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Pollinator communities and pollination services in apple orchards: a trait-based approach

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Al meu pare,
a la meva mare,
a la meva germana i
al meu germà

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Abstract

Biodiversity is being threatened worldwide as a result of human activities such as land use change, exploitation of resources or climate change. During the last 20 years, trait-based approaches have been increasingly incorporated in studies linking biodiversity, community structure and ecosystem functioning, as an alternative to taxonomy-based approaches. One crucial ecosystem function is pollination, which contributes to the sexual reproduction of more than 85% of angiosperm species worldwide. In addition, pollinators provide a crucial ecosystem service through their contribution to agricultural production and human nutrition. However, pollinator diversity is experiencing strong declines in Europe and North America. Agricultural intensification is considered one of the main drivers of these declines.

Functional traits mediate the responses of pollinators (individuals or species) to environmental disturbances (response traits) and, at the same time, contribute to ecosystem function (effect traits). Trait-based approaches have long been used in plant studies and, to a lesser extent, studies on vertebrate animals. However, for many groups of terrestrial invertebrates there is still a lack of consensus on which traits should be measured, their predictive value and how they should be measured. Several studies have addressed the effects of agricultural intensification on pollinator functional composition and others have addressed the role of functional composition on pollination service. However, of studies analysing both processes simultaneously using a response-trait effect framework remain very scarce.

The aim of this thesis is to better understand the mechanisms linking functional composition with pollination service provision in apple orchards. To do so, I measured 10 pollinator traits in 109 species of different pollinator groups to study pollinator functional performance at individual and species level. I also used these traits to study how pollinator functional composition responded to agricultural local and landscape features and how, in turn, these traits affected pollination service at the community level.

First, I developed a standardized method to quantitatively measure hairiness, a salient trait in pollination ecology. The proposed methodology accounts for the two components of hairiness (hair length and hair density) and was used on 109 species from different pollinator groups. Hopefully the method will foster the inclusion of hairiness in pollinator data bases and contribute to our understanding of the relevance of this trait in pollination ecology.

Second, I determined which pollinator traits promote pollination effectiveness and explored whether pollinators with similar pollination effectiveness share similar traits. I found that pollination effectiveness was not dependent on a single trait but on a variety of behavioural and morphological traits. The main traits affecting pollination effectiveness were flower handling behaviour, body size and visit duration. All effective pollinators were top-workers, but otherwise did not necessarily share similar traits.

Third, using a response-trait framework, I analysed how local and landscape features affected pollination service through changes in functional composition in 110 apple orchards across Europe. Pollination service increased with pollinator functional diversity, but only in low-input orchards. As a result, low-input orchards with high pollinator functional diversity reached levels of pollination service similar to those of high-input orchards. The relationship between response and effect traits was better mediated by functional diversity rather than specific functional traits. Functional diversity enabled pollinator communities to better respond to management and landscape intensity and to increase pollination function through complementarity.

Resum

La biodiversitat està amenaçada arreu del món a conseqüència d'activitats humanes com el canvi d'usos del sòl, l'explotació de recursos o el canvi climàtic. Durant els darrers 20 anys, les aproximacions basades en trets s'han anat incorporant de manera creixent en estudis que relacionen la biodiversitat, l'estructura de les comunitats i el funcionament ecosistèmic, com a alternativa a les aproximacions taxonòmiques. La pol·linització és un servei ecosistèmic cabdal que contribueix a la reproducció sexual de més del 85% de les espècies d'angiospermes al món. A més, els pol·linitzadors proveeixen d'un servei ecosistèmic cabdal a través de la seva contribució a la producció agrícola i a la nutrició humana. Tanmateix, la diversitat de pol·linitzadors està experimentant forts declivis a Europa i Amèrica del Nord. La intensificació agrícola és considerada una de les principals causes d'aquests declivis.

Els trets funcionals determinen les respostes dels pol·linitzadors (individus o espècies) a les alteracions ambientals (trets resposta) i, al mateix temps, contribueixen al funcionament ecosistèmic (trets efecte). Les aproximacions basades en trets ja fa temps que s'utilitzen en plantes i, en canvi, no tant en animals vertebrats. Per molts grups d'invertebrats terrestres encara falta consens sobre quins trets cal mesurar, com, i quin poder predictiu tenen. Diversos estudis han analitzat els efectes de la intensificació agrícola sobre la composició funcional, i d'altres han analitzat el rol de la composició funcional sobre el servei de la pol·linització. Tot i això, són pocs els estudis que utilitzen un marc de trets resposta-efecte.

L'objectiu d'aquesta tesi és entendre millor els mecanismes que relacionen la composició funcional amb la provisió del servei de la pol·linització en camps de pomera. Per fer-ho, vaig mesurar 10 trets de pol·linitzadors en 109 espècies de grups diferents per tal d'estudiar el rol funcional individual i a nivell d'espècie. També vaig utilitzar aquests trets per estudiar com la composició funcional de pol·linitzadors responia a factors agrícoles a escala local i de paisatge i com, a la vegada, aquests trets afectaven al servei de la pol·linització a nivell de comunitat.

Primer, vaig desenvolupar un mètode estandarditzat per mesurar quantitativament la pilositat, un tret important en l'ecologia de la pol·linització. El mètode proposat considera dos components de la pilositat (la llargada i la densitat dels pèls) i es va utilitzar en 109 espècies pertanyents a diferents grups de pol·linitzadors. Esperem que aquest mètode incentivi la inclusió de la pilositat en bases de dades de pol·linitzadors i contribueixi al coneixement sobre la importància d'aquest tret en l'ecologia de la pol·linització.

