

## **Introduction**

Insect pollinators play a pivotal role in the sexual reproduction of wild flowering plants, as well as in the production of fruits and seeds of an estimated 75% of global crop species (Klein *et al.*, 2007; Ollerton *et al.*, 2011). The importance of insect pollination as an (agro-)ecosystem service is currently on the rise, as the global area dedicated to pollinator-dependent crops has increased by more than 300% since 1961 (Aizen *et al.*, 2008). For example, apple (*Malus domestica*) is now one of the most economically important fruit crops in the world, with an estimated economic value over \$45 billion for the year 2019 (FAOSTAT, 2020). Wherever they are currently cultivated, apple crops generally rely on insect pollinators such as bees and hoverflies for their sexual reproduction, since they are usually self-incompatible (Delaplane & Mayer, 2000; Pardo & Borges, 2020). Apple blossoms typically attract a wide taxonomic range of pollinators (Nunes-Silva *et al.*, 2020) and different suites of pollinator species in different biogeographic regions of the world (Ramírez & Davenport, 2013), yet producers around the world have converged towards a significant reliance upon managed colonies of the Western honey bee, *Apis mellifera* L., for apple pollination (Delaplane & Mayer, 2000; Garibaldi *et al.*, 2013). This tight functional link between a considerable proportion of our crops, and apples in particular, to this single pollinator species is increasingly viewed as a non-resilient strategy in the context of global change that can potentially affect the beekeeping sector, and hence the availability of managed hives to support the pollination demand of apples and other crops (Klein *et al.*, 2007; Potts *et al.*, 2010; Blitzer *et al.*, 2016).

Because honey bees alone cannot sustain the growth of pollinator-dependent crops, the contribution of alternative managed pollinators and the encouragement of wild pollinators are being increasingly explored. These initiatives are encouraged by reports on the role played by wild pollinators, and especially wild bees, which significantly contribute to crop pollination, and often out-perform honey bees in terms of pollination efficiency at the individual level (Albrecht *et al.*, 2012; Garibaldi *et al.*, 2013; but see Rader *et al.*, 2016). Furthermore, there is now evidence that the diversity of bees, in particular the species richness (i.e., the number of species, a proxy for measuring diversity within a

community) can increase fruit set (a key component when considering crop yield), enhance productivity and improve stability for different types of pollinator-dependent crops (Klein *et al.*, 2003; Hoehn *et al.*, 2008; Garibaldi *et al.*, 2013).

One important limitation to an increasing reliance upon wild and alternative managed pollinators to sustain crop pollination services is that many of these species are currently facing multiple threats (Potts *et al.*, 2010; Vanbergen *et al.*, 2013; Wagner, 2020) which need to be overcome to reduce their associated pollination deficits (Garibaldi *et al.*, 2016). Apart from environmental stressors such as climate change and land-use change, an important pressure has been put on wild bee communities by agricultural intensification (Kremen *et al.*, 2002; Nieto *et al.*, 2014; Grab *et al.*, 2019). Indeed, modern crop management practices still involve the widespread use of pesticides, contribute to habitat fragmentation and pave the way for the introduction of exotic species, all of which have the potential to jeopardize the availability of key resources required for sustaining diverse communities and healthy colonies of pollinators (Potts *et al.*, 2010; Park *et al.*, 2015; González-Robles *et al.*, 2020). As such, organic agriculture has been proposed as a sustainable alternative to conventional farming practices, since in some contexts it has shown increases in species richness and abundance of wild pollinators (Holzschuh *et al.*, 2008; Rundlöf *et al.*, 2016). Perhaps less intuitively, and despite the popular trend in considering honey bees as important allies in crop pollination and as “umbrella” species for the conservation of all pollinators (Wood *et al.*, 2020), recent evidence suggests otherwise with studies describing how honey bees disrupt plant-pollinator interactions (Valido *et al.*, 2019), contribute to pathogen spillover towards wild pollinator species (Fürst *et al.*, 2014) and impact the pollination ecology of individual plant species (Geslin *et al.*, 2017; Agüero *et al.*, 2018; Sørensen *et al.*, 2020). For example, Ropars *et al.* (2020) found a significant and negative association between increased honey bee colony density and the diversity and community structure of wild bees in urban green spaces, but similar results and concerns are echoed by studies in other landscape configurations (Lindström *et al.*, 2016; Torné-Noguera *et al.*, 2016; Ropars *et al.*, 2019).

In a context of (i) an increased consumer interest in organically grown apples in recent years (Peck *et al.*, 2005; The Insight Partners, 2020), (ii) the reported benefits of organic agriculture on biodiversity (Rundlöf *et al.*, 2016), but also (iii) the prevalent use of *A. mellifera* as a managed pollinator for apple production, we aimed to disentangle the impact of honey bee density and management practices (organic vs. non-organic) on wild bee diversity in commercial apple orchards. Contrary to previous studies focusing on either of these stressors for wild bees separately, using mostly artificial experimental setups, and focusing on relatively small geographical scales, we designed a large-scale study with an explicit focus on paired commercial apple orchards varying in honey bee density. Specifically, we used standardized field surveys to investigate the extent to which (i) the dominance of *A. mellifera* and (ii) contrasting pest management practices (organic vs. non-organic) influence the diversity of wild bees (computed through species richness, functional and phylogenetic diversity metrics) associated with apples in different climatic contexts of Western Europe and North Africa. We then provide evidence-based recommendations to growers and policy makers (Park *et al.*, 2015; Kleijn *et al.*, 2019; Pardo & Borges, 2020) to help foster a transition towards more agroecological practices for apples, a key pollinator-dependent crop in Europe, and we also discuss the risks associated with the reliance of a major crop on a single managed pollinator species.

