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USING FUNCTIONAL TRAITS TO PREDICT POLLINATION SERVICES: A REVIEW

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Abstract—Pollination is a fundamental ecosystem service. Predictive and mechanistic models linking pollinator community structure to pollination services increasingly incorporate information on unique functional differences among species, so called effects traits. There is little consensus as to which traits are most important in supporting pollination services at either an individual or community level. Here, we synthesise the state of current knowledge regarding the role and efficacy of traits for predicting pollination, as well as the use of different methods for describing the trait structure of pollinator assemblages. We find a wide range of traits are currently used to predict pollination services, including morphological, behavioural and phenological characteristics. However, we show that the evidence demonstrating their importance is often limited or mixed. There is a trade-off in how traits are used between those that are easier to measure, available for many species but have only limited evidence for their role in pollination, vs. those that are harder to measure but with a more robust link with pollination service delivery. We highlight how community weighted means and measures of functional diversity offer important, albeit different insights into pollination service delivery. We discuss how their relative importance is likely to depend on the goals of the study. To maximise fully the utilisation of traits to predict pollination services, future research should be directed towards the widespread and consistent validation of the links among different traits and the pollination service across crop and semi-natural plant communities. Ideally this also needs to address geographical and taxonomic biases in trait collection.

Keywords—Pollination, effect traits, ecosystem service, functional diversity, review

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INTRODUCTION

With wide-scale evidence of pollinator declines there has become an ever-increasing need to understand how pollinator community structure affects the provision of pollination services (Potts et al. 2010; Goulson et al. 2015; Powney et al. 2019). Understanding this relationship is key to linking pollinator population change to economic consequences for the 75% of crop plants and 87.5% of flowering plants estimated to rely on insects (Klein et al. 2007; Ollerton et al. 2011). Multiple methods exist both to quantify pollinator biodiversity and to link these predictions to the efficacy of pollination ecosystem services (Klein et al. 2003; Hoehn et al. 2008; Garibaldi et al. 2015; Winfree et al. 2015; Woodcock et al. 2019). These revolve around three main measures: abundance, taxonomic classification (most often species richness) and functional trait methods.

Pollination services are underpinned by visitation rates (although abundance is often used as a proxy) that govern interaction frequency with flowers by insects, including bees, but also bats and hummingbirds (Vázquez et al. 2005; Sahli & Conner, 2006). While undoubtedly useful, such measures ignore the underlying variability of these interactions in terms of whether they lead to successful pollen transfer, or indeed if the visit is even legitimate. For example, robbing behaviour common to many bumblebees may bypass the reproductive components of the flower, but is still flower visitation (Newton & Hill, 1983; King et al. 2013, although this can still result in pollination, see Higashi et al, 1988). Although of fundamental importance, the simplicity of visitation rates leaves scope for expansion to derive improved estimates of service delivery from pollinator communities. Species richness partially overcomes the drawbacks of visitation rates in that it superficially accounts for differences in the way species interact with flowers, predicting pollination services to a greater extent than abundance (Klein et al. 2003; Gómez et al. 2010; Mallinger & Gratton, 2015). Two mechanisms may explain why species richness captures the potential of a pollinator community to deliver pollination services above that explained by visitation rates alone: firstly, the sampling effect, where a greater richness of species raises the chance that a highly effective pollinator is included within an assemblage (Klein et al. 2003). Secondly, greater species richness increases the chances of species having complementary ecological requirements, which can maximise the temporal and spatial resource use of a pollinator community (Klein et al. 2003). Such differences may include the temporal distribution of their foraging throughout the day or season: Are they active under different weather conditions, or do they make contact with reproductive parts of the flower; all of this may affect pollination service delivery (Klein et al. 2003; Brittain et al. 2013a). As a metric the information species richness captures assumes all individuals are functionally identical, and so fails to describe functional differences among species that affect how they influence pollination.