En segon lloc, vaig determinar quins trets dels pol·linitzadors promovien l'eficàcia pol·linitzadora i vaig explorar si pol·linitzadors amb eficàcies pol·linitzadores similars compartien també trets similars. Vaig observar que l'eficàcia pol·linitzadora no depenia d'un únic tret sinó de diversos trets morfològics i de comportament. Els trets que tenien més efecte sobre l'eficàcia pol·linitzadora van ser el comportament intrafloral, la mida corporal i la durada de les visites. Tots els pol·linitzadors eficients s'aproximaven a les flors des de dalt però, a banda d'això, no compartien necessàriament altres trets.

En tercer lloc, utilitzant un marc de trets resposta-efecte vaig analitzar com factors locals i de paisatge afectaven al servei de la pol·linització mitjançant canvis en la composició funcional en 110 camps de pomes de diferents zones d'Europa. El servei de la pol·linització va incrementar amb la diversitat funcional de pol·linitzadors, però només en camps de gestió poc intensiva. Així, camps poc intensius amb una alta diversitat funcional van assolir nivells de serveis de pol·linització similars als dels camps de gestió intensiva. La relació entre els trets resposta i efecte es va veure més influenciada per la diversitat funcional que no per trets funcionals concrets. La diversitat funcional va permetre que les comunitats de pol·linitzadors responguessin millor a la gestió i a la intensitat de paisatge, i va incrementar la funció de la pol·linització mitjançant mecanismes de complementarietat.

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General Introduction

The use of functional traits in the study of ecosystem functioning

Biodiversity, including genetic, species, functional diversity of organisms and habitat diversity, is being deteriorated worldwide as a result of human activities such as land use change, exploitation of resources, climate change, pollution, and invasion of alien species among others (Díaz *et al.* 2020). Starting in the 1980s, the scientific community began to focus their attention on the consequences of species loss on the structure of ecological communities, the functioning of ecosystems and the provision and regulation of ecosystem services (Tilman *et al.* 1997; Grime 1998; Tilman 1999; Hooper *et al.* 2005; Millennium Ecosystem Assessment 2005; Cardinale *et al.* 2012).

During the last 20 years, trait-based approaches have been increasingly incorporated in the study of the relationship between biodiversity, community structure and ecosystem functioning as an alternative to taxonomical-based approaches (Díaz & Cabido 2001; Hooper *et al.* 2005; Cadotte, Carscadden, & Mirotchnick 2011; Gagic *et al.* 2015). The functional trait-based approach aims to provide a more mechanistic and predictive framework (McGill *et al.* 2006). By focusing on generalizable properties of organisms and environments trait-based ecology transitions across scales of biological organization and geographic locations to predict community structure and ecosystem functioning (Shipley *et al.* 2016). Functional traits (hereafter "traits") are morphological, biochemical, physiological, structural, phenological and behavioural characteristics that are expressed in phenotypes of individual organisms and are considered relevant to the response of such organisms to the environment (i.e. response traits) and/or their effects on ecosystem properties (i.e. effect traits) (Violle *et al.* 2007).

The trait-based approach account for the functional component of diversity through the analysis of functional composition, including the identity, abundance and range of species traits (Díaz & Cabido 2001; Petchey & Gaston 2006; Violle *et al.* 2007). This approach is useful to understand the ecological mechanisms driving the interaction of individual traits with the environment through their responses and effects across different levels of biological organization (Shipley *et al.* 2016; Wong, Gu, & Lewis 2019).

Understanding the mechanisms promoting ecological stability has been a topic of concern in ecology (MacArthur 1955; Cottingham, Brown, & Lennon 2001). Two main mechanisms have been proposed to explain community responses to disturbances and effects on ecosystem function mediated by functional traits. On the one hand, the ability of species to overcome environmental changes may depend on the mean value of certain functional traits (i.e. functional identity) in a community. This is explained by the mass ratio hypothesis (Grime 1998) according to which community responses and effects are driven by the dominant traits in the community. On the other hand, the complementarity hypothesis contends that non-overlapping single- or multiple-trait distributions (i.e. functional diversity) in a community, will provide a higher resilience to disturbances and more sustainable ecosystem functions and services across space and time (Tilman 2001; Díaz & Cabido 2001). These two mechanisms describe two complementary aspects of community functional composition (Ricotta & Moretti 2011).

If response traits in a community overlap with effect traits, then it becomes critical to understand how functional composition is affected by drivers of change if we aim to

predict changes in ecosystem functioning (Lavorel & Garnier 2002). The response-effect trait framework has been found to be a useful tool to predict how specific drivers will affect specific ecosystem functions (Lavorel & Garnier 2002; Suding *et al.* 2008).

Insect pollination, a threatened ecosystem service

Animal pollination is an important ecosystem function that contributes to the sexual reproduction of more than 85% of angiosperm species worldwide (Ashman *et al.* 2004; Ollerton, Winfree, & Tarrant 2011). In addition, with more than 70% of the world main crops depending on animal pollination, pollinators provide a crucial ecosystem service through their contribution to agricultural production and human nutrition (Klein *et al.* 2007; Brittain *et al.* 2014). However, at a time when the demand for agricultural food products is increasing (FAO 2017), bee diversity is experiencing strong declines in Europe and North America (Biesmeijer 2006; Potts *et al.* 2010; Bartomeus *et al.* 2013). Pollinator declines have been attributed to multiple causes, but there is a general consensus that agricultural intensification is one of the main drivers (IPBES 2016).