## **Material and methods**

### **Study area and sampling method**

From March 29th to May 2nd 2019, we sampled 46 commercial apple orchards (hereafter referred to as “sites”) during the blooming season in Belgium, France, Morocco, the Netherlands, Spain and the United Kingdom (Fig. 1; see **Fig. S1, Table. S1 in Supporting Information**). All sites were managed either according to guidelines and requirements of organic farming practices (hereafter referred to as “organic”) or according to other practices such as integrated pest management (IPM) or conventional agriculture (hereafter referred to as “non-organic”). The sites were grouped into closely located pairs of organic and non-organic orchards. Within each pair, the sites were distant from at least 2km to avoid potential overlapping of pollinator communities (Zurbuchen *et al.*, 2010). This pair strategy allowed to focus on sites with different management practice yet located in close and similar landscapes, and experiencing comparable climatic conditions. Each site was sampled for three days during apple blooming, using a standardized protocol combining active (netting) and passive (pan traps) collection methods (Droege *et al.*, 2005; Portman *et al.*, 2020; Packer & Darla-West, 2021). Active sampling from apple blossoms allowed monitoring of the bee community directly associated with the crop, through randomized transect patterns in the sites during two periods of 90 minutes. The passive sampling was deployed using trios of colored pan traps (fluorescent blue, fluorescent yellow, white), (i.e., nine pan traps in total with three pan traps of each color, set for the day), filled with soap (Westphal *et al.*, 2008; Lebuhn *et al.*, 2016). All collected specimens were digitized and identified to the species level, except for *Bombus terrestris* and *B. lucorum* (difficult to distinguish and pooled together as *Bombus terrestris* agg). All specimens are curated in the entomological collection of the Agroecology Lab (Université libre de Bruxelles (ULB), Brussels, Belgium).

### **Diversity indices**

For each study site, we calculated the proportion of honey bees caught (in %). We then characterized the entire bee community associated with each site, as well as each method of collection, with the following biodiversity metrics: species richness (SR), functional diversity (FD) and phylogenetic

diversity (PD). These diversity indices have been previously used in studies as proxies to assess community characteristics, and are also relevant to measure the efficiency of ecosystem services provided by pollinators (Gagic *et al.*, 2015; Normandin *et al.*, 2017; Woodcock *et al.*, 2019). Species richness (SR) is the computation of the number of different species observed in each site. The functional diversity (FD) of a community represents the diversity of life-history traits of bees within each community (Tilman *et al.*, 2001; Laureto *et al.*, 2015; Normandin *et al.*, 2017). For all but five species recorded, we gathered the following traits (see Carreck, 2016; Normandin *et al.*, 2017): inter-tegular distance (ITD) of female specimens as a proxy for body size and foraging distance (Zurbuchen *et al.*, 2010; Hill *et al.*, 2011), nesting behavior, degree of sociality, modality of pollen transport, season of activity, floral specialization and diet breadth (**Table S2**). Using the ITD of each species, we computed the body mass (in milligrams) and the tongue length (in mm) using the *ITconverter* function of the “BeeIT” package (version 0.1.0) (Cariveau *et al.*, 2016; Kendall *et al.*, 2019). We could not gather all traits for the following species: *Andrena exigu*a (4 specimens), *Andrena tebessana* (2), *Lasioglossum collopiense* (12), *Lasioglossum grisellinum* (1) and *Lasioglossum pseudoplanulum* (12). Therefore, they were discarded for the analyses of functional diversity. We then converted the mixed qualitative/quantitative traits matrix into a Gower distance matrix (Podani, 1999), using the *gowdis* function from the “FD” package (version 1.0-12) (Laliberté *et al.*, 2015) which was used to build a "functional dendrogram" illustrating the similarity in life-history traits among species, with the *hclust* function from the “stats” package (version 4.1.0) (R Core Team, 2016). We then computed FD as the total branch length of this functional dendrogram representing each bee community (Petchey & Gaston, 2007; Mouchet *et al.*, 2010; Mazel *et al.*, 2018). The FD value of bee communities associated with each study site was computed using the *alpha* function of the “BAT” package (version 2.0.1) (Petchey & Gaston, 2006; Cardoso *et al.*, 2015) (**Table S3**). Sites had varying levels of specimen abundance, therefore we set the “raref” option to 1 to rarefy the observed community based on the lowest specimen abundance among all sites, thereby reducing potential comparison biases (Gotelli & Colwell, 2001). Phylogenetic diversity (PD) was also selected as an alternative biodiversity metric as species traits do not always reflect shared evolutionary history (i.e., there are multiple cases of life-history traits convergence in the European bee fauna, see Westrich, 1989; Vereecken, 2017; see also Mazel *et al.*,

