

<sup>1</sup> Trade-offs among plant floral and reproductive  
<sup>2</sup> traits determine interactions with floral visitors

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<sup>12</sup> Plant life strategies are often delimited by vegetative and physiological traits but  
<sup>13</sup> little is known about how floral and reproductive traits drive these strategies, and  
<sup>14</sup> in turn shape plant interactions with floral visitors. Here, we compiled 13 floral, 4  
<sup>15</sup> reproductive and 3 vegetative traits for 1,506 plant species from 28 plant-pollinator  
<sup>16</sup> network studies across 18 different countries. We investigated the associations among

17 these traits, pollinator visitation and the functional role of plant species within the  
18 networks (interaction frequency, normalized degree and specialization). We found  
19 that 51.8% of trait variation was explained by two independent axes that encompassed  
20 plant form and function. Specifically, the first axis indicated the presence of a trade-off  
21 between flower number and flower size (PC1, 26.72%). The second axis indicated a  
22 trade-off for the level of pollinator dependency (PC2, 25.08%). Although the main  
23 axes of trait variation did not fully explain pollinator visitation rates, different plant  
24 life strategies were associated with visitation rates and pollinator functional groups.  
25 Overall, the main traits that determined plant species' functional roles were height,  
26 nectar concentration, pollen grains per flower, number of ovules, style length, selfing  
27 level and flower width. Our results highlight the need to consider plant reproductive  
28 and floral traits to improve understanding of plant life strategies and plant-pollinator  
29 interactions at broader spatial scales.

30 There is an astonishing diversity of floral structures and plant reproductive strategies  
31 among flowering plants (Barrett, 2002; Schiestl & Johnson, 2013), which have long been  
32 of interest to pollination biologists in terms of their relevance to plant-pollinator  
33 interactions. However, most studies that have explored reproductive (e.g., mating and  
34 compatibility systems) and floral trait (e.g., flower size or nectar provision) variation  
35 have concentrated on the individual or community level and thus, broader  
36 macroecological patterns remain poorly investigated (Carvalheiro et al., 2014; Baude et  
37 al., 2016; Munoz et al., 2016; Moeller et al., 2017; Grossenbacher et al., 2017). Indeed,  
38 studies depicting species' life history strategies generally focus on vegetative traits and  
39 rarely consider reproductive traits (Salguero-Gómez et al., 2016; Rüger et al., 2018). As

40 a consequence, a unified framework that explores the compromises among floral traits  
41 and their relevance to plant life strategies is currently lacking (Roddy et al., 2021). At  
42 the same time, there is growing interest in the determinants of plant-pollinator  
43 interactions via trait-based approaches (Fenster et al., 2004) and trait-matching  
44 analyses (Bartomeus et al., 2016). However, floral traits have been overlooked beyond  
45 highly specialised plant-pollinator systems (Dellinger, 2020; Roddy et al., 2021) and the  
46 role of plant reproductive biology remains little explored in plant-pollinator  
47 interactions (but see Tur et al., 2013 and Devaux et al., 2014).

48 With the recent availability of large trait databases, plant ecological strategies are  
49 increasingly being examined (e.g., TRY, Kattge et al., 2011 and COMPADRE,  
50 Salguero-Gómez et al., 2015), and are facilitating the identification of global patterns  
51 and constraints of plant form and function (Salguero-Gómez et al., 2015; Díaz et al.,  
52 2016; Carmona et al., 2021). However, the main focus has been on vegetative traits such  
53 as leaf (Wright et al., 2004) or wood (Chave et al., 2009) trade-offs with little or no  
54 attention given to reproductive and floral traits (E-Vojtkó et al., 2020), also critical to  
55 plant form and function. For instance, short lived versus perennial species tend to have  
56 low versus high levels of outcrossing, respectively (Barrett, 2003; Moeller et al., 2017).  
57 Further, outcrossing levels are positively correlated with flower size (Goodwillie et al.,  
58 2010). In addition, the presence of costly rewards (e.g., pollen or nectar) and showy  
59 flowers or floral displays can only be understood through consideration of plant  
60 species' reliance upon animal pollination (pollinator dependence) and their role in  
61 attracting pollinators (Ollerton et al., 2011). Hence, exploring plant life strategies with  
62 reproductive and floral trade-offs, in conjunction with their pollinator dependence, is  
63 necessary for a balanced understanding of plant economics.

64 Several studies have identified links between plant traits and plant-pollinator network  
65 properties (Lázaro et al., 2008; Bartomeus, 2013; Carvalheiro et al., 2014). Moreover,  
66 plant traits can also define species' network roles (e.g., specialists vs generalists). For  
67 example, species that occupy trait space extremes are more likely to exhibit higher  
68 specialization and be more reliant on trait-matching (Junker et al., 2013; Coux et al.,  
69 2016). This morphological matching between plant and floral visitors can determine  
70 plant-pollinator interactions, and thus shape their interaction network structure (Stang  
71 et al., 2009; Ibanez, 2012). Despite the increasing knowledge of the relevance of traits  
72 on the species network roles, little is known about how plant reproductive and floral  
73 traits determine plant species' network roles at a macroecological scale.

74 Here, we explore the potential trade-offs among plant floral and reproductive traits  
75 and how these influence the structure of plant-pollinator networks. First, we identify  
76 the major axes of floral and reproductive trait variation and trade-offs that determine  
77 plant form and function. Second, we investigate how plant species' position in  
78 trait-space influences interaction strength with different guilds of floral visitors. Finally,  
79 we investigate how the main axes of trait variation and individual traits influence plant  
80 species roles within networks using complementary interaction network metrics (i.e.,  
81 interaction strength, normalized degree and specialization).

## 82 RESULTS

### 83 Plant strategies

84 The phylogenetically informed principal component analysis (pPCA) captured by the

85 first two and three axes 51.8% and 70.97% of trait variation, respectively (Figure 1 and  
86 Figure S5) and had a phylogenetic correlation (**lambda**) of 0.76. The first principal  
87 component (PC1) represented 26.72% of the trait variation and indicated a trade-off  
88 between flower number and flower size. We refer to this axis as the 'flower number -  
89 flower size trade-off as already described in previous studies (Sargent et al., 2007;  
90 Kettle et al., 2011). Hence, one end of the spectrum comprised species with high  
91 investment in flower number and plant height but small flower size, short style length  
92 and low ovule number. The other end of this spectrum comprised species that were  
93 short in height and invested in large flowers, long styles, many ovules, but few flowers.  
94 The main contributing traits to PC1 were plant height, flower number, ovule number  
95 and flower size (loadings > |0.5|; Table S3) but style length also contributed  
96 moderately on PC1 (loading = -0.33). The second principal component (PC2)  
97 represented 25.05% of the trait variation and indicated a trade-off between low and  
98 high pollinator dependence. We refer to this axis as the 'pollinator dependence  
99 trade-off'. The main driver of trait variation on PC2 was autonomous selfing (loading  
100 = 0.85) but the other traits (except ovule number) also made moderate contributions  
101 (loadings from 0.27 to 0.4; Table S3). We found that high pollinator dependence was  
102 associated with larger and higher numbers of flowers, greater plant height and longer  
103 styles. In contrast, species with high levels of autonomous selfing tended to have fewer  
104 and smaller flowers, had shorter styles and were shorter in height. Further, PC3  
105 explained a considerable amount of trait variability (19.17%) and the main contributors  
106 to this axis were style length (loading = -0.66) and the degree of autonomous selfing  
107 (loading = -0.51). The remaining traits, apart from ovule number, were moderately  
108 correlated to changes on PC3 (loadings from -0.23 to -0.46; Table S3). Thus, because

<sup>109</sup> style length was correlated with all traits on PC3 and was the main driver of variation,  
<sup>110</sup> we refer to this axis as the ‘style length trade-off’. Further, the pPCA with the subset of  
<sup>111</sup> species that had nectar and pollen quantity data showed that nectar quantity  
<sup>112</sup> (microlitres of nectar per flower) was positively associated with flower size, style  
<sup>113</sup> length and ovule number (PC1, 23.40%); and pollen quantity (pollen grains per flower)  
<sup>114</sup> was positively correlated with flower number and plant height and negatively  
<sup>115</sup> associated with autonomous selfing (PC2, 21.67%; Figure S6). This pPCA explained  
<sup>116</sup> similar variance with the first two principal components (45.07%) and similar  
<sup>117</sup> associations of traits despite some variability in the loadings (Table S4).