Agricultural intensification affects pollinators through landscape simplification and increases use of external inputs. The loss of and isolation from natural and/or semi-natural habitats leads to reductions of feeding resources (Roulston & Goodell 2011) and nesting habitats (Shuler, Roulston, & Farris 2005). In addition, the increased use of pesticides associated with intensive agriculture at local and landscape scales (Potts *et al.* 2010) has direct negative effects on pollinator fitness and survival (Woodcock *et al.* 2017; Sgolastra *et al.* 2018). Responses of pollinators to agricultural intensification (or to any disturbance) is expected to vary across species depending on their specific traits (Murray, Kuhlmann, & Potts 2009; Roulston & Goodell 2011).

The use of functional traits in pollinator ecology

Advances in trait-based ecology were pioneered by plant ecologists (Cadotte, Carscadden, & Mirotchnick 2011; Lavorel *et al.* 2013), and subsequently adopted by animal ecologists, including studies of terrestrial invertebrates (e.g. Moretti *et al.* 2009; Arnan *et al.* 2013; Pey *et al.* 2014; Arnan, Cerdá, & Retana 2017; Brousseau, Gravel, & Handa 2018a). A first challenge in the application of a functional trait approach to studies on invertebrates has been the definition and measurement of traits, including both morphological and behavioural traits (Pey *et al.* 2014). A second challenge has been to understand correlations between traits and potential trade-offs caused by physiological and/or evolutionary constraints (Brousseau, Gravel, & Handa 2018b).

Important work has been made to synthetize, organize and standardize trait-based approaches in terrestrial invertebrates (Fountain-Jones, Baker, & Jordan 2015; Moretti *et al.* 2017; Parr *et al.* 2017; Brousseau, Gravel, & Handa 2018b). However, there is still a lack of consensus on which are the best traits to measure, how predictive they are and how they should be measured (Stavert *et al.* 2016; Moretti *et al.* 2017). The lack of standardized methodologies and protocols has often prevented the use of important traits and hindered compatibility across databases (Moretti *et al.* 2017). Such compatibility is needed to find generalizable relationships between traits and environment across geographic locations and taxonomic groups (Didham, Leather, &

Basset 2016; Shipley *et al.* 2016). In sum, the application of a functional trait approach to a group of organisms requires a good understanding of which traits are relevant and the availability of standardized protocols to measure and share these traits across databases (Schneider *et al.* 2019).

Pollinator responses to agricultural intensification

Several morphological and behavioural traits have been found to be involved in the response of pollinators to disturbances (Table 1). Some of these traits (e.g. body size, diet specialization) have received a fair amount of attention. By comparison, other traits (e.g. hairiness, foraging behaviour) have been hardly explored (Table 1). At any rate, there is increasing evidence that combination of multiple traits, rather than single traits, are better predictors of the relationship between organisms and environmental gradients (de Bello *et al.* 2010; Violle *et al.* 2012; Díaz *et al.* 2013). Associations between traits linked to important ecological processes such as dispersal ability, resource utilization and reproduction, may better explain responses to environmental disturbances than single traits (Bommarco *et al.* 2010; Bartomeus *et al.* 2018).

Pollinator effects on pollination function

Most plants receive visits from a wide and varied array of pollinators. However, not all pollinators are equally effective at pollinating a given flower species and this variability is modulated by pollinator effect traits (Schleuning, Fründ, & García 2015). The identity and combination of morphological and behavioural effect traits of a pollinator species, or a given individual within a species, affects pollination effectiveness (Phillips *et al.* 2018). Traits that have been identified as determinants of pollination function are listed in Table 1. Importantly, some of these traits act as both effect traits and response traits. Also importantly, some of these traits are strongly correlated (Harder 1985; Peat *et al.* 2005; Moretti *et al.* 2017; Roquer-Beni *et al.* 2020a), and therefore it may be difficult to tease apart the contribution of each trait (Brousseau, Gravel, & Handa 2018b). Most studies rank pollinators based on their effectiveness and then identifiy salient traits of the most effective pollinator species. However, studies directly measuring the importance of various traits are mostly lacking (but see Phillips *et al.* 2018).

At the community level, both functional identity and diversity have been found to better predict pollination function than taxonomic diversity (Gagic *et al.* 2015). Communities with high functional diversity (low trait distribution overlap across space and time), are better suited to enhance pollination services across a variety of environmental conditions (Hoehn *et al.* 2008; Blüthgen & Klein 2011; Albrecht *et al.* 2012; Brittain, Kremen, & Klein 2013; Woodcock *et al.* 2019; Pérez-Méndez *et al.* 2020).

