Wild insect diversity increases inter-annual stability in global crop pollinator communities

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<u>Statement of authorship</u>: DS collated datasets, analysed the data and wrote the manuscript based on initial ideas conceived by AMK. JF wrote the R code for the initial data analyses, and along with MA, MPDG, DK, BJP, SGP & AMK was involved in helping structure subsequent data analyses and in commenting on several early drafts of the manuscripts. BB produced the insect illustrations used in

Figure 1 in addition to contributing data. All other authors provided the data utilised in the analyses and contributed to revisions of the manuscript.

1 Abstract: While an increasing number of studies indicate that range, diversity and abundance of many wild pollinators has declined, the global area of pollinator-dependent crops has significantly 2 3 increased over the last few decades. Crop pollination studies to date, have mainly focused on either identifying different guilds pollinating various crops, or on factors driving spatial changes and 4 5 turnover observed in these communities. The mechanisms driving temporal stability for ecosystem 6 functioning and services, however, remain poorly understood. Our study quantifies temporal 7 variability observed in crop pollinators in 21 different crops across multiple years at a global scale. 8 Using data from 43 studies from six continents, we show that (i) higher pollinator diversity confers 9 greater inter-annual stability in pollinator communities, (ii) temporal variation observed in pollinator 10 abundance is primarily driven by the three most dominant species, and (iii) crops in tropical regions 11 demonstrate higher inter-annual variability in pollinator species richness than crops in temperate 12 regions. We highlight the importance of recognising wild pollinator diversity in agricultural 13 landscapes to stabilize pollinator persistence across years to protect both biodiversity and crop 14 pollination services. Short-term agricultural management practices aimed at dominant species for 15 stabilising pollination services need to be considered alongside longer-term conservation goals focussed on maintaining and facilitating biodiversity to confer ecological stability. 16

17 Introduction:

The crucial role played by pollinators in the reproduction of flowering plants is well-established [1].
Biotic pollination is important for the reproduction of at least 78% of wild plants [2], and insects
contribute to the pollination of 75% of leading global crops [3]. Crop systems have also recently
become more pollinator dependent because of a disproportionate increase in the area cultivated with
entomophilous flowering crops [4]. Given the documented declines of wild insect pollinators in some
NW European and North American landscapes where these crops are grown [1, 5, 6] understanding
temporal variation in assemblages is important to maintain ongoing food security.

25

26 Higher pollinator diversity can lead to increases in fruit and seed set in plants and is an important 27 predictor of crop yields worldwide [7, 8]. Conversely, pollinator communities with lower diversity 28 and fewer species, have been linked to lower fruit set or seed production, and decreased temporal and 29 spatial stability within seasons [9-11], and may be one reason for lower inter-annual stability of yields 30 in pollinator-dependent crops [1]. While biologically diverse communities can enhance ecological 31 resilience [12, 13], and diversity is a key factor affecting system stability [14], most ecological 32 communities are generally made up of a few species that are numerically abundant and may have 33 many rarer species with very few individuals [15].

34

35 Evidence suggests that numerically dominant species may provide most of the ecosystem services [16], with Kleijn et al. [17] finding that ~80% of biotic crop pollination in Europe and North America 36 are fulfilled by $\sim 2\%$ of the pollinator species in a community. In addition, the scale of spatial 37 assessment, is also important, with Winfree et al. [18] showing that the number of wild bee species 38 39 required for reaching a minimum pollination service threshold rapidly increased with spatial scale, 40 indicating that maintaining pollination services across large areas requires many species, including 41 rare ones. Providing stable pollination services for crop systems across several years is needed for 42 sustainable crop production, but the mechanisms driving temporal stability for ecosystem functioning and services still remains an important but poorly understood phenomenon [19]. 43

45 Previous studies aimed at disentangling the mechanisms of temporal stability highlight the role of both diversity and dominance. Lehman & Tilman [20] showed that greater diversity increases 46 47 temporal stability of the entire community but decreases temporal stability of individual populations. 48 The counterview is that dominant species, rather than diversity itself, might regulate temporal stability 49 - for e.g. Sasaki and Lauenroth [21] found that temporal stability in a shortgrass steppe plant 50 community was controlled by dominant species rather than by community diversity. In addition, 51 species asynchrony has also been considered an important mechanism of diversity-stability 52 relationships and may lead to higher stability on the community level even when stability of 53 individual populations decreases with diversity. However, the majority of such studies have utilised 54 long-term observations of the same plant communities over time [for e.g. 22], while such equivalent information on pollinators in general or even crop pollinator communities in particular are lacking. 55 56