It is here that unique species morphological, phenological or behavioural characteristics, termed functional 'effects traits', may be most important in defining the variability in pollination service provision (Gagic et al. 2015; Hoehn, Tscharntke, Tylianakis, & Steffan-Dewenter, 2008; Woodcock et al. 2019). While a wide range of traits and statistical methods are currently being employed to predict pollination services, there exists little consensus as to the ecological relevance and suitability of these different approaches. Indeed, which traits to use represents a fundamental and often under considered basis for studies aiming to identify the role of community functional diversity in the delivery of pollination ecosystem services. Given the proliferation of studies using traits (e.g., Hoehn et al. 2008; Martins et al. 2015; Woodcock et al. 2019; Roquer-Beni et al. 2021), synthesis of the current state of the field is needed to determine the availability and support for different traits to predict pollination effectively. There is also considerable diversity in terms of the methods that are used to describe the functional trait structure of communities, both within and between species (Hoehn et al. 2008; Garibaldi et al. 2015; Woodcock et al. 2019). Here, we review both these applications of functional traits as a method to improve predictions of pollination ecosystem services with a view to identifying key knowledge gaps and targets for future research.

THE ROLE OF POLLINATOR FUNCTIONAL EFFECTS TRAITS

Functional traits are usually split into two categories, response traits and effects traits, although as artificial categories these often overlap to some extent. Response traits describe species dependencies on the environment and can be used to predict or determine the resilience of a community to environmental change (Mori et al. 2013). In contrast, effects traits determine individual pollinator effectiveness, and across species the overall potential of a community to support pollination ecosystem services (Lavorel & Garnier, 2002). It is this latter category that we predominantly focus on this review as it is effects traits that capture the differences between species that dictate the efficacy of pollinators (Lavorel & Garnier, 2002). However, it is worth noting that where correlations between these two classes exist, response traits may determine what effects traits are present at a given location as species filtering can occur in response to environmental conditions (Lavorel & Garnier, 2002 but see Bartomeus, Cariveau, Harrison, & Winfree, 2018).

DEFINING EFFECTS TRAITS

A wide range of traits are currently used to capture the differences among pollinators and how they support ecosystem service provision. Most commonly these describe: i) behavioural interactions with flowers; ii) morphological characteristics that are likely to influence flower choice and pollen transfer and iii) phenological traits that would determine spatio-temporal floral use by species (a summary of key traits and their value in predicting pollination services is presented in the Supplementary Information: Table S1; see Table 1 for an example of how traits are described). Focusing on the level of the individual, effects traits should ideally capture a mechanistic interaction that can directly impact the

Table 1. This table shows a summary of body size as a morphological trait, including general availability of data across species and evidence for a link with pollination. This represents an exert from a comprehensive list of traits provided in the Supplementary Information Table S1.

Trait	Metrics	Overview
Body size (morphological)	**Body dimensions** (including Intertegular distance, length or width of the whole body, thorax or abdomen)	**Trait availability:** Body size is a relatively widely available trait, particularly for bees. Values are often available in the literature (Bommarco et al. 2010; Bartomeus et al. 2013), online repositories/databases (Borges et al. 2020; Speight et al. 2020) and field guides (Falk & Lewington, 2016). **Evidence for link to pollination:** Body size has been shown to be linked with pollination in number of studies (Garibaldi et al. 2015; Jauker et al. 2016; Földesi et al. 2020). Larger pollinators deposit more pollen on plant stigmas (Földesi et al. 2020), and when matched with floral structure, body size predicts crop yields as it can determine access to nectar resources (Garibaldi et al. 2015). Intraspecific variation may be important, with larger individuals of *Osmia rufa* increasing yields of oilseed rape compared to smaller individuals (Jauker et al. 2016). However, some studies suggest body size does not consistently predict pollination efficiency and yield (Bartomeus et al. 2018; Woodcock et al. 2019).

outcome of pollination. For example, of the traits currently used, single-visit pollen deposition, which is the amount of pollen deposited on a plant stigma by an individual, captures a fundamental difference among species (King et al. 2013). This is because for many plants pollen transfer from the anthers to the stigma represents the basic minimum requirement for successful fertilisation, at least where plants have some level of dependency on insect pollination (Lloyd & Schoen, 1992). Single-visit pollen deposition provides an assessment of a clearly defined interaction that can directly affect pollination, which could be viewed to represent a gold standard for an effects trait. However, traits are often not limited to those that just describe key interactions, but also include the use of proxies where logistical constraints limit the direct measurement of a characteristic, for example using body size instead of single-visit pollen deposition (Földesi et al. 2020). Alternatively, traits may also be used to capture more general niche differences among species that could impact pollination, which is often the case where life-history characteristics are used (see Table S1) (Blitzer et al. 2016).