Pollinator response-effect trait framework in orchard pollination

The degree of overlap between response and effect traits will determinate the consequences of a disturbance on a given ecological function (Lavorel & Garnier 2002; Naeem & Wright 2003; Larsen, Williams, & Kremen 2005). As mentioned above, several studies have addressed the effects of agricultural intensification on pollinator functional composition and other studies have addressed the role of functional composition on pollination service. However, there is a lack of studies analysing both processes

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simultaneously. Different pollinators have been found to respond differently to landscape features (e.g. isolation from natural habitats) depending on their traits while, pollination success seems to be enhanced by increased pollinator functional diversity in tropical plantation crops (Klein *et al.* 2008). However, no specific pollinator trait has been found to be responding to agricultural impacts and affecting pollination function at the same time (Bartomeus *et al.* 2018). Clearly, the potential usefulness of a functional response-effect trait framework in pollination ecology needs to be further explored.

Apple as a case study

Apples (*Malus domestica*) are a good system in which to study pollination within a response-effect framework. First, apples benefit from insect pollination both in terms of production and fruit quality (Free 1964; Delaplane, Mayer, & Mayer 2000; Garratt *et al.* 2014a). Most apple varieties are self-incompatible to various degrees, and commercial orchards are usually planted with more than one variety. Second, apple flowers are visited by a wide variety of insects, including bees, hoverflies, other dipterans, beetles, lepidopterans and wasps (Fig. 1) (Garratt *et al.* 2016; Sheffield 2016; Pardo & Borges 2020). *Apis mellifera* L. hives are commonly introduced in orchards to increase pollination levels (Free 1993; Delaplane, Mayer, & Mayer 2000; Stern, Eisikowitch, & Dag 2001), but at the individual level, wild bees such as mason bees (e.g. *Osmia* spp.), bumble bees (*Bombus* spp.) and mining bees (e.g. *Andrena* spp.) have been shown to be more effective pollinators (Vicens & Bosch 2000a; Thomson & Goodell 2001; Gardner & Ascher 2006; Sheffield 2014; Mallinger & Gratton 2015; Park *et al.* 2016). Third, apples are grown under a variety of management systems and environmental conditions (Fig. 2). Since the late 1980s the European Union is promoting a wide range of measures at different scales (from local to regional) in order to revert the negative effects of agricultural intensification and enhance biodiversity in agricultural landscapes (Primdahl *et al.* 2003). These measures, mostly implemented on a voluntary basis, include reducing on-farm management intensity (e.g. reducing pesticide use and promoting biological pest control and organic fertilizers), preserving historical land-uses (e.g. unmanaged field margins, pastures and semi-natural grasslands) and promoting agri-environmental structures such as hedgerows and buffer strips to enhance non-cropping areas and to increase connectivity to natural and semi-natural habitats (Ekroos *et al.* 2016). Fourth, apples are one of the most important fruit crops. They are planted on more than 4.9 million of harvested hectares worldwide ('FAOSTAT' 2018).

Motivation and research aims

Among the many challenges imposed by global change, finding a sustainable balance between supplying the increasing food demand and preserving biodiversity is particularly urgent. In this context, pollinators play a crucial role as they provide pollination services and, at the same time, are vulnerable to agricultural intensification. The aim of this thesis is to better understand the mechanisms linking functional composition to responses to agricultural changes and to pollination service provision in agricultural crops. First, I measured a wide range of traits in apple pollinators and analysed pollinator functional performance at individual and species levels. Then I used

those traits to link pollinator functional composition with agricultural landscape features and pollination service provision at the community level (Fig. 3).

Figure 1: Wild bee (*Eucera nigrilabris*) approaching apple flowers.

Figure 2: Commercial apple orchard in Lleida

Chapter outline

Chapter 1

Hairiness is a salient trait of insect pollinators, with potential importance both as response and effect trait (Table 1). Yet, effective standardized protocols to effectively measure this trait are not available. For this reason, we developed a method to quantitatively measure hairiness in insect pollinators and we synthesized the methodology in a standardized protocol. We described procedures to measure hair density and hair length and proposed a simple hairiness index integrating both components.

Chapter 2

Differences in pollination effectiveness among pollinators have been widely documented. By comparison, the morphological and behavioural pollinator traits underlying these differences have been less investigated. We explored the link between pollinator traits and pollinator effectiveness. We aimed to determine which morphological and behavioural traits promote pollination effectiveness in apple. We also compared pollinator species in terms of pollinator effectiveness to establish whether effective pollinators share similar traits or not.

