Kozlov et al., 2015; Linstädter et al., 2014; Ruiz-Jaen & Potvin, 2011), clarifying regional or ecosystem-specific plant functional traits indicators is a field of study that is essential in developing habitat and regionally specific monitoring or measurement programs for ecosystem services.

Despite the acceptance and clear prevalence of trait–service relationship in the literature, there has been some recent doubt as to the ability of plant functional traits alone to predict changes in ecosystem functioning, which would extend to changes in ecosystem service provision (van der Plas et al., 2020). Such studies have pointed out the limits to the predictive ability of using functional traits alone to predict service provision or changes in ecosystem function (Lanta et al., 2011). This caution around treating functional traits as the “Holy Grail” in ecology is also found other studies which recommend inclusion of traits to increase the accuracy of estimates and service mappings but refrain from using traits alone to measure ES (Xu et al., 2021; Graux et al., 2016). While these functional traits often show clear correlation along with mechanistic basis for their influence and prediction of ecosystem processes and services, it is important that their limitations also be understood.

With increased knowledge on the functional trait effects, we have a deepened understanding of which functional traits are dominant in specific landscapes—whether it is due to management or based on the surrounding landscape—and this knowledge has the potential to provide insight into the ecosystem services provided, and the trade-offs that occur. Given the thorough understanding of plant functional trait responses to land-use intensification, anthropogenic disturbances, and climate change that has been developed in the past decade, these functional trait responses could be scaled up to provide initial answers about these same disturbance effects on ecosystem service provision (Bjorkman et al., 2018; Miedema et al., 2019; Pérez-Camacho et al., 2012). The next step in ecology is to combine these two, filling in the knowledge gaps and informing restoration, management, and ecological theory using these plant functional traits as indicators of the presence and trade-offs of ecosystem service. This is particularly relevant with the discovery of common trends in functional relationships across the globe—indicating the potential of worldwide indicators of service provision (Bruehlheide et al., 2018; Gross et al., 2017; Reich et al., 1997). Combination of this knowledge, a literature of ES built off of the foundation of the study of ecosystem functions, would greatly improve their management, allowing stakeholders and conservationists alike to predict and respond to the changes caused by climate and land-use change related disturbances (Chillo et al., 2018; Jones et al., 2019).

CONCLUSION

Plant functional traits offer great potential as indicators of ES delivery and ES changes, allowing for accurate measurement, mapping, and the development of unique management and recovery strategies in the face of climate change and urban expansion. A deeper understanding of the influence of dominant plant functional traits on ecosystem processes and the services they provide could lead to a future where management and policy are informed to the point where ecosystems could be engineered, if necessary, to provide the ecosystem services needed (Storkey et al., 2015). The use of these plant functional traits to improve measures of ecosystem service delivery has wide implications for developing accurate models of the effects of climate change, as well as scientifically defensible, policy-relevant, and widely accepted ES quantification methods (Heink et al., 2016; Polasky et al., 2015). While a great deal of the foundation has been laid for the application of plant functional traits in this capacity, there is still a great deal to be uncovered, notably the influence of microbes on both plant functional trait filtering as well as on ecosystem processes (and thus on ES). This along with research into habitat-dependent plant functional trait indicators and the development of consistent and comparable trait measures for under-represented services such as medicinal services, refugium, and nursery functions and genetic provision is the next step in consistent and accurate measures of ecosystem services.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data utilized for this research come from previously published works, cited in Appendix S2.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.

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