While effects traits are derived at the level of the individual, how effects traits interact with abundance is key to understanding community-level pollination services (Winfree et al. 2015; Woodcock et al. 2019). For example, some traits, such as those that describe phenological characteristics like daily activity periods, are inherently related to abundance (Table S1). These traits are predominantly capturing variation in abundance at different times of the day/season, which is a strong driver of pollination services (Fründ et al. 2013; Winfree et al. 2015), rather than the direct efficacy of individual pollinators. Similarly, the value of traits to predict ecosystem functions, like pollination, is often mediated by abundance (Gagic et al. 2015; Woodcock et al. 2019). Gagic et al. 2015 showed that functional diversity indices that do not account for abundance often performed no better in predicting ecosystem functions, including pollination, than measures based solely on species diversity and abundance. This suggests that simply understanding the diversity of traits within a community is not always enough to predict functioning. To assess community-level pollination, a link between species level traits and pollination must be established for appropriate traits to be selected (covered in this section of the review and also see Table S1 for a summary of different traits). We also need an understanding of pollinator community structure based on both traits and abundance (covered in section 3 of this paper).

SELECTING EFFECTS TRAITS

Ideally, effects traits are selected where there is either previous evidence of a mechanistic role associating that trait to successful pollination or a reasonable hypothetical link. Unfortunately, the ease with which traits are derived has been a strong determinant of their use. For example, single-visit pollen deposition is likely to be one of the best estimates of pollination efficacy. However, this is time consuming to measure as it relies on observing visitations of bees to virgin flowers as well as the additional requirement of counting individual pollen grains under a microscope (King et al. 2013). Similarly, the derivation of other traits, like hairiness, may depend on expensive technology not widely available, e.g., high-resolution cameras (Stavert et al. 2016) (Table S1). These logistical constraints have often-forced researchers to select more-easily derived proxies that may not have as strong support for a role in pollination. For example, the time an individual spends foraging on a flower is relatively easy to measure and is often included in trait studies, despite little evidence that it leads to greater pollen deposition (Table S1) (see Thomson & Goodell, 2002). That is not to say that traits like the time spent on a flower are unimportant, but that currently there is limited evidence to suggest that they are capturing a key interaction driving pollination success. Conversely, traits like body size, which are easy to measure and generally widely available in trait databases (see Table 1), have been shown to be correlated with single-visit pollen deposition. These may therefore provide a useful proxy in the absence of community-wide data on stigmal pollen deposition rates (Földesi et al. 2020). With any proxy there is always the risk that multiple mechanisms maybe responsible for the importance of a trait. For example focusing on body size, while it is correlated with single-visit pollen deposition, also determines the availability of pollen and nectar resources to pollinators, which is also important in determining pollination service delivery (Garibaldi et al. 2015). As a result, careful interpretation is needed where proxies are used and where a trait could influence pollination by multiple pathways. This also highlights that where possible it is important to try and directly quantify the trait of interest.