Chapter 3

In agricultural systems, pollinator communities are exposed to agricultural intensification at different scales. Using a response-trait effect approach, we aimed to determinate how single traits and functional diversity respond to agricultural intensification and affect pollination service in apple pollinator communities across Europe. We also asked whether the effect of pollinator functional composition on apple pollination services is dependent on orchard management. Finally, we established whether traits that determine pollinator responses to changes in agricultural systems overlap with traits that affect pollination.
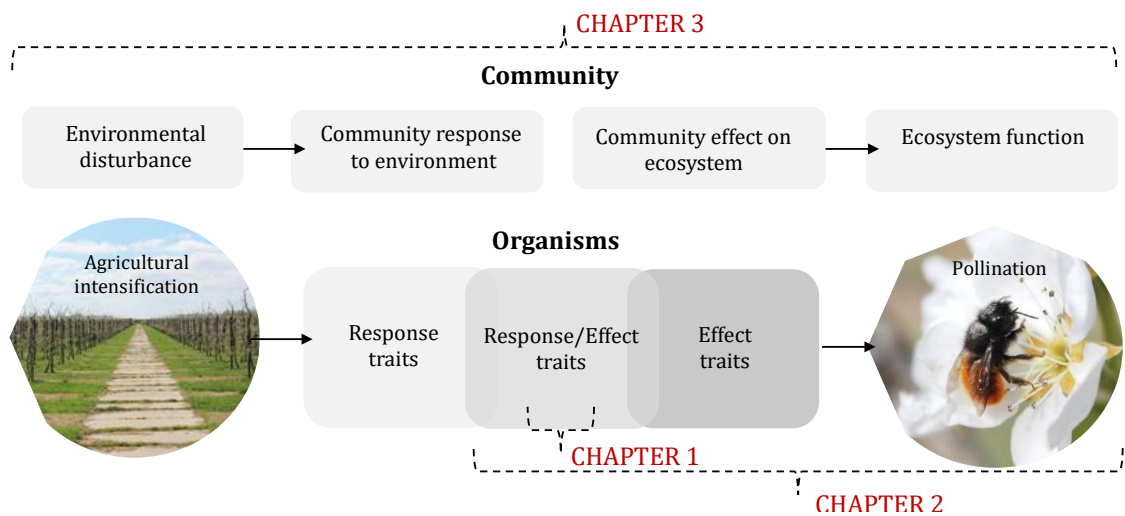
Figure 3: Conceptual framework of the thesis. Each chapter focuses on different levels and aspects of the response-trait effect framework applied to pollination in agricultural landscapes.

Table 1:Pollinator traits used in pollination studies in agricultural landscapes. Trait type (R: response, E: effect) is indicated

Name	Type	Description
Body size	R	Body size has been associated with foraging range (Greenleaf *et al.* 2007; Klein *et al.* 2008), thermoregulation capacity (Stone & Willmer 1989), ability to fly at low temperatures (Stone, 1993) and phenology (Osorio-Canadas *et al.* 2016). Because they are more mobile, large bees may be more capable than small bees of finding resources in disturbed habitats (Klein *et al.* 2008; Jauker *et al.* 2013). At the same time, large bees require greater amounts of feeding resources, which can be limiting in intensive agricultural areas, and are likely to be more exposed to pesticides while foraging (Williams *et al.* 2010; Brittain & Potts 2011). Importantly body size is correlated to other functional traits such as hair length and tongue length.
	E	Pollinator size conditions pollination effectiveness. Large pollinators usually deliver more pollen grains, partly due to higher rates of visit legitimacy (Kandori 2002; Sahli & Conner 2007; Willmer & Finlayson 2014).
Hairiness	R	Hairiness is associated with thermoregulation (Heinrich 1993). Bee species with longer hairs have been found to fly at lower temperatures along altitudinal gradients (Peters *et al.* 2016).
	E	Hairiness influences pollen collection (Thorp 2000) and has been positively related to pollination effectiveness (Stavert *et al.* 2016; Phillips *et al.* 2018).
Tongue length	E	Tongue length may influence pollination effectiveness on certain flower types (Harder, 1983; Inouye, 1980). Long-tongued species are more specialized in flower use than short-tongued species (Peat, Tucker, & Goulson 2005)
Pollen transportation structures	E	Pollen transportation structures may influence pollen collecting behaviour, flower specialization, pollen carrying capacity, and consequently, the likelihood of pollen transfer (Parker *et al.* 2015; Portman, Orr, & Griswold 2019).
Voltinism	R	Univoltine species have been found to be particularly vulnerable to disturbances if these overlap with their reproductive period (Brittain & Potts 2011; De Palma *et al.* 2015). On the other hand, multivoltine species require flower resources for longer periods and may thus be more vulnerable in agricultural landscapes with intense but short-flowering periods (Roulston & Goodell 2011).
Lecty (adult and larval)	R	Pollinators with narrow floral host ranges (e.g. oligolectic and monolectic bees) are likely to be more susceptible to agriculture intensification than species that can feed on alternative host plants (Williams *et al.* 2010; De Palma *et al.* 2015). However, specialised pollinators may benefit from certain agricultural practices if their preferred host plant is a crop or an associated weed (Forrest *et al.* 2015; Bartomeus *et al.* 2018). In addition to flower resources for adults, pollinators require appropriate larval feeding resources. Larval diet differs widely among pollinator groups. Bee larvae feed on pollen and nectar but larvae of other groups are insectivorous (hoverflies, wasps) or saprophagous (flies) among others.
	E	Loss of dietary generalists may alter plant-pollinator interactions (Memmott, Waser, & Price 2004). Different larval diets imply different levels of dependency on flowers, with consequences on visitation rates and pollination service.