2018 on FD-PD relationships). In this context, we built a phylogeny (**Appendix S1**) based on fragments from the mitochondrial cytochrome oxidase I (*COI*) and low-wavelength opsin (LW *Rh*) genes, hereafter referred to as multi-gene (Danforth, 1999; Boyle & Adamowicz, 2015) (**Fig. S2; Table S4**). We computed PD based on the multi-gene tree (and also on the taxonomic tree for comparison) by summing the lengths of connecting species found in each community of bees, an efficient geographic measure of the evolutionary history shared among species forming a community (Faith, 1992; Faith & Baker, 2006; Grab *et al.*, 2019). The function *pd* from the package “picante” (version 1.8.2) (Kembel *et al.*, 2010) then computed values of phylogenetic diversity for each site (Faith, 1992; Vereecken *et al.*, 2020) (**Table S3**).

### Statistical analyses

All regressions were calculated using only the net samples, since we aimed to analyze the bee community directly associated with apple crops (i.e., foraging on apple blossoms). To test the hypothesis that the proportion of honey bees (in % of the local community) drives significant changes in species richness, functional and phylogenetic diversity of the wild bee communities, we used linear and generalized linear mixed models (LMMs and GLMMs) and computed the three diversity indices as response variables. In all models, the management type (organic *versus* non-organic), the proportion of honey bees, the interaction between these two factors, along with the agriculture cover in the surrounding landscape, were computed as fixed effects.

Spatial autocorrelation between sites was tested using the *fitme* function of the “spaMM” package (version 3.4.1) (Rousset & Ferdy, 2014), and was accounted by using the site pair number as random effect (**Fig. S3**). To avoid potential sampling biases, we also computed the sampler group as random effect (Roulston *et al.*, 2007). Pearson’s correlation coefficient were used to test for correlations between the different response variables (Birkhofer *et al.*, 2018; Vereecken *et al.*, 2020). For every study site, we computed the proportion of agriculture cover in a buffer area of 1500m (mean foraging distance of honey bees according to Couvillon *et al.*, 2015), to account for the surrounding landscape. This was done using the *geobuffer\_pts* function from the “geobuffer” package (version 0.0.0.90) (Stefan, 2019), from the

2019 Copernicus Global Land Cover (100m x 100m resolution) (Buchhorn *et al.*, 2019). That proportion of agriculture cover was computed as a fixed effect.

For SR as the response variable we first computed a generalized linear mixed regression model with a Poisson error distribution using the *glmer* function from the “lme4” package (version 1.1-23) (Zeileis *et al.*, 2008; Bates *et al.*, 2015). Functional and phylogenetic diversity (taxonomic and Multi trees) were modelled with a gaussian error distribution, using the *lmer* function of the “lme4” package (version 1.1-23) (Bates *et al.*, 2015). Pan traps allowed to test for potential sampling biases (i.e., more relative time dedicated to the collection of honey bees by netting could result in less time dedicated to the collection of other bees during the timed field surveys) (**Fig. S4, Table S5 for SR analyses**), while the communities obtained from pooling all bees together helped to check if a congruence was observed in the overall trends, without additive/subtractive effects (Portman *et al.*, 2020).

Following the theoretical framework of Moullot *et al.* (2013), we then created a visual functional trait space, by transforming species trait values into (x,y) spatial coordinates using the *pcoa* function of the “ape” package (version 5.4) (Paradis & Schliep, 2019) on the Gower matrix previously created. Each bee species was represented in a two-dimensional plot using Principal Coordinate Analysis (PCoA) axes. We aimed to explore how the communities’ functional diversity changed with (i) increasing dominance of *A. mellifera* and (ii) management practices.

For the first analysis, we divided the netted community into two distinct and contrasting groups of sites, each with roughly a quarter of all specimens caught (details in the Results section) (**Fig. S5**). The first group consisted of all study sites with less than 35% of honey bee proportion (nine sites, hereafter referred to as “Low *Apis* sites”). The second group consisted of all sites having above 70% proportion of honey bee (14 sites, hereafter referred to as “High *Apis* sites”). The 23 remaining sites, with a honey bee proportion between 35% and 70%, were named “Medium *Apis* sites”. This allowed for the comparison of clusters of sites with distinct and contrasting levels of honey bee dominance. Hence, the following analyses have been computed after removing *A. mellifera* from the dataset. Similarly, we

compared the functional spaces occupied by the species from organic and non-organic sites. Four metrics of functional diversity were used for comparison: functional richness (FRic, i.e. portion of functional space filled by species communities), functional evenness (FEve, i.e. distribution of abundance among species in the functional space), functional divergence (FDiv, i.e. relative abundance of species with extreme functional traits), and functional specialization (FSpe, i.e. differing contribution of generalist species —close to the center of the functional space, and specialist species —showing extreme trait combinations— to the functional space) (Mason *et al.*, 2005; Mouchet *et al.*, 2010; Schleuter, 2010).