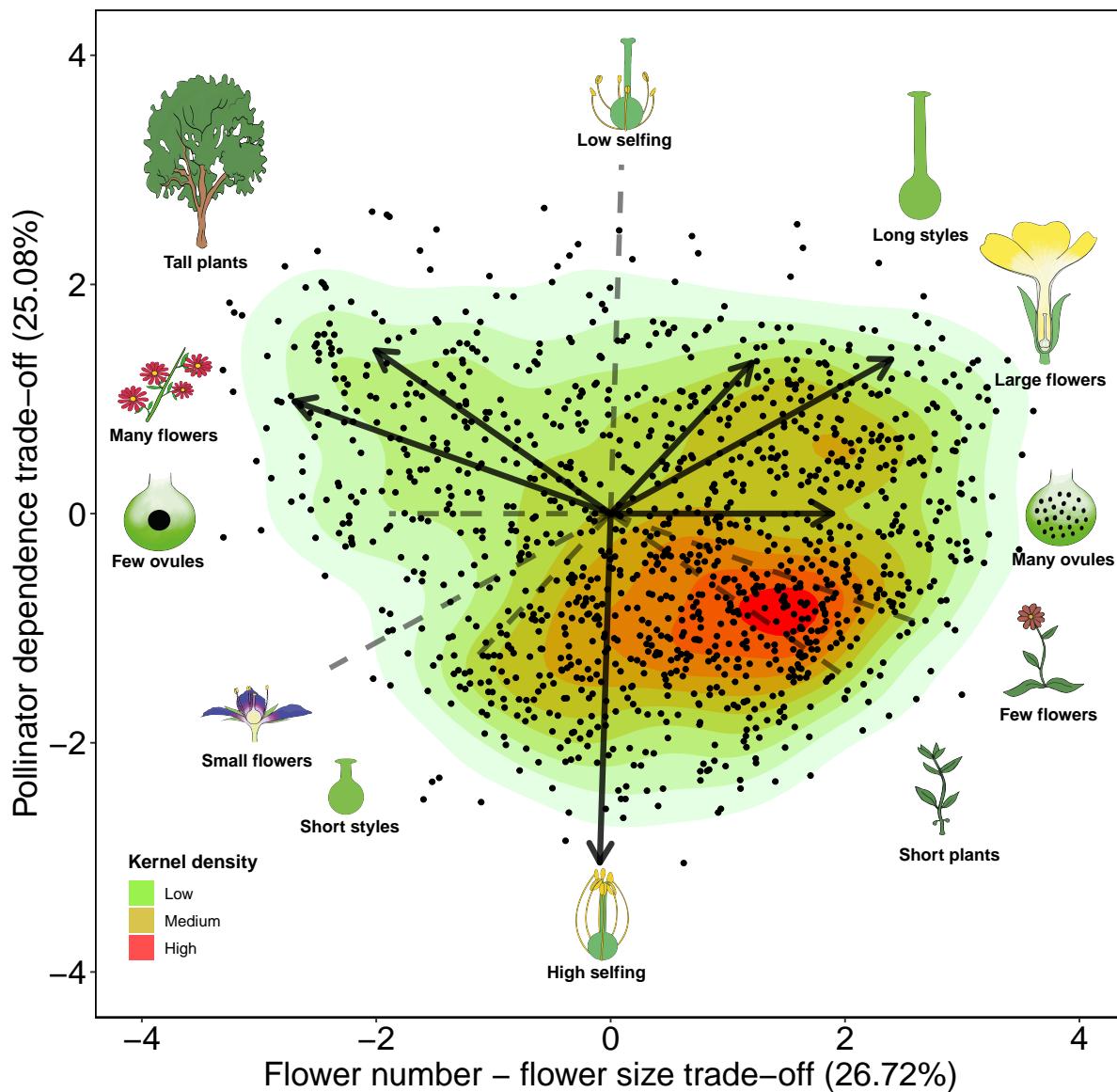


Figure 1: Figure 1. Life history strategies for 1,236 plant species from 28 plant-pollinator networks studies across the first two axes of trait variation from a phylogenetically informed principal component analysis (pPCA). The solid arrows indicate the direction of the different quantitative traits (flower number, plant height, style length, flower size, ovule number and level of autonomous selfing) in the 2-d plane. The length of the arrows indicate the weight of the variables on each principal component and the labelled icons at their end represent the extreme form of the trait continuum. The dashed lines show the opposed direction of trait variation and the non-labelled icons at their end illustrate the opposing extreme of the continuum.

- <sup>118</sup> We found that most categorical traits were statistically associated with the first two
- <sup>119</sup> axes of trait variation (Figure 2 and Table S2). Flower symmetry, which was only
- <sup>120</sup> associated with PC2 (Sum of squares = 8.51, F-value = 14.72,  $p < 0.01$  ), and nectar

<sup>121</sup> provision, which was independent of PC1 and PC2 (PC1: Sum of squares = 0.37,  
<sup>122</sup> F-value = 0.29 , p = 0.59; PC2: Sum of squares = 0.83, F-value = 1.43, p = 0.23) showed  
<sup>123</sup> lack of statistical association. In addition, we found statistical differences (Tukey test)  
<sup>124</sup> between the different levels of categorical traits in the trait space (Figure S7).  
<sup>125</sup> Regarding self compatibility, we found larger differences on PC2 (i.e., species with  
<sup>126</sup> unisexual flowers that were self incompatible were statistically differentiated from  
<sup>127</sup> species with partial or full self compatibility; Figure S7 A and B). Life forms differed  
<sup>128</sup> statistically across both axes of trait variation and followed a gradient of larger life  
<sup>129</sup> forms (trees and shrubs) with higher pollinator dependence to smaller ones (herbs)  
<sup>130</sup> with lower pollinator dependence (Figure S7 C and D). Consequently, lifespan also  
<sup>131</sup> followed this gradient but perennial and short lived species only differed statistically  
<sup>132</sup> on PC2 (Figure S7 E and F). Species with unisexual flowers (monoecious and dioecious)  
<sup>133</sup> were clustered on both extremes of the first two principal components and had the  
<sup>134</sup> highest pollinator dependence and highest number of flowers (Figure S7 G and H).  
<sup>135</sup> Moreover, we found that the campanulate and capitulum flower shapes were  
<sup>136</sup> differentiated from tube, papilionaceous, open and brush shapes in the trait space. The  
<sup>137</sup> former morphologies had larger flowers and greater pollinator dependence, while the  
<sup>138</sup> latter had higher flower number and greater autonomous selfing (Figure S7 I and J).  
<sup>139</sup> Regarding flower symmetry, zygomorphic flowers were associated with lower levels of  
<sup>140</sup> pollinator dependence, whereas actinomorphic flowers had higher levels of pollinator  
<sup>141</sup> dependence (Figure S7 K and L).