Name	Type	Description
Flight season duration	R	Flight season duration (or activity period) depends on weather conditions which vary between years and regions and s affected by climate change (Memmott *et al.* 2007). Availability of flower resources throughout the entire activity period is essential to ensure the sustainability of pollinator populations (Baker 1963).
Flight season duration	E	Longer flight seasons increase the number of flowering species with which a pollinator overlaps. Pollen movement among individual plants and resulting outcrossing rates depend on the overlap between the period of pollinator activity and the blooming period of the plant population (Herrera 2000).
Nesting habits (substrate and construction)	R	Landscape intensification can alter the availability of nesting sites and substrates (Klein *et al.* 2002; Winfree, Griswold, & Kremen 2007; Williams *et al.* 2010), negatively affecting below ground nesting bees (Williams *et al.* 2010) as well as above-ground nesters (Forrest *et al.* 2015).
Sociality	R	Sociality (and associated feeding requirements) may influence sensitivity to landscape intensity. Solitary bees are associated with more restrictive habitat requirements, have smaller foraging ranges and lower reproductive capacity than social bees. For these reasons, they have been found to be more susceptible to landscape intensification (Steffan-Dewenter *et al.* 2002; Klein *et al.* 2008; Jauker *et al.* 2013; De Palma *et al.* 2015). On the other hand, social bees require continuous brood production, which may increase time stress and resource requirements. Social bees tend to have low effective population sizes, which may render their populations more susceptible to human impacts (Chapman & Bourke 2001; Williams *et al.* 2010).
flower handling behaviour	E	Flower handling behaviour, the way in which the pollinator positions itself and moves on the flower, conditions stigma contact and, therefore, pollinator effectiveness (Bosch & Blas 1994; Thomson & Goodell 2001; Park *et al.* 2016).
Nectar or pollen collectors	E	Some studies have found pollen collectors to be more effective than nectar collectors (Bosch & Blas 1994; Monzón, Bosch, & Retana 2004; Tepedino, Arneson Horn, & Durham 2016) but other studies have found the opposite (Williams & Thomson 2003; Young, Dunning, & von Hasseln 2007).
Buzz pollinator capacity	E	Some plants species require buzz-pollination (Vallejo-Marín *et al.* 2010). Only some bee species have the capacity to effectively buzz flowers.
Mobility across plants or rows	E	In crops requiring transfer of pollen across varieties, low levels of geitonogamy and mobility between plants and/or rows is an important trait to ensure cross-pollination (Bosch & Blas 1994; Vicens & Bosch 2000a; Brittain *et al.* 2013; McBrydie, Howlett, & Pattemore 2017).
Visit duration	E	Visit duration has been positively related to pollen grain deposition in some studies (Conner, Davis, & Rush 1995; Phillips *et al.* 2018), but this relationship is not supported or even reversed in others (King, Ballantyne, & Willmer 2013; Zych *et al.* 2013).

1

A novel method to measure hairiness in bees and other insect pollinators

Laura Roquer-Beni, Anselm Rodrigo, Xavier Arnan, Alexandra-Maria Klein, Felix Fornoff, Virginie Boreux, Jordi Bosch

ABSTRACT

Hairiness is a salient trait of insect pollinators that has been linked to thermoregulation, pollen uptake and transportation, and pollination success. Despite its potential importance in pollination ecology, hairiness is rarely included in pollinator trait analyses. This is likely due to the lack of standardized and efficient methods to measure hairiness.

We describe a novel methodology that uses a stereomicroscope equipped with a live measurement module software to quantitatively measure two components of hairiness: hair density and hair length. We took measures of the two hairiness components in 109 insect pollinator species (including 52 bee species). We analysed the relationship between hair density and length and between these two components and body size. We combined hair density and length measures to calculate a hairiness index and tested whether hairiness differed between major pollinator groups and bee genera.

Body size was strongly and positively correlated to hair length and weakly and negatively correlated to hair density. The correlation between the two hairiness components was weak and negative. According to our hairiness index butterflies and moths were the hairiest pollinator group, followed by bees, hoverflies, beetles, and other flies. Among bees, bumblebees *(Bombus)* and mason bees *(Osmia)* were the hairiest taxa, followed by digger bees (Anthophorinae), sand bees *(Andrena)* and sweat bees (Halictini).

Our methodology provides an effective and standardized measure of the two components of hairiness (hair density and length) thus allowing for a meaningful interpretation of hairiness. We provide a detailed protocol of our methodology, which we hope will contribute to improve our understanding of pollination effectiveness, thermal biology and responses to climate change in insects.

Keywords: functional diversity, functional trait, pilosity, pollinating efficiency, protocol, thermoregulation

1.1 -Introduction

Functional traits are morphological, physiological or phenological characteristics measurable at the individual level, that are believed to influence the fitness of an organism, to be a response of the organism to environmental changes or to reflect the effect of the organism on ecosystem function (Violle *et al.* 2007). A growing number of studies are exploring the relationship between functional trait diversity, environmental change and species composition, and emphasizing the importance of functional diversity in ecosystem processes (e.g.: Elmqvist *et al.* 2003; Hooper *et al.* 2005; Petchey & Gaston 2006; Suding *et al.* 2008; Arnan *et al.* 2013). Trait-based studies were mostly pioneered by plant ecologists and extensive trait data bases are available for many plant taxa and communities (e.g.: McIntyre *et al.* 1999; Lavorel & Garnier 2002; Díaz *et al.* 2007). Compared to plants, we know much less about animal functional diversity, especially of terrestrial invertebrate communities (Moretti *et al.* 2017; Parr *et al.* 2017). This is partly caused by the lack of standardized protocols to measure functional traits in terrestrial invertebrates (Didham, Leather, & Basset 2016; Moretti *et al.* 2017). Consequently, some important traits are often not measured or measured in ways that are not comparable across studies, rendering databases insufficient, non-uniform or taxa-limited.