## **Results**

### **Patterns of diversity in commercial apple orchards**

A total of 9,253 bees were caught by net in the 46 sites sampled during the 2019 flowering period (**Table S6; Appendix S2 for pan traps**). They consisted of 108 species (11 *Bombus* species, 96 wild bee species, and the domesticated bee *A. mellifera*), from five different families (Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae). The family Andrenidae showed the highest number of species, with 43 species (16.8% of total abundance), followed by the Halictidae with 21 species (1.3% of abundance), the Megachilidae with six species (3%), and finally the Colletidae with two species (0.2%). Apidae was the bee family represented by the highest number of specimens (37 species, i.e., 78.7% of the total abundance). The honey bee *A. mellifera* represented 54% of the total abundance in our database, with 4,994 specimens caught across all sites; its relative abundance ranged between 18.9% and 100% of collected specimens per site (**Fig. S5**). The next most abundant species in our dataset was *Bombus terrestris* agg. (1,463 specimens), *Andrena haemorrhoa* (285 specimens) and *Bombus pratorum* (169 specimens).

### **Effect of honey bee dominance and management on wild bee diversity**

Our results indicated a strong and significant correlation between all diversity metrics (response variables). Looking at pairwise correlations, we see Pearson's correlation coefficients of 0.75 for SR-FD ( $P = 1.376e-09$ ), 0.99 for SR-Multi PD ( $P < 2.2e-16$ ), 0.75 for FD-Multi PD ( $P = 2.433e-09$ ), and 0.96 for Taxonomic PD-Multi PD ( $P < 2.2e-16$ ). With these correlations, we showed hereafter that honey bee dominance has a strong effect on all variables, although the magnitude and their implications varied (**Fig. 3**).

We found a highly significant and negative effect of honey bee dominance on the species richness of wild bees (GLMM with Poisson error distribution for count data) in the studied sites, with an estimate of -2.62 (conditional  $R^2 = 0.84$ , CI 95% = [-4.17, -1.06],  $P = 0.001$ ) (**Fig. 3A, 3B; Table S7**). The

estimate (in log-mean) converted into an incidence rate ratio (IRR = 0.07) indicated that for every 20-percentage point increase in *A. mellifera* dominance, there was a predicted decrease of 13.7% in wild bee species richness. The agriculture cover in a 1500m buffer area (estimate = -0.81, CI 95% = [-2.03, 0.41], P = 0.192), along with the type of management (estimate = 0.07, CI 95% = [-0.36, 0.51], P = 0.748) and the interactions, had no significant impact on predicted species richness (**Table S7**). Similar trends were found for the pan traps and pooled data (**Fig. S6, S7, S8; Table S8**).

Secondly, our results indicated that the dominance of *A. mellifera* has also a highly significant and negative effect on FD, with an estimate of -1.95 (conditional  $R^2 = 0.82$ , (CI 95% = [-2.89, -1.00], P < 0.001) (Fig. 3C, 3D). Here, we removed the random effect “site pair” because it had no variance, resulting in a singular fit. For every 20-percentage point increase in *A. mellifera* dominance, we saw a decrease by 0.38 of the total branch length of the tree linking all species in a community (Petchey & Gaston, 2006). The highest functional diversity was 2.93 (with 28 species), and the lowest was 0.62 (*A. mellifera* only), hence for every 20-percentage point increase in *A. mellifera* dominance, we would expect to lose 13.3% of functional diversity in the communities. Agriculture cover (estimate = 0.2, CI 95% = [-0.65, 1.05], P = 0.652), management type (estimate = 0.12, CI 95% = [-0.27, 0.50], P = 0.552) and the interactions did not play a significant role here (**Table S7**). Results for pan traps and pooled data are displayed in **Fig. S9, S10** and **Table S8**.

Finally, the mixed linear regression for phylogenetic diversity (multi-gene tree) also shows a highly significant and negative effect of *A. mellifera* dominance (estimate = -6.64, conditional  $R^2 = 0.87$ , CI 95% = [-9.16, -4.11], P < 0.001) (Fig. 3E, 3F; **Table S7**). According to our model, a decrease by 18.7% of the total branch length of the phylogenetic tree can be expected for every 20-percentage point increase in honey bee dominance. Again, the management type was not significant (P = 0.371), neither is the interaction between management and *A. mellifera* dominance (P = 0.792) (**Table S7**). However, in this case the agriculture cover was significant (estimate = -2.47, CI 95% = [-4.76, 0.17], P = 0.035), along with the interaction between agriculture cover and honey bee proportion (estimate = 6.03, CI 95% = [-1.20, 10.86], P = 0.014). These results suggested that the effect of honey bee dominance on the

phylogenetic diversity of wild bees was more extreme in areas with low agriculture cover (**Fig. S11, Fig. S12, Table S8** for pan traps and pooled data). Similar results were obtained for the Linnean taxonomic phylogeny (**Fig. S13, S14**).

### Functional community space

Roughly a quarter of the total specimen abundance (2,302 specimens on 9,253 total) was found in Low *Apis* sites, then half (4,736) in Medium *Apis* sites, and the last quarter of abundance (2,215) in High *Apis* sites. After removing *A. mellifera*, the five following bee families were found in both Low and High *Apis* sites: Apidae (respectively 58.8% and 69.2% of abundance), Andrenidae (32.7% VS 27.5%), Megachilidae (3% VS 2.1%), Halictidae (5% VS 0.5%) and Colletidae (0.5% VS 0.7%) (**Fig. S15**).