The availability of certain traits in identification guides or online repositories is also likely to influence their use (Table S1). This is most likely to be the case where general ecological traits are selected, including characteristics like sociality and nesting preferences, which while widely available do not have any particular mechanistic basis for their link to pollinator efficacy (Bartomeus et al. 2018) (Table S1). Traits that capture the general ecology of a species, and could predominantly be viewed to be response traits, may be useful in creating different functional groups that could be expected to have differing per-capita efficiency or complementary resource use (Blitzer et al. 2016). However, this is only likely to be useful where differences in effect traits are nested (or correlated) with different response-based functional groups, for which there is currently limited evidence to suggest this is the case (Bartomeus et al. 2018; Greenwell et al. 2019). Often less-freely available are what we refer to here as high-resolution traits, like the amount of conspecific pollen carried by an individual pollinator, metrics of hairiness or single-visit pollen deposition rates, that have a strong mechanistic basis for assumed pollination success (Table S1). Besides difficulties in measuring traits like these for a large number of species, environmental differences may drive variation. For example, changes in foraging behaviour in response to weather may mean any measurements are specific to the context in which they were assessed rather than a general fixed characteristic of a species (Goulson, 1999; Peat & Goulson, 2005). Therefore, they may be less applicable between studies compared to less flexible traits, such as descriptors of species life histories or morphology.

In addition to these issues, the relevance and importance of individual traits are likely to vary with plant fertilisation systems (Bartomeus et al. 2018). For example, traits such as nectar robbing or buzz pollination are unlikely to be relevant for a large number of plant species, but would be key indicators of pollinator effectiveness in field bean and tomato respectively (Kendall & Smith, 1975; De Luca & Vallejo-Marín, 2013). Individual traits are unlikely to capture pollination efficacy completely. For example, while single-visit pollen deposition may be argued to be one of the best estimates of pollination ecosystem service delivery, without an assessment of pollen species, even where high amounts of pollen are deposited, it may be irrelevant as the pollen could come from other plant species (Brosi & Briggs, 2013). The goals of the study and study system are therefore an important consideration for the traits selected to predict pollination. For example, if the focus is on a specific crop species then traits like single-visit pollen deposition and conspecific pollen load are likely to be important as they are providing a high-resolution estimate of the efficacy of individual pollinators (Brittain et al. 2013b; Marzinzig et al. 2018). In contrast, when whole plant communities are being focused on, traits like tongue length and species flight times are useful because they will determine the availability of different plant species to pollinators and could capture complementary resource use (Lonsdorf et al. 2009; Garibaldi et al. 2015). As such, perennial cropping systems like orchards may be traits far simpler to use to predict pollinator service provision from community structure than either rotational cropping systems or natural plant communities underpinned by greater floral diversity.

MEASURING POLLINATION SERVICES

A number of different methods are used to link traits to the pollination services. For example, while an important effects trait, single-visit pollen deposition is also used as a way of validating the efficacy of traits that are easier to derive, such as body size (Földesi et al. 2020). Single-visit pollen deposition captures the potential of a pollinator at the point of delivery, therefore provides a measure of pollination services that can be assessed against other traits. Pollination services are also often considered in the context of an agronomic input (Fijen et al. 2018; Garratt et al. 2018), where yield/seed set is of key economic importance and so the main variable of interest. While a key measure of service delivery, yield/seed set can be confounded by factors that can occur post-pollination (e.g., adverse weather, herbivory, agricultural inputs) so does not solely account for the effects of pollinators and therefore certain traits (Ballantyne et al. 2015). Such post-pollination factors may obscure the mechanistic link between a trait and pollination service delivery, thus pose an issue if this is the sole aim of a study. Therefore, study goals are key to trait selection and validation - it is unlikely that one size fits all.

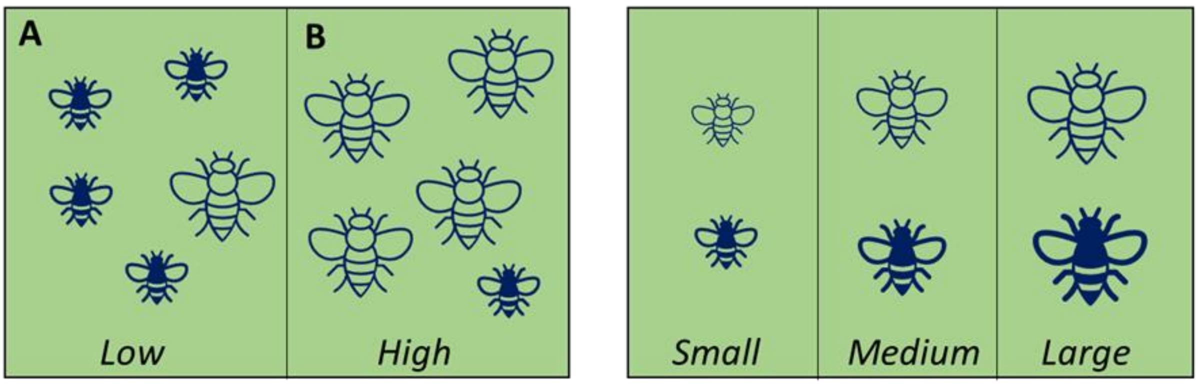
UNDERSTANDING THE LINK BETWEEN POLLINATOR COMMUNITY STRUCTURE AND THEIR EFFECTS TRAITS TO PREDICT POLLINATION SERVICES