Pollinators play a key role in the functioning of terrestrial ecosystems and provide an essential ecosystem service in terms of crop pollination (Klein *et al.* 2007). However, several studies in Europe and North America have shown that pollinator diversity is declining (Biesmeijer 2006; Colla *et al.* 2012; Bartomeus & Winfree 2013; Powney *et al.* 2019). Within this context, functional traits are increasingly being incorporated in pollinator studies. Various studies have established links between environmental changes and species susceptibility (Murray, Kuhlmann, & Potts 2009; Roulston & Goodell 2011) and between biodiversity and ecosystem functioning (Fontaine *et al.* 2006; Gagic *et al.* 2015). Commonly used functional traits in pollinator ecology studies include body size, mouthpart length, sociality, trophic specialization (lecty), voltinism, flight period and nesting habits (e.g.: De Palma *et al.* 2015; Aguirre-Gutiérrez 2016; Coutinho, Garibaldi, & Viana 2018; Woodcock *et al.* 2019) .

One particularly important trait in pollinator insects is hairiness (pilosity). Hairiness creates an insulation layer that mitigates convective loss of heat generated by the vibration of thoracic muscles, thus playing an essential role in thermoregulation (May 1979; Heinrich 1993). Some studies have found differences in hair length between bees from different climates (Peat *et al.* 2005) and along elevation gradients (Peters *et al.* 2016), suggesting that hairiness could act as a response trait to climatic changes. Hairiness can also be considered an effect trait involved in pollen collection and transfer (Müller 1995; Thorp 2000; Amador *et al.* 2017), potentially affecting pollination effectiveness (Stavert *et al.* 2016; Phillips *et al.* 2018; Woodcock *et al.* 2019).

Notwithstanding the importance of hairiness in pollinator ecology, information on how to measure this trait is scarce and inconsistent across studies (Moretti *et al.* 2017). As a result, hairiness data are mostly lacking in pollinator data bases and, when available, are not comparable across studies. Some studies use thorax hair length as a measure of

hairiness (Peat *et al.* 2005; Peters *et al.* 2016). Others use the percentage of body surface covered by hair (Kühsel 2015; Phillips *et al.* 2018). However, these measures do not account for the two components of hairiness (hair length and hair density; Moretti *et al.*, 2017). Other studies do consider both components, but use a semi-quantitative scale (Woodcock *et al.* 2019). Finally, Stavert and collaborators (2016) proposed an innovative method that uses a measure of entropy obtained from images of the insect's body surface as a proxy for hairiness. However, we could not apply this method to pollinators with shiny cuticles, which yielded high levels of entropy due to light reflection.

The aim of our study is to develop a method to quantitatively measure hairiness in insect pollinators. We describe procedures to measure hair density and hair length and propose a simple hairiness index integrating both components. These procedures are then synthesized in a standardized protocol. We apply this protocol to three different body parts of 109 insect pollinator species and show that our methodology discriminates pollinator groups and bee genera in terms of hairiness. Finally, because body size is another functional trait that has been related to both thermoregulation (Stone & Willmer 1989; Heinrich 1993) and pollination effectiveness (Kandori 2002; Willmer & Finlayson 2014; Jauker, Speckmann, & Wolters 2016), we explore the relationship between hair density, hair length and body size.

1.2-Materials and Methods

1.2.1- Insect specimens

We used a collection of pollinator insects from Sweden, Germany and Spain composed of 109 species including Anthophila (bees; 52 species), Syrphidae (hover-flies, 27), Bombyliidae (bee-flies, 2), other flies (9), Coleoptera (beetles, 9), Lepidoptera (butterflies and moths, 5), Vespidae (wasps, 3) and Symphyta (saw-flies, 2). Bees comprised the following genera: *Andrena* (20 species), *Bombus* (10), *Lasioglossum* (8), *Halictus* (3), *Osmia* (5), *Apis* (1), *Anthophora* (1), *Eucera* (2), *Xylocopa* (1) and *Nomada* (1). For the analyses, *Lasioglossum* and *Halictus* species (Halictini) were grouped together, as well as *Anthophora, Eucera, and Xylocopa* species (Anthophorinae) (Table A2.1). Because bees show marked sexual dimorphism, we only worked with females.

1.2.2- Body size

We used body length as an estimator of body size (mean ± SE sample size = 5.44 ± 0.39 specimens per pollinator species). For bees, in addition to body length we measured intertegular span (hereafter ITS) using a stereomicroscope (mean ± SE sample size = 6.62 ± 0.68 specimens per species). ITS is the most commonly used estimator of body mass in bee studies (Cane 1987; Cariveau *et al.* 2016; Osorio-Canadas *et al.* 2016; Kendall *et al.* 2019). For this reason, we used ITS in the analyses involving only bees and body length in the analyses involving all pollinators. ITS and body length in bees were highly correlated (Spearman ρ = 0.87; P < 0.001).

1.2.3- Hairiness

The two components of hairiness (hair density and hair length) were measured in three body parts: the dorsal surface of the mesothorax, the ventral surface of the thorax and the face (Fig. 1.1A-D). We selected these body parts because the flight muscles involved in endogenous heat production are located in the thorax (Heinrich 1993) and because the thorax and the face act as surfaces of pollen exchange in the pollination of many flower species (Willmer 2011). We measured a mean of three specimens per species (mean ± SE = 2.96 ± 0.11). Measurements were taken with the stereomicroscope LEICA M165C equipped with a LAS live measurement module software (Leica Microsystems, Wetzlar, Germany). This module allows taking length and surface measurements on live images in real units (Fig. 1.1E-F).