To illustrate how the bee communities from Low and High *Apis* sites varied, all species were positioned spatially by coordinates from Axis 1 [19.35% of variance], Axis 2 [11.35% of variance] and Axis 3 [9.53% of variance] of the PCoA. The resulting two-dimensional functional space from the Low *Apis* sites (blue) is visually bigger than the High *Apis* sites (red) (Fig. 2 A-C). We compared both functional spaces by testing variations in mean FRic, FEve, FDiv and FSpe. The mean FRic decreases from 2.33% to 0.92% between the Low *Apis* sites and High *Apis* sites, with mean species richness going from 19.44 to 9.22 (and abundance changing from 1,237 to 425 specimens caught, after removing *A. mellifera*). Except for FRic ( $P = 0.0078$ ), the other metrics (mean FEve, mean FDiv and mean FSpe) were not significantly different between the two groups of sites, and were therefore not considered as relevant (**Table S9; Fig. S16** for Medium *Apis* sites). We observed a difference in the bee species represented in each functional space. 27 species were found in sites ranging from Low to High *Apis* sites, and therefore likely to represent species less impacted by the proportion of *A. mellifera*. (**Table S10**). They consisted in 10 *Andrena* spp., seven *Bombus* spp., three *Nomada* spp., two *Lasioglossum* spp., two *Osmia* spp., along with *Anthophora plumipes*, *Colletes cunicularius* and *Xylocopa violacea*. We also found 26 species only represented in the functional space from Low *Apis* sites, and not above (**Table S11**). Therefore, they are likely to represent species more impacted by the proportion of *A. mellifera*, coming from the following eight genera: nine *Andrena* spp., eight *Lasioglossum* spp., three *Nomada* spp., two

*Bombus* spp., including *Eucera longicornis*, *Halictus rubicundus*, *Seladonia tumulorum* and *Sphecodes ephippius*. These were primarily generalist and ground nesting species. A total of 13 species were solitary bees and seven were primitively eusocial; the six remaining species were cleptoparasites, except for *Halictus rubicundus*. Concurrently, seven bee species were only found in the functional space above 70% of *A. mellifera* proportion, and not below (**Table S12**). They consisted of four *Andrena* spp., two *Eucera* spp. and *Nomada fucata*. These were all ground nesting and mainly solitary species, except for *Nomada fucata*. Apart from *Eucera nigrescens*, all six species were generalists in their floral choices. All details are provided in **Table S13** for species in Medium *Apis* sites. Considering the regression results on management influence, the simple comparison between organic and non-organic sites was disregarded.

As for the general functional traits, we found that the relative proportion of larger bees with longer tongues increased with honey bee proportion. Species over 80mg tended to be more represented in High *Apis* sites (57%) compared to Low *Apis* sites (48%). Also, species with a tongue size over 6mm occurred more frequently in High *Apis* sites (69%) than in Low *Apis* sites (60%). However, no patterns were detected for the other traits (**Fig. S17**).

## **Discussion**

Collectively, our results showed that across 46 apple orchards in western Europe, the dominance of honey bees was consistently and statistically associated with lower wild bee richness, functional diversity and phylogenetic diversity, irrespective of the local management strategies. This was unexpected, since organic agriculture has previously been shown to increase species richness and abundance of wild pollinators (Holzschuh *et al.*, 2008; Rundlöf *et al.*, 2016; *contra* Porcel *et al.*, 2018; Pardo *et al.*, 2020). Landscape structure and composition had also very little impact on our results, except for phylogenetic diversity which, in line with other studies using other metrics, was negatively impacted by an increased proportion of agricultural land around study sites at the landscape scale in line with previous studies investigating the decrease of biodiversity in sites with high proportion of agricultural land (Forrest *et al.*, 2015; Grab *et al.*, 2019; Neumüller *et al.*, 2020).

We also observed a significant decrease in the functional richness of wild bee functional space when *A. mellifera* dominated bee communities, suggesting that wild species exhibiting particular combinations of ecological and behavioral traits tended to be less abundant under conditions of high honey bee density. These results, never obtained for apple orchards and at such a large geographic scale, were consistent with previous studies conducted in contrasting habitats (e.g. semi-natural habitats or other crops, in France and French Polynesia) (Henry & Rodet, 2018; Legras *et al.*, 2018; Jeavons *et al.*, 2020). In particular, we found that large and generalist species occurred more frequently in sites with high honey bee dominance, compared to small and specialist species. A potential explanation for this apparent paradox is that honey bees induce floral competition favoring species exhibiting disruptive combination of ecological and behavioral traits in the same habitats, acting as a filter through the available spectrum of pollinators, and resulting in primarily generalist and opportunistic species, and particularly larger bees (a trait associated with increased foraging distances), as “winner” species in the spatial and habitat context investigated here (Shavit *et al.*, 2009; Jeavons *et al.*, 2020; Wignall *et al.*, 2020). Even though different functional groups may vary in their response to a disturbance in their native environment

(Forrest *et al.*, 2015; Odanaka & Rehan, 2019; Wignall, Brolly, *et al.*, 2020), such trend of declining functional diversity could result in threatened and weakened pollination services, according to Rader *et al.* (2014). There is still a lack of studies investigating the impact of honey bees on wild bee species with different foraging and nesting habits (Wojcik *et al.*, 2018), most studies having focused on exploitative competition with bumble bees (Forup & Memmott, 2005; Balfour *et al.*, 2015; Wignall *et al.*, 2020).