Complexity in understanding the impacts of traits on pollination not only arises from trait selection but the method used to define the trait structure or diversity of a pollinator community. Functional traits have been utilised in a number of different ways to predict pollination services, but broadly their use falls into two groups: 1) the assessment of community weighted means of individual traits (Garibaldi et al. 2015; Bartomeus et al. 2018; Woodcock et al. 2019; Roquer-Beni et al. 2021) and 2) functional diversity measures (see Mammola et al. 2021 for an overview), which in general describe the breadth of traits within a community and can be weighted by abundance (Hoehn et al. 2008; Blitzer et al. 2016; Woodcock et al. 2019; Roquer-Beni et al. 2021). In the following section, we discuss the underlying theory of the different ways to define pollinator communities based on their functional trait structure.

COMMUNITY WEIGHTED MEANS

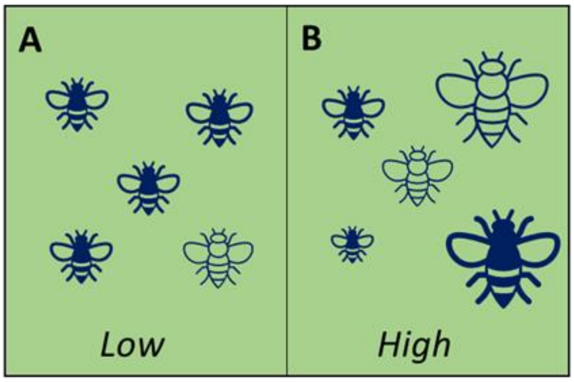
Community weighted means (CWM) are based on single traits, where the expression of a trait (e.g., body size) is weighted by the abundance or biomass of individuals in a community (Fig. 1a) (Lavorel et al. 2008). CWMs can also be used to quantify the categorical expression of traits, for instance the proportion of individuals in a community that express a particular tongue length. The theoretical basis for linking CWM to the prediction of pollination services is an assumption that one (or a few) traits play a dominant role in pollination provision (Lavorel et al. 2008; Woodcock et al. 2019). This follows the principles outlined under the Mass Ratio Hypothesis, whereby the impact of each species on the ecosystem function is proportional to their abundance (or equivalent metric) (Grime, 1998). Therefore, using the example of body size, a community with a proportionally higher number of larger species would be expected to maximise pollination as larger species on average deposit more pollen, although this may not be the case for smaller flowers (Fig. 1a) (Földesi et al. 2020). A number of studies have found that CWMs, or similar measures focusing on individual traits, are useful predictors of pollination services (Gagic et al. 2015; Garibaldi et al. 2015).

A particular benefit of CWMs is that they elucidate a mechanistic link between a species trait and pollination services (Garibaldi et al. 2015). For example, Garibaldi et al. (2015) showed that body size and tongue length, when matched with crop traits (describing flower morphology) were the best predictors of fruit set in a number of crops. In this example, the body size and tongue length of



a) Community weighted mean

b) Functional groups



c) Functional diversity

Figure 1. A contrast of hypothetical pollinator communities composed of species representing different body sizes and how this can lead to different community-level trait measures for; (a) community weighted means (CWM). Here, the mean value for a community, in our case body size, is calculated based on the relative abundance of individuals and the body size of each of those individuals. In our example, community A has a lower mean body size than B; (b) functional groups. Here, species are put into functional groups based on common attributes in our example species are sorted into three groups based on body size, and; (c) functional diversity based on body size. Functional diversity in its simplest form accounts for the range of traits within a community and the overall difference among species in the expression of those traits. In our example community A has lower functional diversity than community B as it has a smaller range of body sizes.