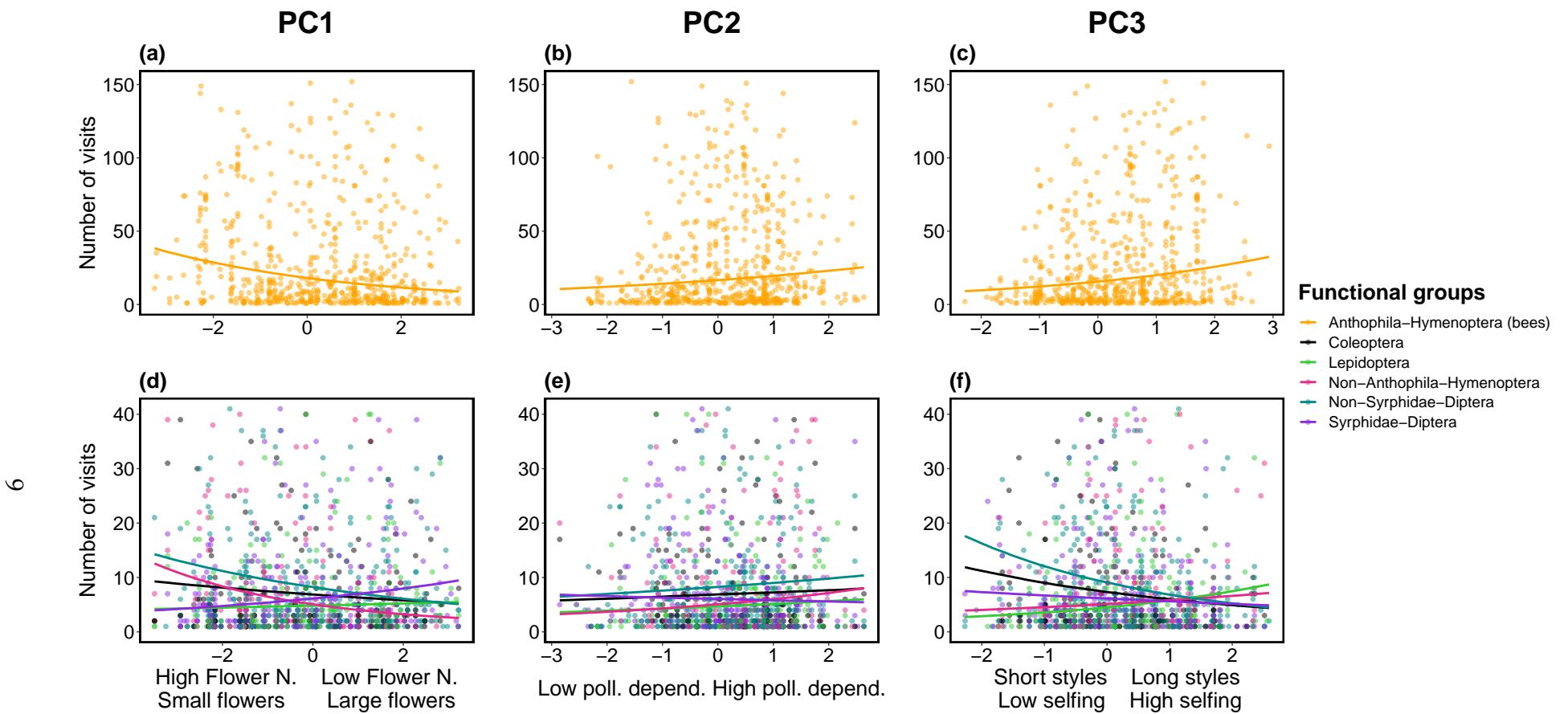


Figure 2: Location of the different qualitative traits that showed statistical association with the first two axes of trait variation. These different traits included: compatibility system (a), life form (b), lifespan (c), breeding system (d), flower shape (e) and flower symmetry (f).

<sup>142</sup> Phylogenetic signal of traits

<sup>143</sup> OLD

<sup>144</sup> Among flowering plants there is an astonishing diversity of floral structures and plant

<sup>145</sup> reproductive strategies (Barrett 2002, Schiestl and Johnson 2013). Subsequently,

<sup>146</sup> pollination biologists have long studied their relevance on plant-pollinator interactions.

<sup>147</sup> However, despite recent efforts exploring reproductive (e.g., mating and compatibility

<sup>148</sup> system) and floral traits (e.g., flower size or nectar provision) with large sets of species

<sup>149</sup> (Carvalheiro et al. 2014, Baude et al. 2016, Munoz et al. 2016, Grossenbacher et al. 2017,

<sup>150</sup> Moeller et al. 2017), most studies focus on the individual, community level or specific

<sup>151</sup> taxa and macroecological patterns remain poorly investigated. For instance, studies

<sup>152</sup> depicting species' life history strategies generally focus on vegetative traits and rarely

<sup>153</sup> consider reproductive traits on the main axes of trait variation (Díaz et al. 2016,

<sup>154</sup> Salguero-Gómez et al. 2016). In addition, there is not a unified framework that explores

<sup>155</sup> the compromises of floral traits and their relevance on plant life strategies (Roddy et al.

<sup>156</sup> 2021). Similarly, there is growing interest in understanding what determines

<sup>157</sup> plant-pollinator network structure. Approaches with traits range from the description

<sup>158</sup> of pollination syndromes (e.g., Dellinger 2020), to more specific trait-matching analysis

<sup>159</sup> (Bartomeus et al. 2016), but again the reproductive biology of the species has received

<sup>160</sup> little attention (but see Tur et al. 2013 and @devaux2014) and floral traits have been

<sup>161</sup> overlooked beyond highly specialised plant-pollinator interactions (Dellinger 2020,

<sup>162</sup> Roddy et al. 2021).

<sup>163</sup> With increased availability of large trait databases, plant ecological strategies have

<sup>164</sup> begun to be examined more frequently (e.g., TRY, Kattge et al. 2011 and COMPADRE,  
<sup>165</sup> Salguero-Gómez et al. 2015), highlighting global patterns and constraints of plant form  
<sup>166</sup> and function (Díaz et al. 2016, Salguero-Gómez et al. 2016, Carmona et al. 2021).  
<sup>167</sup> However, these resources and their research have mainly focused on vegetative traits  
<sup>168</sup> such as the leaf (Wright et al. 2004) or wood (Chave et al. 2009) trade-offs and  
<sup>169</sup> neglected reproductive and floral traits that also can influence the spectrum of trait  
<sup>170</sup> variation. For instance, short lived and perennial species tend to have high and low  
<sup>171</sup> levels of outcrossing respectively (Barrett 2003, Moeller et al. 2017) and outcrossing  
<sup>172</sup> levels have been shown to be positively correlated with flower size (Goodwillie et al.  
<sup>173</sup> 2010). In addition, the presence of costly rewards (e.g., pollen or nectar) and showy  
<sup>174</sup> flowers or floral displays cannot be understood without considering pollinators that  
<sup>175</sup> are thought to be responsible for approximately 87.5% of the pollination of flowering  
<sup>176</sup> plants (Ollerton et al. 2011). Hence, exploring plant life strategies with reproductive  
<sup>177</sup> and floral trade-offs, in conjunction with their known pollinators seems necessary for a  
<sup>178</sup> correct understanding of the plant economics.