57 A few multi-year, single crop studies exist showing that pollinator communities can vary over 58 longer time periods [9, 23, 24]. What implications this may have for stability remains unknown 59 due to lack of synthesized knowledge on temporal dynamics of crop pollinator communities and 60 underlying driving factors. For example, evidence for the contribution of managed pollinators to the 61 temporal stability of the overall crop pollinator community is largely lacking. Such knowledge gaps, 62 if addressed, could lead to better understanding of the stability and long-term resilience of global crop systems that rely on insect pollination. Temporal stability of ecosystem functioning increases 63 predictability and reliability of ecosystem services and understanding the drivers of stability across 64 65 spatial scales is important for land management and policy decisions [25].

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Here we synthesise data from multiple studies to examine factors that affect temporal stability of crop
pollinator communities, which in turn has implications for stability of pollination services provided.
Using data from 43 studies across six continents, we characterise the annual variation observed in
crop pollinators and explore the following questions 1. Is temporal stability of crop pollinator
communities primarily driven by diversity of pollinator communities or by inter-annual stability of
dominant species? 2. What crop characteristics if any (e.g., annual/perennial, flower morphology,

- mass flowering / non mass flowering crops) influence inter-annual stability of crop pollinator
- 74 communities? 3. Does inter-annual variation observed in pollinator communities differ between
- 75 climatic regions (i.e. tropics and temperate study areas)?
- 76

77 <u>Material and methods:</u>

78 Data collection: We collated datasets from 12 countries across six continents on 21 crop species to 79 examine the variations in richness and abundance of insect pollinators in crop systems. The criteria 80 for inclusion in the analyses were as follows: Data on crop pollinator species / morpho-species were 81 required (a) from the same crop for two or more years, (b) with consistent sampling methods used 82 across years, (c) focused on flower visitation data, and (d) in the case of annual crops, field sites were 83 required to be within 500m of the crop field used for recording in previous years to make sure they 84 could be visited by the same pollinator communities. Our final dataset included information on 375 85 crop fields (hereafter referred to as sites) from 43 studies (see Supplementary Table S1 for additional information). Data were standardised to ensure that species names and taxonomic groups were 86 87 consistent across all studies prior to analyses.

88

89 Each dataset was classified on the basis of climatic region (tropical/temperate), crop type 90 (annual/perennial), plant family and flower type (open / not open) – based on nectar accessibility criteria in Garibaldi et al. [26]. In addition, we distinguished crop species that exhibit mass-flowering 91 92 (MFC) - i.e. short duration intense bloom with high floral density, from those with extended flowering 93 periods with lower density and more sparse blooms. Some crops are clearly defined as mass flowering 94 in the literature [27-31], while others remain ambiguous. To overcome this uncertainty, we requested 95 the original authors to indicate if their crop was considered as MFC in their study and that is reflected 96 in the dataset and subsequent analyses (see Supplementary Table S2). Almonds (Prunus dulcis), 97 apples (Malus domestica), highbush blueberry (Vaccinium corymbosum), cranberry (Vaccinium 98 angustifolium), red clover (Trifolium pratense), field beans (Vicia faba), oilseed rape or canola (Brassica napus), pears (Pyrus communis), pak choi (Brassica rapa subsp. chinensis) and turnips 99 100 (Brassica rapa subsp. rapa) were classified as MFC. Non mass-flowering crops in our analyses

101 include avocado (Persea americana), bitter gourd (Momordica charantia), brinjal (Solanum

102 *melongena*) – also known as eggplant or aubergine, cashew (Anacardium occidentale), cotton

103 (Gossypium hirsutum), kiwifruit (Actinidia deliciosa), mango (Mangifera indica), mustard (Brassica

104 *napus*), onion (*Allium cepa*), pumpkin (*Cucurbita pepo*), ridge gourd (*Luffa acutangula*), spine gourd

105 (*Momordica dioica*), strawberry (*Fragaria x ananassa*) and watermelon (*Citrullus lanatus*). Note:

106 Brassica napus includes oilseed rape (OSR) – a MFC in Europe and North America but a different

107 subspecies considered as a type of mustard in India which is not grown as MFC.