Despite the increasing evidence for the benefits associated with harnessing pollinator diversity to crop pollination (Klein *et al.*, 2003; Blitzer *et al.*, 2016; Woodcock *et al.*, 2019), apple growers follow a prevalent and almost institutionalized reliance upon honey bees as “agricultural insurance” for apple pollination (Pardo & Borges, 2020; Park *et al.*, 2020). Whilst complete reliance on wild pollinators for large scale agriculture may be challenging because of their unpredictability and vulnerability (Rader *et al.*, 2009), Breeze *et al.* (2014) nevertheless suggested that a strong dependence on honey bees is also commercially dangerous, should their numbers plummet following unpredictable events such as unfavorable temperatures, novel diseases or parasites (Hristov *et al.*, 2020; Traynor *et al.*, 2020). In the case of commercial apple orchards, an efficient management of diverse wild bee assemblages could help producers to be less dependent on domesticated honey bees for pollination services and crop yields, while maintaining a strong market security (Breeze *et al.*, 2014; Blitzer *et al.*, 2016; Park *et al.*, 2020).

Apple production is also dependent on pest management. Whether the orchards are considered conventional (and IPM) or organic, they all strongly overlap in production expectations, soil quality and pest management strategies (Marliac *et al.*, 2015; Goldberger & Lehrer, 2016; Orpet *et al.*, 2020). Organic farming by itself does not seem to be sufficient to help protect bee diversity (Forrest *et al.*, 2015). Therefore, our results that local management practices had no significant effect on species richness, functional or phylogenetic diversity were not surprising. In line with Hill's theory (1985) for a transition of agriculture systems into sustainable agroecosystem, three stages of progress can be considered : efficiency in the way conventional products are applied; substitution of traditional products by biological controls; and finally redesigning the production strategies into sustainable and ecology-friendly approaches (Pretty, 2020). Currently, management practices in apple orchards appear to have

stagnated in the substitution stage, with better inputs coming, but without implementing a real redesign strategy (Park *et al.*, 2018; Porcel *et al.*, 2018; Joshi *et al.*, 2020). In order to have beneficial effects on biodiversity, management practices should not only involve varying substitution of the inputs used, but they should also be complemented by certain measures of natural habitats and resource conservation, and include a mix of different and locally-adapted management strategies (Puech *et al.*, 2014; Merfield *et al.*, 2015; Orpet *et al.*, 2020). There is now substantial evidence to support the view that pollinator conservation through the local restoration of their ecological requirements is a key target to promote the redesign of our agroecosystems, with associated increased benefits in terms of sustainability and profitability for key insect-dependent crops such as apple, among other crops (Wezel *et al.*, 2014; Gliessman, 2016; Pretty, 2020).

More experiments are needed to support the evidence of adopting these recommendations, and particularly towards the potential of pollinator biodiversity for crop pollination, at the scale of commercial apple orchards. Further studies should also investigate the effect of climate and land use changes on wild bees associated with apple orchards, and disentangle the effect of those known stressors for wild pollinators. Including measures of yields and fruit sets could help further recommendations to be used by agronomists. We think that a multiscale approach is mandatory to embrace the complexity of wild pollinator management associated with worldwide crops, and that it could help create a useful tool for policy makers, applicable in various field situations. This, in return, could empower growers to be more resilient in their production, while simultaneously unlocking the full potential of ecological agroecosystems.

## **Acknowledgements**

The FNRS/FWO joint program “EOS – Excellence of Science” for the project “CliPS: Climate change and its effects on Pollination Services (project 30947854)” funded and made it possible to elaborate this study. Thanks to the apple growers who allowed access to their land and shared their knowledge. Thanks to A.Pauly, A.Dorchin and S.Robert and D.de Grave for providing species identification and help with the species traits. Thanks to M.Garratt, L.Roquer, J.Bosch, P.Lhomme, E.Hulsmans, L.Fockaert for contacting the producers and finding the study sites. A great many thanks to A.Anselmo, A.Danneels, A.Vandewal, B.Martinet, B.Valkenboy, E.Zambra, F.Denis, G.Ghisbain, H.Hainaut, H.Van Ryckel, M.Gerard, N.Dudermel, S.De Greef, V.Eklund and V.Nocent for undertaking the fieldwork.