<sup>179</sup> Several key studies have progressed knowledge of the link between traits and network  
<sup>180</sup> properties (Lázaro et al. 2008, Bartomeus 2013, Carvalheiro et al. 2014, Klumpers et al.  
<sup>181</sup> 2019). Functional traits can determine whether species interact, and thus define the  
<sup>182</sup> species network role (e.g., specialist vs generalist). For instance, species with high  
<sup>183</sup> investment in floral display tend to have higher visitation rates (Stang et al. 2006,  
<sup>184</sup> Novella-Fernandez et al. 2019) and greater specialization is generally associated with  
<sup>185</sup> occupation of the trait space extremes (Junker et al. 2013, Coux et al. 2016). In addition,  
<sup>186</sup> the structure of the pollination network highly depends on the degree of trait-matching  
<sup>187</sup> between plants and pollinators (Stang et al. 2009, Ibanez 2012, Peralta et al. 2020).

<sup>188</sup> However, little is known about the consequences of reproductive traits and floral  
<sup>189</sup> rewards on plant species roles. In addition, although some attempts have been made to  
<sup>190</sup> evaluate trait relationships in plant-pollinator interactions at a global scale (Carvalheiro  
<sup>191</sup> et al. 2014, Rech et al. 2016), macroecological patterns have been little explored.

<sup>192</sup> Here, we explore the major axes of plant reproductive trait variation. We investigate  
<sup>193</sup> how these traits influence the structure of plant-pollinator networks by compiling a  
<sup>194</sup> unique dataset comprising 20 plant functional traits for 1,506 species from 64 unique  
<sup>195</sup> networks and 8 metawebs. First, we evaluate the major axes of reproductive trait  
<sup>196</sup> variation and tradeoffs that determine plant form and function. Second, we investigate  
<sup>197</sup> how plant species' position in trait-space influences interaction strength with different  
<sup>198</sup> pollinator functional groups. Finally, we assess the relevance of the main axes of trait  
<sup>199</sup> variation and traits in understanding the plant species role within the networks with  
<sup>200</sup> complementary species level metrics (i.e., interaction strength, normalized degree and  
<sup>201</sup> specialization).

## <sup>202</sup> METHODS

### <sup>203</sup> Plant-pollinator network studies

<sup>204</sup> We selected 28 studies from 18 different countries that constituted a total of 64  
<sup>205</sup> plant-pollinator networks. All these studies censored plant-pollinator interactions in  
<sup>206</sup> natural systems and were selected in order to have a wide representation of  
<sup>207</sup> geographical areas of the world. Although these studies differ in sampling effort and

<sup>208</sup> methodology, all studies provided information about plant-pollinator interactions  
<sup>209</sup> (weighted and non-weighted) allowing us to build a database of plants that are likely  
<sup>210</sup> to be animal pollinated. Some of these networks have been already used in past studies  
<sup>211</sup> of plant-pollinator networks (Olesen et al. 2007, Fortuna et al. 2010, Carvalheiro et al.  
<sup>212</sup> 2014) and are available on the online networks archives The Web of Life (Fortuna et al.  
<sup>213</sup> 2014) and Mangal (Poisot et al. 2016). In total, our network dataset (Table S1)  
<sup>214</sup> constituted 60 weighted (interaction frequency) and 4 binary networks, each sampled  
<sup>215</sup> at a unique location and year, as well as 8 meta-webs where sampled interactions were  
<sup>216</sup> pooled across several locations and multiple years.

## <sup>217</sup> **Taxonomy of plants and pollinators**

<sup>218</sup> All plant species names, genera, families and orders were retrieved and standardized  
<sup>219</sup> from the taxonomy data sources NCBI (<https://www.ncbi.nlm.nih.gov/taxonomy>)  
<sup>220</sup> (plants) and ITIS (<https://www.itis.gov/>) (pollinators) using the R package taxize  
<sup>221</sup> (version 0.9.99, Chamberlain et al. 2020). We filled the ‘not found’ searches manually  
<sup>222</sup> using <http://www.theplantlist.org/> and <http://www.mobot.org/> for plants and  
<sup>223</sup> <http://www.catalogueoflife.org/> for floral visitors.

## <sup>224</sup> **Functional traits**

<sup>225</sup> We selected 20 different functional traits based on their relevance to plant reproduction  
<sup>226</sup> and data availability (Table 1). The selected traits were quantitative (12) and categorical  
<sup>227</sup> (8) and belonged to three different trait types: vegetative, floral and reproductive. For

228 each species, we undertook an extensive literature and online search across a wide  
229 range of resources (plant databases, online floras, books, journals and images) from a  
230 total of 30,120 cells (20 columns x 1,506 spp) we were able to fill 23,969 cells (79.6% of  
231 the dataset, see Figure S1 for missing values information per variable).

## 232 **Phylogenetic Distance**

233 We calculated the phylogenetic distance between different plant species using the  
234 function get\_tree from the package rtrees (downloaded from github,  
235 <https://github.com/daijiang/rtrees>), which downloads phylogenetic distances from  
236 the extended R implementation of the Open Tree of Life (Smith and Brown [2018](#))  
237 developed by Jin and Qian ([2019](#)).

## 238 **Data Imputation**

239 Missing values were imputed with the function missForest (Stekhoven and Bühlmann  
240 [2012](#)) which allows imputation of data sets with continuous and categorical variables.  
241 We accounted for the phylogenetic distance among species on the imputation process  
242 by including the eigenvectors of a principal component analysis of the phylogenetic  
243 distance (PCoA) which has been shown to improve the performance of missForest  
244 (Penone et al. [2014](#)). To extract the eigenvectors, we used the function PVRdecomp  
245 from the package PVR (Santos et al. [2018](#)) based on the conceptual framework of  
246 Diniz-Filho et al. ([2012](#)). Although the variable of autonomous selfing had a high  
247 percentage of missing values (68%), we were able to solve this by back transforming

Table 1: List of the 20 traits compiled in this study divided in quantitative and categorical traits. The different types of trait (vegetative 'V', floral 'F' and reproductive 'R'), total records found for the 1,506 species and categories of the qualitative traits are also provided.

Quantitative traits			Categorical traits			
Type	Traits	Records	Type	Traits	Categories	Records
V	Plant height (m)	1470	V	Lifepan	Short-lived Perennial	1466
F	Flower width (mm)	1472	V	Life form	Herb Shrub Tree	1472
F	Flower length (mm)	1401	F	Flower shape	Brush Campanulate Capitulum Open Papilionaceous Tube	1458
F	Inflorescence width (mm)	1496	F	Flower symmetry	Actinomorphic Zygomorphic	1478
F	Style length (mm)	1497	F	Nectar	Presence Absence	1408
F	Ovules per flower	1457	R	Autonomous selfing	None Low Medium High	987
F	Flowers per plant	1468	R	Compatibility system	Self-incomp. Partially self-comp. Self-comp.	1253
F	Nectar ( $\mu$ l)	531	R	Breeding system	Hermaphrodite Monoecious Dioecious	1489
F	Nectar (mg)	455				
F	Nectar concentration (%)	558				
F	Pollen grains per flower	533				
R	Autonomous selfing (fruit set)	992				

<sup>248</sup> the qualitative column of autonomous selfing to numerical. The categories of 'none',  
<sup>249</sup> 'low', 'medium' and 'high' were converted to representative percentages of each  
<sup>250</sup> category 0%, 13%, 50.8% and 80% respectively. This reduced the percentage of missing  
<sup>251</sup> values for this column from 68% to 35% and allowed the imputation of this variable.  
<sup>252</sup> However, we were unable to impute nectar and pollen quantity due to the high  
<sup>253</sup> percentage of missing values (Figure S1). The imputed dataset had 9.7% of missing  
<sup>254</sup> values with a total of 8 categorical and 8 numerical variables. Finally, we conducted an  
<sup>255</sup> additional imputation for the subset of species with quantitative information of nectar  
<sup>256</sup> and pollen; all variables had lower than 30% of missing values ( $N = 636$ ) and the total  
<sup>257</sup> proportion of missing values in this dataset considering all variables was 13%.