108

109 Characterising year to year variation in crop pollinators: Initially, crop pollinators recorded were 110 classified into taxonomic groups which included the following: (i) honeybees (including Apis mellifera, Apis cerana, Apis dorsata and other recorded as Apis sp.); (ii) bumblebees (all Bombus sp.); 111 (iii) other bees (wild solitary and social bees including stingless bees but excluding bumblebees and 112 113 honeybees); (iv) butterflies and moths; (v) hoverflies; (vi) other Diptera (flies excluding hoverflies); (vii) wasps, and (viii) beetles. The single most dominant taxonomic group and species were identified 114 at all study sites (see Figure 1) based on recorded abundance and a binary (change / no change) 115 116 analysis was used to determine whether the most dominant group and species remained constant 117 across all years of sampling.

118

119 To characterise between year variation in crop pollinators, (i) a coefficient of variation (CV) of total pollinator abundance and (ii) a CV of pollinator species richness were calculated for each site across 120 121 all years of the study. The CV (which incorporates a bias correction) is defined as the ratio of the 122 sample standard deviation 's' to the sample mean \bar{x} - i.e. $CV = s / \bar{x}$, and shows the extent of variability in relation to the mean of the population. These measures were calculated using species 123 124 level data for each study site and the mean and standard deviation of these two measures were also 125 calculated for each individual study (Supplementary Figure S1). In addition, the CV of abundance and CV of richness were calculated for each site for every pairwise year comparisons (i.e. Y1& Y2; 126 127 Y2&Y3; Y3&Y4 etc) to account for studies having different number of years of data.

Other calculated indices included (a) CV of honeybee abundance, (b) CV of proportion of honeybees, (c) CV of the most dominant pollinator species across all years and (d) the mean Shannon index of pollinator diversity (H') were calculated across years. The Shannon diversity index was chosen as it accounts for evenness of the species present, thus reflecting effective diversity, and is less sensitive to sampling effects than species richness [32, 33]. Since a subset of studies (28 out of 43) also recorded temperature at the study sites, a standard deviation (SD) of temperature was also calculated as a measure of variation in local climatic condition across years.

136

137 Factors influencing the observed variation: In order to examine the potential drivers of inter-annual variation in crop pollinator communities, linear mixed-effects models were constructed using (i) CV 138 of total pollinator abundance and (ii) CV of pollinator species richness. These two indices were 139 140 calculated across all years of each study and for every pairwise year in each study to account for 141 studies with different numbers of years of observations and ensure checks for sensitivity and robustness. The models included descriptors of pollinator communities such as Shannon diversity (H') 142 of pollinators, CV of dominant species, and change in dominant pollinator species between years 143 (Y/N) as fixed effects. External predictors including climatic region (tropical/temperate), crop type 144 145 (annual/perennial), crop family, flower type, MFC (Y/N) and SD of site temperature were also included as other explanatory variables. Study ID was included in all models as a random effect and 146 147 for models where the response variables were calculated for every two years of the study, site ID nested within the study ID were used as random effects (and identified as relevant indicated by 148 149 positive variance estimates).

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The calculated indices were tested for collinearity and correlated variables were not used within the same models (see correlation matrix in Table S3 of supplementary material). Similarly, categorical predictors which exhibited significant collinearity were not used as variables within the same models. A series of candidate models were constructed for each response variable. Each candidate model was 'dredged' to obtain a series of plausible intermediate models. Intermediate models with Δ AICc value < 7 of the model with lowest AICc were averaged (using the default zero average method) to obtain the final outputs. Residual plots for final models were used to check for heteroscedasticity. Models
were fitted using maximum likelihood (ML) and analysed using the 'lme4' [34] and 'MuMIn' [35]
packages. All statistical analyses were carried out in R v. 4.0.3 statistical software [36].