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## Figures

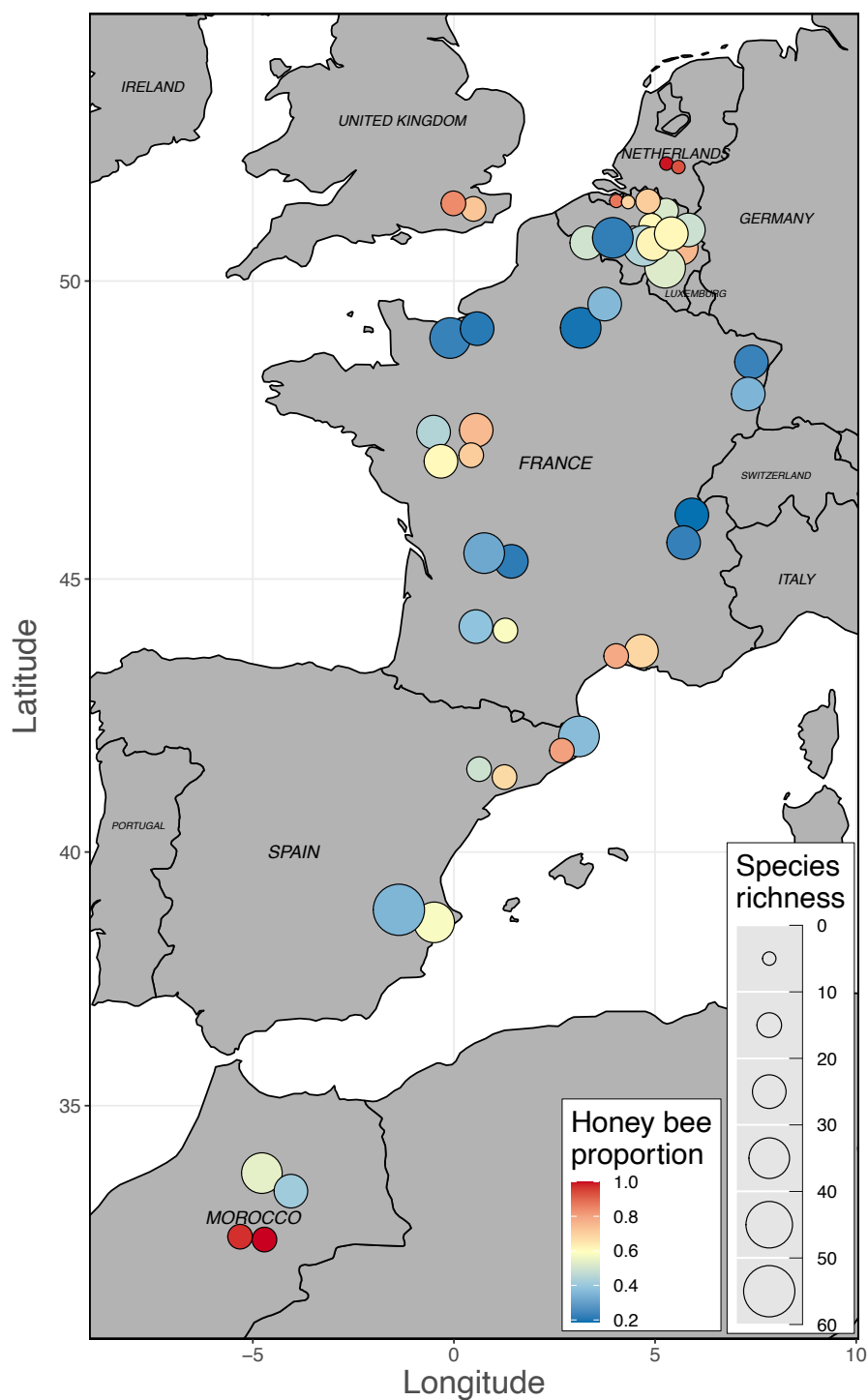


Fig. 1: Map of the 46 apple orchards sampled. Each circle is sized according to the number of species found in the orchard; and the colors indicate the proportion of *A. mellifera* found in each orchard. See Fig. S1 for detailed sites of Belgium.