the pollinator species dictated their access to nectar resources in different crop species, and therefore affected subsequent pollination (Garibaldi et al. 2015). Garibaldi et al. (2015) also showed that the CWM approach better predicted crop yields than functional diversity metrics, although this is not consistently found (see Woodcock et al. 2019; Roquer-Beni et al. 2021). CWMs are also useful as the measurements are generally ecologically meaningful, e.g., a mean value for body size measured in mm is easy to interpret. While this may seem trivial, this is not always the case for more-derived functional diversity metrics (discussed below) and, as such, may prove easier to provide targets for management intended to maximise certain aspects of a pollinator community to support service delivery.

As with any diversity measure, CWM has drawbacks. While CWMs do allow traits to be isolated, they may suggest only single traits are important for pollination services when it is more likely that a multitude of traits determines the overall effectiveness of a pollinator community (Hoehn et al. 2008; Woodcock et al. 2019; Roquer-Beni et al. 2021). Another issue, is that CWMs may be predominantly capturing abundance rather than causative effects of the traits they are based on (Woodcock et al. 2019). In a meta-analysis assessing how pollinator community structure could predict oilseed rape yields, Woodcock et al. (2019) found that while many traits, such as hairiness and body size, were significantly correlated with oilseed rape yield, after controlling for abundance these correlations were no longer significant. Overall, CWM can offer valuable insights into the mechanistic link between pollinators and pollination success. However, careful consideration of traits and assessment methods is needed to avoid overly simple models of pollination.

FUNCTIONAL GROUPS

This is a method used to define functional diversity based on multiple traits simultaneously and sits alongside continuous measures of functional diversity described in the next section. Here, species are sorted into discrete groups based on their traits in an attempt to assess niche partitioning based on the ecological requirements of different pollinator species (Fig. 1b) (Hoehn et al. 2008; Blitzer et al. 2016). Unlike CWM's, the Complementarity Hypothesis underpins the role of functional diversity in promoting pollination services, whereby a lower overlap between traits of species within a community is more likely to promote successful pollination (Hoehn et al. 2008). By this process niche partitioning among species provides greater coverage (complementarity) of pollination services potentially both spatially and temporally depending on the traits considered (Blitzer et al. 2016; Hoehn et al. 2008; Woodcock et al. 2019). Increased functional group richness has been shown to increase pumpkin and apple seed set, and has also been found to predict pollination services to a greater extent than species richness or abundance (Hoehn et al. 2008; Blitzer et al. 2016). The functional group richness approach overcomes one of the limitations of CWMs, in that it distinguishes between clusters of species based on multiple traits that may be important for pollination services. One of the main drawbacks is the selection of functional groups can be potentially arbitrary in nature, for example, dividing pollinators into size classes based on body size is not necessarily going to be based on biologically meaningful values. Alternatively, categorisation based on clustering algorithms that form groups using a statically robust threshold are an option, although again this is not necessarily going to reflect closely niche partitioning in the real world (Woodcock et al. 2019).

FUNCTIONAL DIVERSITY

A large number of methods exist that provide continuous measures of functional diversity that are often (although not exclusively) based on different geometric attributes of multi-dimensional functional space and can be used to derive different aspects of functional diversity such as evenness, richness and dispersion (see Laliberte & Legendre, 2010; Blonder et al. 2018; Mammola & Cardoso, 2020). Similar to functional group richness, continuous measures of functional diversity are able to account for multiple traits overcoming one of the drawbacks of CWM and can account for abundance (Mammola et al. 2021). However, an important distinction between functional diversity metrics and the categorisation of communities into effect trait groups is that there is no allocation (either arbitrarily or based on some kind of threshold) into discrete groups (although categorisation may be present in the traits used), rather variation within a community is continuous (Fig. 1c). This may explain why functional dispersion – a continuous measure of functional diversity – was found to be a better predictor of oilseed rape pollination than the functional group richness (Woodcock et al. 2019). As for the functional groups, the mechanistic underpinning of functional diversity metrics relates to complementarity resulting from niche partitioning among species, providing greater coverage of pollination services (Woodcock et al. 2019).