160

161 Influence of dominant pollinator species: To test whether variation in total crop pollinator abundance 162 was driven primarily by variation of the most dominant pollinator species, a paired t-test was used to 163 determine whether CV of total pollinator abundance was significantly different from CV of 164 abundance of the single most dominant pollinator species. The same test was repeated using the 165 combined CV of abundance of the two-most, three-most and four-most dominant species to determine 166 how many dominant pollinator species were required to influence the overall variation in total abundance observed. While abundance of dominant species will always be a subset of the total 167 pollinator abundance, these tests were conducted to determine how many dominant species it took to 168 169 match the change in overall pollinator abundance across years and determine the minimum number of 170 species that drive the temporal variation in overall pollinator abundance. A Welch Two Sample t-test was used to determine if inter-annual variation in pollinator abundance differed between sites 171 dominated by honeybees versus other pollinator species. Sites where there was mixed dominance 172 173 between honeybees and other pollinators were excluded from this analysis.

174

175 Dominance species and stability effect: To further understand mechanisms of stability and particularly the relationship of the dominant species to the whole community, we calculated the correlation 176 177 between the changes in abundance of the dominant species and the changes in abundance of the rest 178 of the community. Negative correlation (negative covariance) suggests asynchrony, which is 179 considered a key driver of stability and a main mechanism of diversity-stability relationships [37]. 180 Negative correlations could indicate density compensation or different responses to environmental 181 variation [12]. In general, higher the asynchrony (i.e. more negative the correlation), the stronger the 182 contribution to stability. With our short time serious, many correlations are -1 or +1, without an even continuous gradient in the degree of asynchrony. Therefore, we separated sites by asynchronous (r \leq 183 184 0) or synchronous (r > 0) fluctuations of the dominant pollinator species in comparison to the rest of

the pollinator community, and for each group separately, repeated the paired t-test of the CV of thedominant species vs. the whole community.

187

188 <u>Results:</u>

189 *Characterising year to year variation in crop pollinators*

Honeybees were dominant across 41.9% of studies with other wild bees (32.6%) representing the next most dominant group (Figure 1A). At the site level, other wild bees were the most dominant group at 41.6%, with honeybees (38.0%) the second most dominant (Figure1B). The dominant taxonomic group did not change between years in most of the studies or the sites, whereas the dominant species varied between years in approximately half the studies and half the sites (Table 1). The mean (\pm SD) of the CV of total pollinator abundance, and the CV of total pollinator richness for all sites within each study is provided in Supplementary Figure S1.

197

198 *Factors influencing the observed variation*

The relative variability of total pollinator abundance across all years was significantly related to the Shannon diversity (Table 2, Estimate = -0.16, z = 3.96, p<0.0001, Figure 2A). It was also significant whether the most dominant species varied between years: systems where dominant species stayed the same showed less inter-annual variation in overall pollinator abundance (Table 2, Estimate = -0.08, z = 2.23, p = 0.03, Figure 2B). However, in models using CV of abundance for every two years, the variability in dominant species showed no significant relationship (Table 2, Estimate = -0.05, z = 1.42, p = 0.16)

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Having a diverse pollinator community also reduced the inter-annual variation in pollinator species richness (Table 2, Estimate = -0.16, z = 5.61, p<0.0001, Figure 3A) and this was true for indices calculated across all years of the studies as well as every two years of the studies (see Table 2). The relative change in species richness between years was related to the change in the abundance of the most dominant species, with study systems showing larger changes in species richness if there was increased inter-annual variation in dominant species abundance across all years (Table 2, Estimate = 213 0.09, z = 3.31, p<0.001, Figure 3B). This was also significant in models accounting for change in 214 species richness for every two years (Table 2, Estimate = 0.12, z = 3.77, p<0.001). However, any 215 change in dominant species across years showed no significant relationship with relative change in 216 species richness. The change in pollinator species richness also varied between climatic regions with 217 crops grown in temperate systems showing less inter-annual variability in pollinator species richness 218 than crops in tropical areas (Table 2, Estimate = 0.15, z = 2.22, p = =0.03, Figure 3C).