## <sup>258</sup> Plant strategies

<sup>259</sup> We explored the trade-offs between different quantitative plant functional traits with a  
<sup>260</sup> phylogenetically informed Principal Component Analysis (pPCA). We did not include  
<sup>261</sup> the quantitative variables of flower length and inflorescence width because they were  
<sup>262</sup> highly and moderately correlated to flower width (Pearson's correlation = 0.72,  $p < 0.01$   
<sup>263</sup> and Pearson's correlation = 0.36,  $p < 0.01$  respectively), and thus we avoided  
<sup>264</sup> overemphasizing flower size on the spectrum of trait variation. In addition, we  
<sup>265</sup> explored the location of different qualitative traits in the trait space. Prior to the  
<sup>266</sup> analyses, we excluded outliers and standardized the data. Due to the high sensitivity  
<sup>267</sup> of dimensionality reduction to outliers, we excluded values in the 2.5th-97.5th  
<sup>268</sup> percentile range (Legendre and Legendre 2012). Then, we log transformed the  
<sup>269</sup> variables to reduce the influence of outliers and z-transformed ( $X= 0$ ,  $SD=1$ ) so that all

variables were within the same numerical range. We performed the pPCA using the function `phyl.pca` from the package `phytools` (version number 0.7-70, Revell 2012) with the method `lambda` ( $\lambda$ ) that calculates the phylogenetic correlation between 0 (phylogenetic independence) and 1 (shared evolutionary history) and we implemented the mode covariance because our variables are on the same scale after the log and z-transformation (Abdi and Williams 2010). Moreover, to corroborate that our imputation of missing values did not affect our results, we conducted a pPCA on the full dataset without missing values (Figure S2). We found little difference between the variance explained with the imputed dataset (51.08%) and the dataset without missing values (56.26%). In addition, the loadings on each principal component had a similar contribution and correlation patterns, with the exception of plant height which showed slight variations between the imputed and non imputed dataset. Finally, we explored with the imputed dataset with quantitative information of pollen and nectar the compromises in the trait space of these two floral rewards with the other quantitative traits. For this, we considered solely one variable of nectar quantity (microlites of nectar per flower) in order to avoid overemphasizing nectar on the spectrum of trait variation.

## Phylogenetic signal of traits

We calculated the phylogenetic signal of the different quantitative traits on the imputed dataset with the full set of species ( $N = 1506$ ) with the package `phytools` version 0.7-70 (Revell 2012) and we used Pagel's `lambda` ( $\lambda$ ) as a measurement of the phylogenetic signal. For pollen and nectar traits, phylogenetic signal was calculated on the imputed

<sup>292</sup> dataset that included these traits (N = 636).

## <sup>293</sup> Networks analysis

<sup>294</sup> Our analyses were conducted on the subset of 60 weighted networks with interaction  
<sup>295</sup> frequency sampled in a unique flowering season and site. Although floral visitors are  
<sup>296</sup> not always pollinators and the frequency of visits does not consider each pollinator  
<sup>297</sup> species efficiency (Ballantyne et al. 2015), interaction frequency provides valuable  
<sup>298</sup> information of the impact of pollinators (Vázquez et al., 2005; Vázquez et al., 2012).

<sup>299</sup> Although not all networks were sampled using the same method, our aim was not to  
<sup>300</sup> compare patterns across networks but within each network in order to obtain a general  
<sup>301</sup> picture of associations between traits and the main axes of trait variation and plant  
<sup>302</sup> species functional roles.

### <sup>303</sup> *Functional groups visitation patterns*

<sup>304</sup> We explored the relevance of pollinator functional groups and the main axes of trait  
<sup>305</sup> variation (pPCA with imputed dataset) on pollinator visitation per plant species. For  
<sup>306</sup> this, we divided floral visitors into six main groups that differ in life form and  
<sup>307</sup> behaviour: (i) Hymenoptera-Anthophila (bees), (ii) Hymenoptera-non-Anthophila  
<sup>308</sup> (other non-bee Hymenoptera), (iii) Diptera-Syrphids, (iv) Diptera-Non-Syrphids, (v)  
<sup>309</sup> Lepidoptera and (vi) Coleoptera. In addition, because Hymenoptera was the most  
<sup>310</sup> represented group with 2,256 records counted and had the highest frequency of visits  
<sup>311</sup> of all groups, we also explored visitation patterns of the most represented families of  
<sup>312</sup> Hymenoptera on the trait space (Andrenidae, Apidae, Colletidae, Halictidae and

<sup>313</sup> Megachilidae). Apis mellifera was the species with the largest proportion of records  
<sup>314</sup> (7.55% from the total) which is consistent with the results of Hung et al. (2018) that  
<sup>315</sup> showed that A. mellifera was the most frequent visiting species on a similar dataset of  
<sup>316</sup> 80 interaction plant-pollinator networks on natural systems. Hence, to control for the  
<sup>317</sup> relevance of Apis mellifera on the observed visitation patterns of bees, we conducted  
<sup>318</sup> an analogous analysis excluding A. mellifera. We found that A. mellifera, was driving,  
<sup>319</sup> in part, some of the observed trends on PC1 (Figure S3). However, we did not find  
<sup>320</sup> major changes on PC2 and PC3.

<sup>321</sup> *Plant species functional roles*

<sup>322</sup> We investigated if the main axes of trait variation and traits explained plant species  
<sup>323</sup> functional roles. We considered all uncorrelated traits apart from the principal  
<sup>324</sup> components because this allowed us to consider quantitative and categorical traits. For  
<sup>325</sup> this, we also used a modelling approach and conducted decision trees which help to  
<sup>326</sup> interpret visually how the different traits determine species functional roles. We  
<sup>327</sup> selected simple and complementary plant species level metrics with a relatively  
<sup>328</sup> straightforward ecological interpretation relevant to our research goals: (i) sum of  
<sup>329</sup> visits per plant species; (ii) normalized degree calculated as the number of links per  
<sup>330</sup> plant species divided by the possible number of partners which helps comparison  
<sup>331</sup> across networks; and (iii) specialization ( $d'$ ) (Blüthgen et al. 2006), which measures the  
<sup>332</sup> deviation of an expected random choice of the available interaction partners and  
<sup>333</sup> ranges between 0 (maximum generalization) and 1 (maximum specialization).  
<sup>334</sup> Normalized degree and specialization were calculated with the specieslevel function  
<sup>335</sup> from the R package bipartite (version 2.15, Dormann et al. 2008).