An important drawback associated with the use of functional diversity measures, particularly from a mechanistic standpoint, is that they are not easy to interpret. Multiple traits are often included in a single measure, therefore one or all traits could be affecting pollination (this highlights one of the benefits of the CWM approach) (Lavorel et al. 2008; Petchey & Gaston, 2006). Theoretically, it is possible to overcome this issue by calculating the functional diversity measure using every possible combination of traits and reassessing the strength of the correlation with pollination service delivery, but in reality this could be computationally very intensive and so is rarely undertaken. In addition, continuous measures of functional diversity provide an overall measure of trait diversity that could potentially be equivalent between two communities of very different composition in terms of trait components. This is to say that a specific level of functional diversity could be achieved in multiple ways and may not necessarily have the same level of service delivery associated with it. As a result, the use of functional diversity indices as a conservation target may be problematic for practical applications. This issue can be overcome to a certain extent, as methods exist to track the trait composition of a community, for example using Jaccard measurements based on the overlap of community trait structure (Carmona et al. 2019; Mammola & Cardoso, 2020). Overall, both functional diversity and CWM's provide complementary approaches to determining how pollinator community structure supports pollination services and provide ecologically important information.

FUTURE DIRECTIONS FOR PREDICTING POLLINATION SERVICES

The rapid increase in the derivation of different traits (e.g., Rader et al. 2016, Stavert et al. 2019, Woodcock et al 2013), and methods for analysing trait diversity and composition offers new avenues for understanding how pollinator community structure supports pollination ecosystem services. However, there are fundamental issues regarding the importance of traits as a mechanisms for predicting pollination services that remain either unclear or are poorly defined. Below we outline these key areas.

THE PRACTICALITIES AND LIMITATIONS OF USING FUNCTIONAL TRAITS

VALIDATION OF TRAITS

A large number of traits have been used to measure pollination ecosystem services (outlined in Table S1), however, few studies have consistently validated traits against key measures of service delivery using experimental approaches. Currently, much of the evidence regarding the importance of different traits is based on correlations with either yield or seeds set, with a few studies directly manipulating differences in traits between assemblages (Jauker et al. 2016). In the majority of cases the link is largely on the basis of reasonable ecological inference based on known or assumed mechanisms, but lacks empirical evidence. While there are practical limitations regarding the manipulation of traits amongst species experimentally, this approach can offer novel mechanistic insights into how traits impact pollination. For example, Fründ, Dormann, Holzschuh, & Tscharntke (2013) found in a cage study that differences in bee floral preferences and daily foraging times led to greater seed set due to functional complementarity. There are a number of traits highlighted in Table S1, such as pollen carrying behaviour and the location of corbicula (pollen baskets), that are likely to impact pollinator effectiveness, however, there is currently limited experimental evidence to demonstrate this directly.

More broadly, there remains significant scope for research into the quantification of the relative importance of different traits in predicting pollination services across broad taxonomic groups of plants. This would ideally be done by assessing a wide range of traits and then partitioning out their relative importance. For example, the importance of each trait could be determined through the ranking of the predictive power of different models to gain an accurate understanding of whether certain functional traits are consistently important, or vary depending on different plant families/species. While assessing traits' importance in this way relies on a correlative approach, given the complexity of trait diversity in natural pollinator assemblages it is likely to be more practical when compared with direct experimental testing. Through systematic sampling utilising both correlation and experimentation, it is likely that the limitations of current traits-predicted pollination services will become apparent. This will open up insights into the importance of novel traits.