219

220 Other factors tested including crop family, flower type, annual versus perennial crop type, mass

221 flowering, or site temperature did not show any significant relationship with variability observed in

- the abundance or richness of species across years.
- 223

224 Influence of dominant pollinator species

225 It took the pooled abundance of the three most dominant pollinator species to match the relative variability of total pollinator abundance (respective mean CVs: 0.58 vs 0.55, t = 1.09, df = 362, p = 226 227 0.2, difference in means = 0.03). The relative variability of total pollinator abundance at the site level was found to be significantly lower than that of the single (t = 9.56, df = 362, p-value <0.001, 228 229 difference in means = 0.17) and top two most dominant species (t = 6.34, df = 362, p-value < 0.001, difference in means = 0.07). Sites where honeybees were dominant species (mean CV = 0.46) were 230 found to have significantly lower variability (t = 3.25, df = 295.26, p = 0.001) than sites where other 231 232 bees were dominant species (mean CV = 0.60).

233

234 Where the dominant species changed asynchronously to the rest of the community, the difference

between the CV of the dominant species and CV of total abundance was strong, with less than half the

variability in the whole community than in the dominant species (t = -11.02, df = 125, p-value <

237 0.0001, mean of total 0.31, mean of single most dominant species 0.67; difference in means = 0.36).

238 In contrast, CV of total abundance was only slightly lower than CV of the dominant species where the

dominant species changed synchronously with the rest of the community (t = -3.48, df = 219, p-value

= < 0.001, mean of total 0.65, mean of single most dominant species 0.71, difference in means = 0.06,

Figure 4). In simple terms, the stability of the whole pollinator community only increased to aconsiderable degree when other species buffered changes by asynchronous fluctuations.

243

244 **Discussion:**

245 This study is the first to use a global dataset to explore inter-annual variation in crop pollinator 246 communities and has revealed several important features of community stability. Our findings 247 indicate that: (i) crop pollinator communities with higher pollinator diversity are more stable between 248 years, and (ii) the variation observed in pollinator communities is driven by dominant species changes 249 across years. The importance of other species in addition to the stability of the dominant species was 250 in line with mechanisms of diversity-stability relationships: while stability of the dominant species was similar to the total community where the dominant species fluctuated synchronously with the rest 251 252 of the community, community abundance was much more stable than abundance of the dominant 253 species where these fluctuations were asynchronous. Neither the variation in abundance nor the 254 variation in species richness was significantly affected by any crop characteristics.

255

256 Our results show that sites with higher pollinator species diversity experience less variation in total 257 crop pollinator abundance and less change in pollinator species richness between years. These results concur with studies from individual cropping systems which have shown that diversity provides 258 greater spatial and temporal stability and resilience [12, 23], and supports the theory that ecological 259 systems with higher species diversity are better buffered against inter-annual variation in species 260 261 abundance, and possibly more resilient to changes in the longer term [14]. This has implications 262 beyond ecological resilience, as stable pollination services could help mitigate risks and uncertainties 263 for farmers growing pollinator dependent crops, providing economic resilience..

264

In addition to diversity, our results demonstrate that dominant species play a significant role in interannual stability of crop pollinator communities. Honeybees were found to be the single most dominant species in 18 out of 43 datasets and in 140 out of 375 sites which concurs with the findings of Kleijn *et al.* [17]. Sites where honeybees were the dominant species across all years also showed

269 greater inter-annual stability in abundance when compared to sites dominated by other species. Unlike wild pollinators, managed pollinators are often placed near crops, and due to hive management 270 271 practices may show less variability in abundance between years. Managed pollinators are considered 272 to supplement rather than substitute pollination by wild insects in most crop pollination systems [38], 273 but there is experimental evidence to suggest that managed bees in high numbers could displace wild 274 pollinators from crop fields [39]. Our study systems from Argentina, for instance, were entirely reliant 275 on managed Apis mellifera and no other species were recorded. The management of bees could 276 therefore be an important contributor to the inter-annual variability observed in the crop pollinator 277 community depending on placement of hives, stocking densities and how much these vary from one 278 year to the next. Careful targeting of managed pollinators could be used to increase the stability of 279 pollination [40-42], particularly in those crops for which inter-annual variation is high due to 280 fluctuations in populations of the dominant wild pollinators.