<sup>336</sup> **Analyses**

<sup>337</sup> First, we implemented Bayesian generalized linear mixed models using the R package  
<sup>338</sup> `brms` (version 2.14.6, Bürkner 2017). We modelled the frequency of visits as a function  
<sup>339</sup> of the main axes of trait variation and floral visitors functional groups  
<sup>340</sup> ( $\text{Visits} \sim \text{PC1xFG} + \text{PC2xFG} + \text{PC3xFG}$ ). Because we were interested in possible differences  
<sup>341</sup> among main visitor guilds to plants with different strategies, we included the  
<sup>342</sup> interaction between the main axes of trait variation and the distinct floral visitor  
<sup>343</sup> functional groups. We added a nested random effect with networks nested on the  
<sup>344</sup> study system to capture the network variability per study and within networks. We  
<sup>345</sup> specified this model with a zero inflated negative binomial distribution and weakly  
<sup>346</sup> informative priors from the `brms` function. Moreover, we included the phylogenetic  
<sup>347</sup> covariance matrix as a random factor due to the possible shared evolutionary history  
<sup>348</sup> of the species and therefore lack of independence across them.

<sup>349</sup> Second, we modelled the distinct plant species metrics (sum of visits, normalized  
<sup>350</sup> degree and plant specialization) as a function of the three main axes of trait variation in  
<sup>351</sup> three different models for each metric (plant species level metric  $\sim \text{PC1} + \text{PC2} + \text{PC3}$ ). In  
<sup>352</sup> addition we also explored how all uncorrelated traits (13) explained these metrics in  
<sup>353</sup> three other models (plant species level metric  $\sim$  plant height + lifespan + life form +  
<sup>354</sup> flower shape + flower symmetry + flower width + style length + ovule number +  
<sup>355</sup> flowers per plant + nectar provision + autonomous selfing + compatibility system +  
<sup>356</sup> breeding system). For each response variable (metric), we used different distribution  
<sup>357</sup> families: zero inflated negative binomial for the sum of visits, weibull for normalized  
<sup>358</sup> degree and zero one inflated beta for specialization. Moreover, we included a nested

<sup>359</sup> random effect with networks nested on the study system and a phylogenetic random  
<sup>360</sup> effect for species (as detailed above) in each model.

<sup>361</sup> All analyses were conducted in R Version 4.0.3. In addition, all models were run for  
<sup>362</sup> 3,000 iterations with 1000 warm up iterations. We set delta () to 0.99 to avoid divergent  
<sup>363</sup> transitions and visualized the posterior predictive checks with the function pp\_check  
<sup>364</sup> using the bayesplot package (version 1.7.2, Gabry et al., 2019).

<sup>365</sup> [ADD REGRESSION TREE TO METHODS] We conducted regression trees in order to  
<sup>366</sup> explore the relevance of traits on the species plant functional role. We repeated the  
<sup>367</sup> procedure as the modelling analysis and we ran a decision tree for each plant level  
<sup>368</sup> species metric (interaction frequency, normalized degree and specialization). We used  
<sup>369</sup> the full dataset

<sup>370</sup> rpart 4.1-15 (Therneau et al., 2019) rpart.plot 3.0.9 (Milborrow 2018)

## <sup>371</sup> RESULTS

### <sup>372</sup> Plant strategies

<sup>373</sup> The phylogenetically informed principal component analysis (pPCA) captured with  
<sup>374</sup> the first two and three axes 51.8% and 70.97% of the trait variation respectively (Figure  
<sup>375</sup> 1 and Figure S4) and had a phylogenetic correlation ( $\lambda$ ) of 0.76. The first principal  
<sup>376</sup> component (PC1) represented 26.72% of the trait variation and showed the flower  
<sup>377</sup> number versus flower size compromise. Thus, as flower number and plant height

increase, flower size, style length and ovule number decrease; and, as flower size, style length and ovule number increase, flower number and plant height decrease. The main contributing traits to PC1 were plant height, flower number, ovule number and flower size (loadings > |0.5|; Table S2) but style length also contributed moderately on PC1 (loading = -0.33). The second principal component (PC2) represented 25.05% of the trait variation and showed the trade-off between low and high pollinator dependence and we refer to this axis as the pollinator dependence trade-off. The main driver of trait variation of PC2 was autonomous selfing (loading = 0.85) but the other traits (except ovule number) also made a moderate contribution to PC2 (loadings from 0.27 to 0.4; Table S2). We found that high pollinator dependence was associated with larger and higher number of flowers, greater plant height and longer styles. In contrast, species with high levels of autonomous selfing had a general lower investment in flower number and size, plant height and style length. Further, PC3 also explained a considerable amount of variability (19.17%) and the main contributors to this axis were style length (loading = -0.66) and the degree of autonomous selfing (loading = -0.51). The remaining traits, apart from ovule number, were moderately correlated to changes on PC3 (loadings from -0.23 to -0.46; Table S2). In addition, the pPCA with the species subset that had nectar and pollen quantity showed that nectar quantity (microlitres of nectar per flower) was positively associated with flower size, style length and ovule number (PC1, 24.70%); and pollen quantity was positively correlated with flower number and plant height and negatively associated with autonomous selfing (PC2, 20.59%; Figure S5). This pPCA also showed similar explained variance with two components (50.06%) and similar associations of traits despite some variability in the loadings (Table S3).