TRAIT AVAILABILITY

The overriding constraint on the wide-scale use of functional traits, particularly in understanding importance of different traits across diverse pollinator systems, is the limited availability of information. While this is true for some traits, e.g., stigmatic deposition rates are only available for handful of species and crops, it is a wider problem particularly for faunas deriving from less-well studied parts of the world (Millard et al. 2020; Orr et al. 2021). Europe has relatively good coverage of certain traits for particular taxonomic groups, for example, hoverflies, due to the existence of a large database (Speight et al. 2020).Less information is available in formal databases and the scientific literature for areas that exhibit high pollinator diversity, such as Africa and South America (Orr et al. 2021). Such differences are likely to reflect biases in formal research funding (Nuñez et al. 2021). Given the importance of pollination globally, directing greater resources to understanding pollination systems in these areas will prove important in fully understanding the impacts of ongoing biodiversity change for both people and nature (Nuñez et al. 2021). Another prevalent bias is a focus on a small subset of taxa, predominantly bees (Millard et al. 2020). While some other taxa have reasonable coverage, such as the aforementioned hoverflies (Speight et al. 2020), traits are less frequently derived for other key taxa, such as non-syrphid flies, beetles and moths (Rader et al. 2016). Deriving traits for a larger number of taxa would ultimately help elucidate the importance of whole pollinator communities in supporting service provision.

INTRASPECIFIC VARIATION

Intraspecific variation is often overlooked in functional trait assessments where trait averages are frequently used despite the fact that intraspecific variation can be as important as interspecific variation in predicting ecosystem functions (Des Roches et al. 2018). The effects of intraspecific variation in body size on pollination have been investigated to a limited extent (Willmer & Finlayson, 2014; Jauker et al. 2016) and it has been shown that larger individuals of pollinators tend to be better pollinators. Such intraspecific variation may show a strong phylogenetic origin, with eusocial species (e.g., *Bombus*) being particularly prone to significant intraspecific size variation (Chole et al. 2019). Differences in the size between casts may also act to restrict access to some flowers (Suzuki, 1994). Experimentally determining the degree to which traits, such as hairiness and single-visit pollen deposition, vary within species and how this variation impacts pollination services may provide important new insight into assessment of pollination services. Interestingly, intraspecific variation in body size has been shown to be affected by landscape characteristics (Warzecha et al. 2016; Elzay & Baum, 2021), suggesting intraspecific variation in these traits could be interacting with environmental change to further affect the vulnerability of this ecosystem service. From an analytical perspective the integration of within-species variation into pollination assessments is likely to become easier with new methods, like trait probability densities, that directly account for intraspecific variation (Carmona et al. 2019).

CONCLUSION

Functional traits are an important tool for identifying how pollinator community structure supports the delivery of pollination ecosystem services. Use of traits provides insights into the mechanisms underpinning pollination and opportunities to understand how biodiversity change could impact service provision, and also how service provision could be best conserved and enhanced. Currently, biodiversity indicators have been developed for pollinators that give us long-term trends in how the distributions of pollinators are changing, however, these do not account for species traits or the functional structure of pollinator communities. As taxonomic diversity and functional diversity can show opposite patterns over large timescales (Greenop et al. 2021), biodiversity indicators based on traits could be key to identifying changes in pollination service delivery that would otherwise go unnoticed or be difficult to quantify. However, for such functional indicators to be most effective we first need to understand how pollinator community structure through traits drives service provision. This review has identified important knowledge gaps in terms of the lack of widespread and consistent approaches to validating the links between different traits and the pollination service between crop and semi-natural plant communities. Future research needs to address these deficiencies in order to maximise the benefits of using traits as predictors of economically important services, such as pollination.

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AUTHOR CONTRIBUTION

AG, BW and RP contributed to the conception and writing of the manuscript. AG undertook the review and wrote the first draft which was commented on by all authors.

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No potential conflict of interest was reported by the author(s).

DATA AVAILABILITY STATEMENT

This paper presents a literature review and as such there is no associated data with this paper.

APPENDICES

Additional supporting information may be found in the online version of this article:

Table S1. Traits commonly used to predict pollination ecosystem services, their general availability across species and evidence for a link with pollination.

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