281

While we can say with a high level of certainty that most honeybees recorded in the USA and 282 283 European studies were from managed hives, it is difficult to distinguish between managed and wild 284 honeybees in other studies. For example, in China and India, while almost all Apis mellifera were 285 managed and all Apis dorsata wild, it is difficult to distinguish between wild and managed Apis cerana with any degree of certainty. In addition, certain areas - particularly in Western Europe, utilise 286 Bombus terrestris as a managed pollinator, and managed and wild individuals of this species are 287 indistinguishable from each other. Therefore, we cannot draw specific conclusions on the effect of 288 289 managed pollinators on the changes in richness and turnover of wild pollinator communities but raise 290 this as a possible question to be explored in future studies.

291

From our results, we also infer that a significant part of the year to year variation in crop pollinator abundance is driven by as few as three of the most dominant species within each system (see list of dominant species by study in supplementary Table S4). This is consistent with the findings of Kleijn *et al.* [17] who showed that the three most dominant pollinator species account for two-thirds of flower visits recorded. Even if only few species are quantitatively important in crop pollination

systems, enhancing stability by managing for diversity effects delivered through asynchrony among
species could be really effective as our results above have indicated. It is worth noting that while
delivery of crop pollination services may be predominantly driven a few key functional pollinator
species [17], depending on the context, the diversity and abundance of other pollinators may
complement or largely replace the functional role of dominant species [43].

302

303 The Winfree et al. [18] study – which explored functional consequences of spatial turnover in crop 304 pollinator communities - indicated that more species would be required to fulfil the minimum 305 pollination service threshold if dominance effects were to be removed or lost, but that is based on the 306 assumption that another species would be unable to take over the dominant role through increased 307 abundance. This raises questions of which systems would remain resilient in the event these specific 308 dominant species are lost due to future environmental conditions. For example, field beans flower 309 morphology excludes small solitary bees and depends predominantly on effective flower visits from 310 long-tongued bumblebees [44, 45], may be less resilient to loss of dominant pollinators when 311 compared to crops like oilseed rape dependent on a diverse suite of pollinators [44].

312

313 While no effect of climatic region was observed on the inter-annual change in pollinator abundance, there was less variation in pollinator species richness in temperate crops than in crops grown in the 314 tropics. Studies from temperate regions (n=29) showed a higher average Shannon diversity (H'=1.21) 315 than studies from the tropics (n=13, H'=1.19) but the difference was not statistically significant 316 (Figure S2, t=0.26, df= 356, p=0.74), and it is difficult to disentangle whether this result may be due 317 318 to differences in sampling effort. The difference between the temperate and tropical studies could not 319 be attributed to contrasting temperature regimes in the different climatic regions as we did not detect a 320 significant effect of temperature on inter-annual stability of crop pollinators in any of the models. 321 Pollinator populations are known to be sensitive to weather conditions [31] with temperature 322 influencing pollinator phenology [46] as well as plant-pollinator interactions [47]. Our analyses indicated that the crops in the tropics experienced significantly less variation in temperature than 323 324 those in temperate regions (t = 6.71; df = 34.74; p < 0.001, Supplementary Figure S3) but insufficient

climate data across all the datasets (only 28 studies of the 43 recorded temperature), meant this aspectcould not be fully explored within this study.

327

328 Of the 43 studies utilised, 25 studies had two years of data, 14 studies three years of data and four 329 studies with four or more years of repeated sampling. With these differences in number of years of 330 sampling, our global synthesis has only provided a first step to looking at temporal dynamics. 331 Estimates of temporal dynamics may vary with the number of years sampled and every effort has 332 been made to account for these differences by analysing changes in observed in every two years of 333 each study. It is to be noted that results of the models with the pairwise year calculations were 334 consistent with the model using data across all the years, but further measures to account for any differences caused by varying number of sampling years, and are beyond the scope of this manuscript. 335 336 Also, the diversity-stability effect identified, may be linked to sampling effort with lower sampling 337 leading to high CV values and low diversity between years. As this is a collated dataset consisting of various studies that have taken place across several geographic regions across multiple 338 339 years and we cannot retrospectively change the sampling effort, we acknowledge that the CV may be 340 sensitive to these underlying effects and raise this as a point to be considered in future studies.