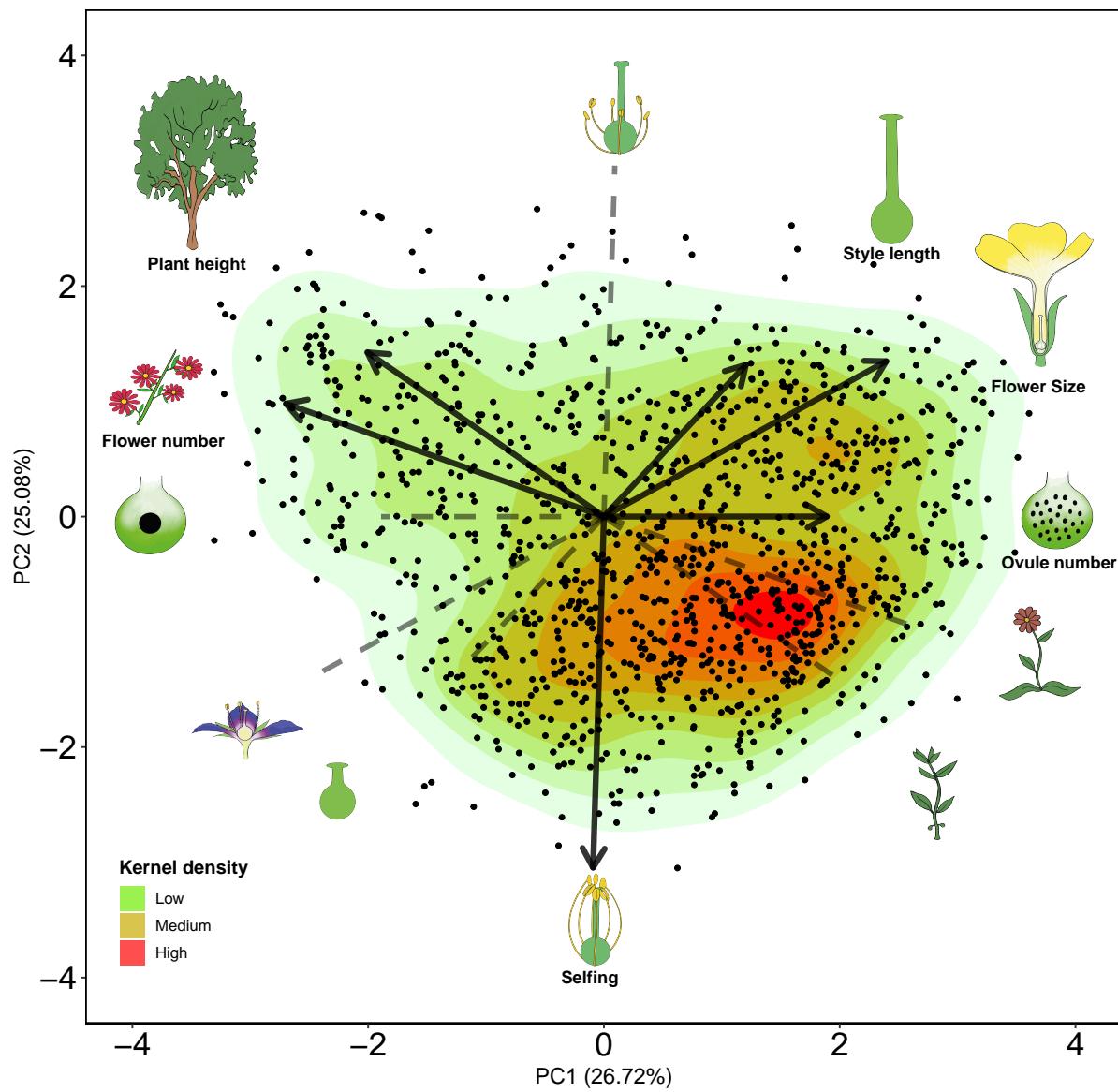


Figure 3: Life history strategies for 1,236 plant species from 29 plant-pollinator networks studies across the first two axes of variation from a phylogenetically informed principal component analysis (pPCA). The solid arrows indicate the direction and weights of the six quantitative traits (flower number, plant height, style length, flower size, ovule number and autonomous selfing level) and the labelled icons at their end represent the extreme form of the trait continuum. The dashed lines indicate the opposed direction of trait variation and the non-labelled icons at their end illustrate the other extreme of the continuum.

<sup>402</sup> Evaluation of qualitative variable positions in the trait space revealed statistical  
<sup>403</sup> association on both axes of trait variation for compatibility, breeding system, life form,  
<sup>404</sup> lifespan and flower shape (Figure 2 and Table S4). In addition, flower symmetry was

405 associated with PC2 (Sum of squares = 8.51, F-value = 14.72 , p < 0.01 ). Nectar  
406 provision was independent of both axes (PC1 Sum of squares = 0.37, F-value = 0.29 , p  
407 = 0.59; PC2 Sum of squares = 0.83, F-value = 1.43 , p = 0.23). Concerning self  
408 compatibility, we found larger differences in pollinator dependence the trade off (i.e.,  
409 species with unisexual flowers and self incompatibility were statistically differentiated  
410 from species with partially and fullyself compatibility in trait space; Figure S3 A and B).  
411 Life forms differed statistically across both axes of trait variation and followed a  
412 gradient of larger life forms (trees and shrubs) with higher pollinator dependence to  
413 smaller ones (herbs) with lower pollinator dependence (Figure S3 C and D).  
414 Consequently, lifespan also followed this gradient but perennial and short lived  
415 species just differed statistically on PC2 (Figure S3 E and F). Species with unisexual  
416 flowers (monoecious and dioecious) were clustered on both extremes of trait variation  
417 with the highest pollinator dependence and flower number investment (Figure S3 G  
418 and H). Moreover, we found that the campanulate and capitulum flower shapes were  
419 differentiated from tube, papilionaceous, open and brush shapes in the trait space. The  
420 former morphologies tended to occupy positions with larger flowers and greater  
421 pollination dependence, while the latter positions had higher number of flowers and  
422 autonomous selfing (Figure S3 I and J). Regarding flower symmetry, zygomorphic  
423 flowers were associated with lower levels of pollinator dependence, whereas  
424 actinomorphic flowers had higher pollinator dependence (Figure S3 K and L).

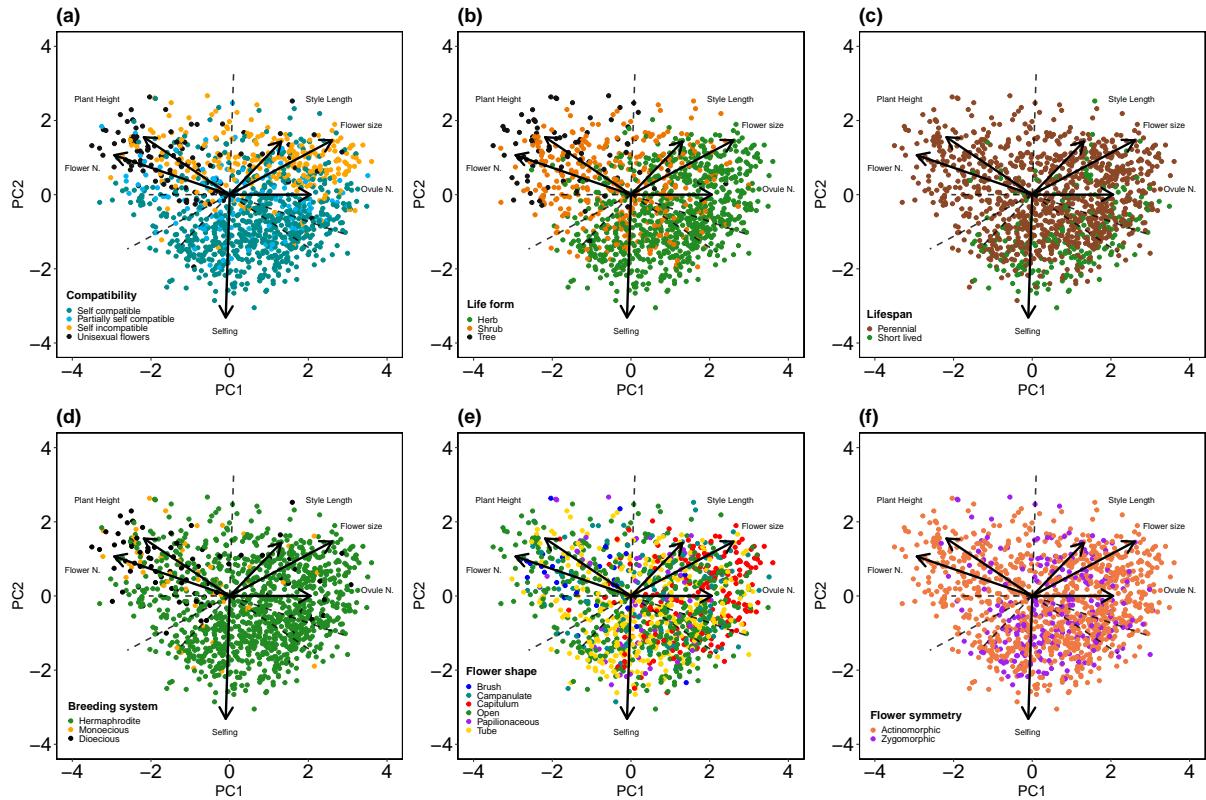


Figure 4: Location of the qualitative traits in the trait space for traits that showed a statistical association with the main axis of trait variation. These different traits included: compatibility system (a), life form (b), lifespan (c), breeding system (d), flower shape (e) and flower symmetry (f).