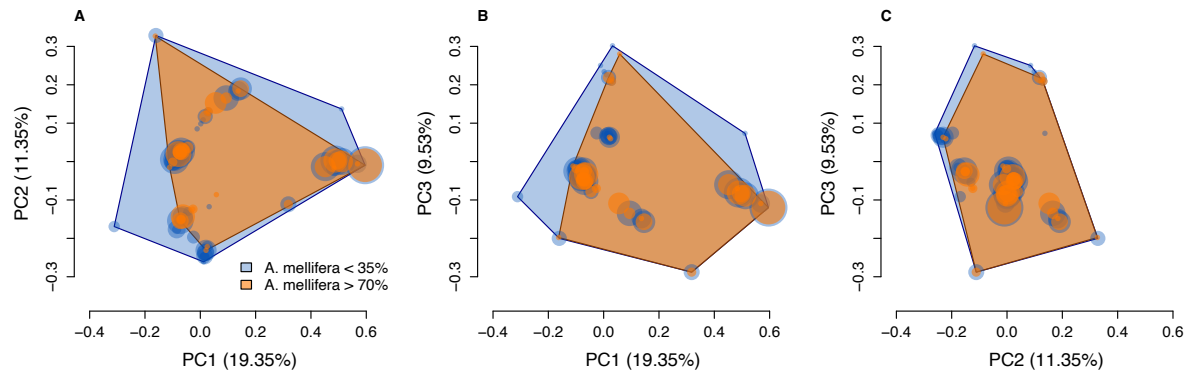


Fig. 2 : Functional space occupied by species in sites up to 35% (i.e., Low Apis sites, polygons in blue), and above 70% (i.e., High Apis sites, polygons in orange), of *A. mellifera* proportion. Each circle within the polygons represents a species positioned spatially by coordinates from the Axis 1 [19.35% of variance], Axis 2 [11.35% of variance] and Axis 3 [9.53% of variance] of the Principal Coordinates Analysis. The diameter of each circle represents the relative abundance of the species. Plot A is a projection on PC1 and PC2, plot B shows PC1 and PC3, and plot C shows PC2 and PC3.

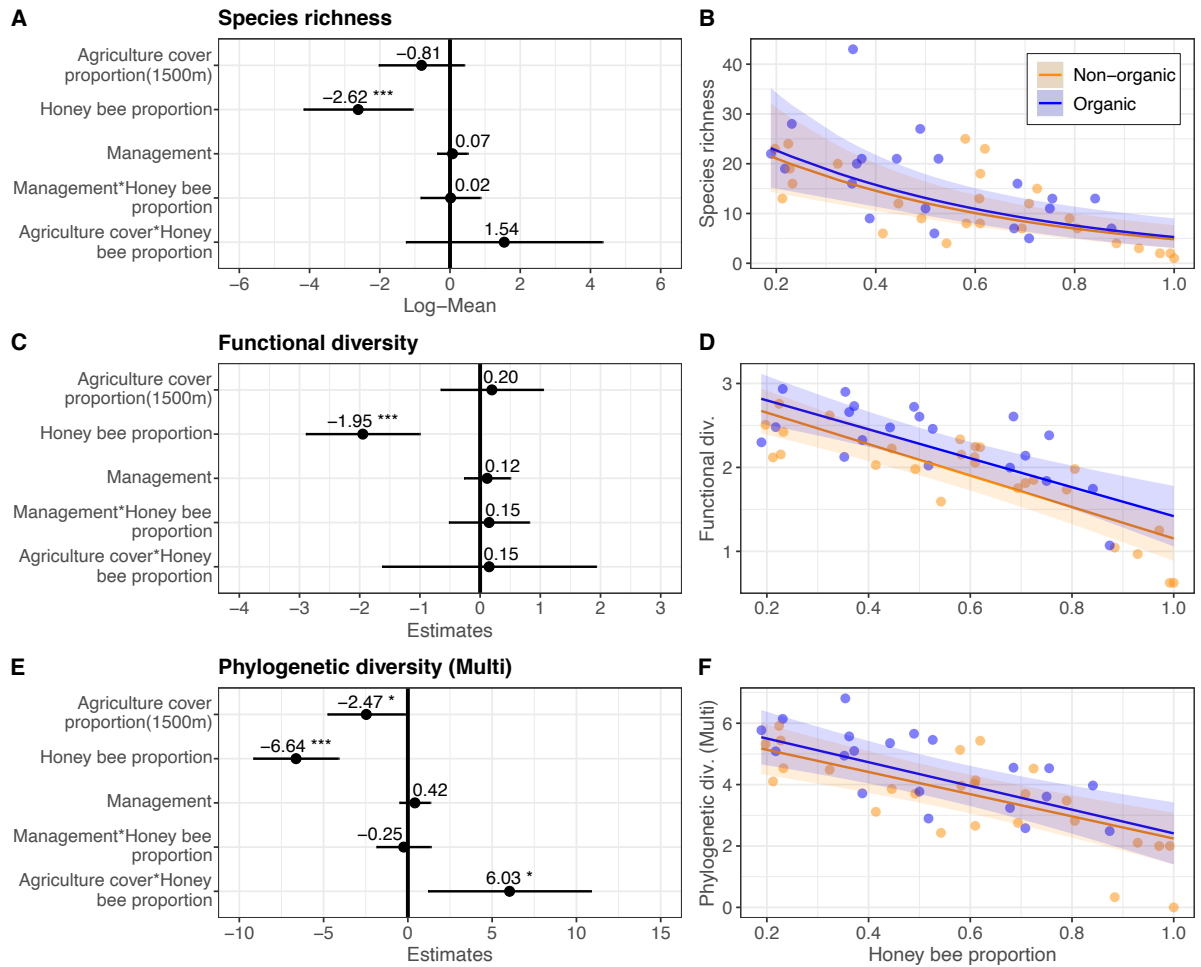


Fig. 3: Generalized linear mixed models results for the species richness (SR), functional diversity (FD) and Multi-gene phylogenetic diversity (Multi PD). The predictor variables are the proportion of *A. mellifera* for all sites, the management type (organic versus non-organic), and the interaction between the two. Random effects are the sampler group and the sites pair number. Plots A-C-E show the estimates computed respectively for SR, FD and Multi PD regressions, with a confidence interval of 95%. And plots B-D-F show the predicted values of SR, FD and Multi PD for increasing dominance of honey bees (expressed in percentage of the total community, for each site).