341

342 Many studies to date, have focused on spatial variations observed between crops, fields and across 343 different landscapes [29, 48, 49], while relatively few studies have considered temporal variation 344 caused by differences in crop flowering times [31, 40, 50] and even these focussed only on within 345 season variation. To the best of our knowledge, our study is the first to explore temporal variation 346 in pollinator communities across different crops. Our results highlight the importance of considering both wider pollinator diversity as well as abundance of dominant species in understanding 347 348 inter-annual stability of crop pollinators. Temporal stability of ecosystem functioning increases the predictability and reliability of ecosystem services and understanding the drivers of stability across 349 350 spatial scales is important for land management and policy decisions [25]. Stability in the availability 351 of pollinators is also important from an agro-ecological resilience perspective as increased variation in

- animal pollination could reduce average yield and yield stability [51]. We further propose that the
- 353 stability and ecological resilience brought about by enhancing the diversity of pollinator communities
- 354 will contribute beyond agriculture and should be considered alongside longer-term conservation
- 355 targets focussed on maintaining and enhancing wider biodiversity.
- 356
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Table 1: The proportion of studies and sites showing inter-annual changes in the dominant taxonomic groups and species of crop pollinators; actual no. of studies and sites shown within parentheses. Note: One study with five sites (Pisa01) had only morphospecies level data

	Study Level		Site Level		
	Change	No change	Change	No Change	
Taxonomic	27.9%	72.1%	31.2%	68.8%	
Group	(12)	(31)	(117)	(258)	
Species	48.1%	51.2%	50.8%	49.2%	
(excl Pisa01)	(20)	(22)	(188)	(182)	

Table 2: Results of model averaging of candidate models that were within AICc $\Delta 7$ of the model with the lowest AICc value.

Response variable	Fixed effects remaining in the averaged model	Estimate	Adjusted SE	z value	p value		
	Models with CV calculated across all years of the studies Conditional $R^2 = 0.33$; Marginal $R^2 = 0.09$						
CV total pollinator abundanc e	Same dominant species H' index Climatic region MFC	-0.08482 -0.15584 0.08302 -0.08627	0.03802 0.03932 0.09064 0.08326	2.231 3.964 0.916 1.036	0.0257 * 7.38e-05 *** 0.3598 0.3001		
	Models with CV calculated for every two years of the studies Conditional $\mathbf{R}^2 = 0.35$: Marginal $\mathbf{R}^2 = 0.06$						
	Same dominant species H' index Climatic region MFC	-0.05286 -0.10368 0.11703 -0.10889	0.03726 0.03792 0.08691 0.03726	1.418 2.734 1.347 1.322	0.15607 0.00626** 0.17812 0.18609		
CV of pollinator species richness	Models with CV calculated across all years of the studies Conditional $R^2 = 0.56$; Marginal $R^2 = 0.19$						
	Climatic region CV of most dominant species [^] H' index MFC	0.16877 0.09774 -0.16173 0.00435	0.08576 0.02957 0.02879 0.11645	1.968 3.305 5.616 0.037	0.049096 * 0.000951 *** < 2e-16 *** 0.970190		
	Models with CV calculated for every two years of the studies Conditional $R^2 = 0.37$: Marginal $R^2 = 0.09$						
	Climatic region CV of most dominant species [^] H' index MFC	0.111412 0.121180 - 0.048424 0.002177	0.079390 0.032136 0.037559 0.051874	2.138 3.771 2.242 0.073	0.032545* 0.000163 *** 0.024961 * 0.942094		

[^] *CV* of most dominant species remained significant when it was the single most dominant, two most dominant as well as three most dominant species.



Figure 1: Most dominant taxonomic group of crop pollinators across years at (A) study and (B) site levels with number of studies and number of sites in parentheses.



Figure 2: The relative change in total abundance of crop pollinators between years are driven by (A) species diversity (Shannon index) with 95% CI, and (B) the change in dominant species.





dominant species (showing 95% CI), (B) average species diversity (Shannon index) and (C) the climatic region.



Figure 4: Relative change in single most dominant species (grey) compared to relative change in overall abundance (white) when split into asynchronous (left side) and synchronous (right side) pollinator communities.