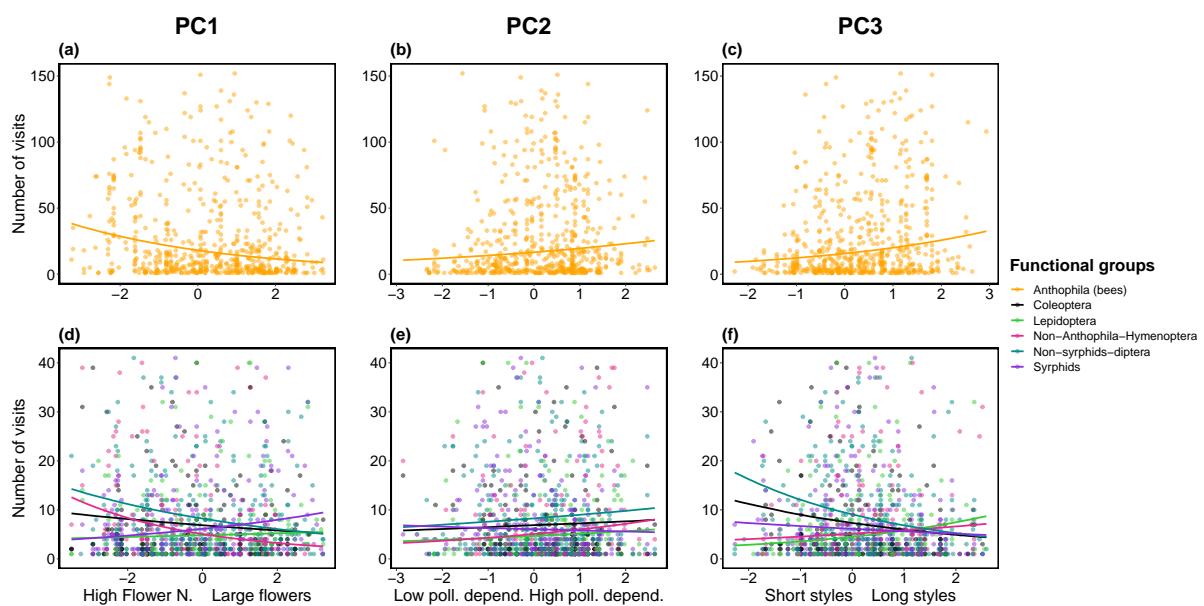
## 425 Phylogenetic signal of traits

426 We found a strong phylogenetic signal with statistical association ( $P < 0.01$ ) for all  
 427 quantitative traits (Table S4). The traits with the highest phylogenetic signal were ovule  
 428 number ( $\lambda = 1$ ) and plant height ( $\lambda = 0.96$ ), followed by flower length ( $\lambda = 0.75$ ), flower  
 429 width ( $\lambda = 0.73$ ) and flower number per plant ( $\lambda = 0.69$ ). Finally the traits that showed  
 430 lower phylogenetic signal were inflorescence width ( $\lambda = 0.57$ ), style length ( $\lambda = 0.49$ )  
 431 and autonomous selfing ( $\lambda = 0.34$ ).

432 Add \*pollen and nectar traits

433 **Visitation patterns**

434 The overall visitation records of functional groups differed considerably. There were  
435 2,256 for bees, 1,768 for non-syrphid-Diptera, 845 for syrphids, 437 for Lepidoptera, 432  
436 for Coleoptera and 362 for non-bee-Hymenoptera. The main axes of trait variation  
437 explained little of the visitation patterns (conditional R<sup>2</sup> = 0.31; marginal R<sup>2</sup> = 0.06) but  
438 showed interesting trends for the different functional groups (Figure 3). Furthermore,  
439 the additional model with interaction between the most represented families of  
440 Hymenoptera and the main axis of trait variation (marginal R<sup>2</sup> = 0.30; conditional R<sup>2</sup> =  
441 0.03) showed that the family Apidae was the main driver of the observed patterns  
442 (Figure S2). Although *Apis mellifera* contributed substantially to floral visitation, the  
443 general pattern of bee visitation did not change when *A. mellifera* were removed (FSX).



<sup>445</sup> **Plant species metrics**

<sup>446</sup> The three main axes of trait variation did not explain the position or role of the plant  
<sup>447</sup> species in the network (visits ~ PCs: conditional R<sup>2</sup> = 0.11, marginal R<sup>2</sup> = 0.02;  
<sup>448</sup> normalized degree ~ PCs: conditional R<sup>2</sup> = 0.24, marginal R<sup>2</sup> = 0.02 and specialization  
<sup>449</sup> ~ PCs: conditional R<sup>2</sup> = 0.37, marginal R<sup>2</sup> = 0.03). However, the functional groups  
<sup>450</sup> showed different visitation patterns across the three main axes of trait variation (Figure  
<sup>451</sup> 3). On the flower number versus size compromise, all functional groups showed  
<sup>452</sup> higher visitation rates on plant species with greater vegetative investment and more  
<sup>453</sup> flowers except syrphids which showed the opposite trend (higher visitation on species  
<sup>454</sup> with larger flowers and associated traits). Remarkably, on the pollinator dependence  
<sup>455</sup> trade-off, all pollinator functional groups showed an increasing visitation pattern for  
<sup>456</sup> species with higher pollinator dependence. Lastly, we found that bees, Lepidoptera  
<sup>457</sup> and non-bee Hymenoptera visited more species with larger style length and  
<sup>458</sup> Coleoptera, Non-Syrphids Diptera and Syrphids had greater visitation patterns on  
<sup>459</sup> species with shorter styles. Furthermore, with the full model that included all traits, we  
<sup>460</sup> found that a considerable amount of variance for plant species network metrics was  
<sup>461</sup> explained by the different qualitative and quantitative traits (Visits ~ Traits: conditional  
<sup>462</sup> R<sup>2</sup> = 0.32, marginal R<sup>2</sup> = 0.07; Normalize degree ~ Traits: conditional R<sup>2</sup> = 0.46,  
<sup>463</sup> marginal R<sup>2</sup> = 0.16; Specialization ~ Traits: conditional R<sup>2</sup> = 0.49, marginal R<sup>2</sup> = 0.14).

<sup>464</sup> **DISCUSSION**

<sup>465</sup> Our work highlights that in plant-pollinator networks, plant species have displayed  
<sup>466</sup> clear trade-offs in life strategies. These trade-offs can be differentiated on two main  
<sup>467</sup> axes of trait variation: the flower number-size trade-off and the pollinator dependence  
<sup>468</sup> trade-off. In addition, we found that relevant qualitative traits were aggregated within  
<sup>469</sup> trait space, showing clear delimited strategies of different plant species within  
<sup>470</sup> plant-pollinated systems. Moreover, the distinct pollinator functional groups showed  
<sup>471</sup> changes in their interaction strength along these axes of trait variation. Although the  
<sup>472</sup> main axes of trait variation explained little the variation of plant species network  
<sup>473</sup> metrics, the full model of uncorrelated traits explained partially the plan level metrics.

<sup>474</sup> **CONCLUSIONS**

<sup>475</sup> Wrap up

<sup>476</sup> **ACKNOWLEDGEMENTS**

<sup>477</sup> On the shoulders of giants.

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## **693 SUPPLEMENTARY MATERIAL**