Hair density (number of hairs/mm^2). In each of the three above-mentioned body parts, we selected 3 representative areas of approximately 0.1 mm^2 and counted the number of hairs in each area. In some cases, notably in species with high hair density and in specimens in which hairs formed clumps due to manipulation during capture and/or preservation, it was easier to count hairs at their insertion points, usually signalled by a micropore on the cuticle (Fig. 1.1E, see Appendix 1 for details). Counting micropores has the added advantage that can be applied to specimens that have lost hairs (e.g., due to aging: Southwick 1985; Bosch & Vicens 2006; or to poor manupulation) to obtain a measure of original hair cover.

The results of these three measurements were used to calculate a mean hair density for each body part. In some species, hairiness patterns were clearly not uniform within a body part (notably in the face). In these cases (11.3 % of the 327 species/body parts we measured), we sampled approximately 0.1 mm^2 of the area occupied by each hairiness pattern separately, and the overall hair density mean was weighted by the area occupied by each hairiness pattern.

Hair length (mm). The length of 8-9 hairs of each body part was measured using the length measuring tool of the software (Fig. 1.1F). Again, in body parts with clearly distinct hairiness patterns, hair length of 8-9 hairs was measured separately for each part and the overall mean hair length was weighted by the surface occupied by each hairiness pattern.

The time spent measuring hairiness (hair length + hair density in three 0.1 mm^2 areas of the three body parts) was about 15 minutes per specimen. A detailed protocol describing our method can be found in Appendix 1.
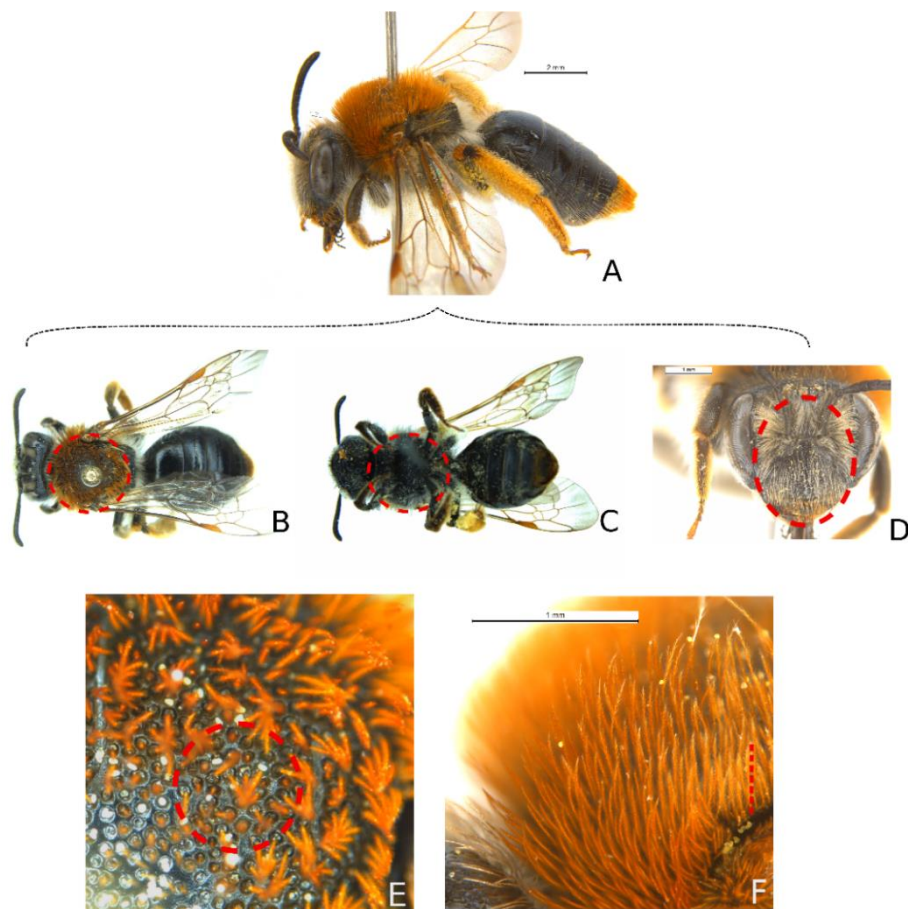
Figure 1.1: Pinned *Andrena haemorrhoa* female (A), body parts in which hairiness was measured (B: dorsal surface of the mesothorax, C: ventral surface of the mesothorax, D: face), and close-up images of the dorsal mesothorax showing measurements of hair density (E) and hair length (F)

1.2.4- Data analysis

All analyses were conducted in R v.3.3.2 (R Core Team. 2016), first with all pollinator species, and then with bees only.

1.2.4.1- Relationships between hair density, hair length and body size

For each body part separately, we tested whether hair density and hair length were correlated. We also tested the correlation of each of these two hairiness components with body size. Because hair density and length were only weakly correlated (see results), we calculated, for each body part, a hairiness index (hair density x hair length). Finally, we examined whether the hairiness components and the hairiness index of the three different body parts were correlated. We used either Pearson or Spearman correlation depending on data distribution.

1.2.4.2- Hairiness comparisons among pollinator groups and bee taxa

We calculated the coefficients of variation (SD/mean x 100) of the two hairiness components within and between species, separately for each body part. Because our method accounts for hair loss and since we only measured female specimens, we expected greater variability between than within species.

We explored whether hair density, hair length and hairiness index differed between pollinator groups and bee taxa using one-way ANOVA and Kruskal-Wallis tests (depending on data distribution), followed by post-hoc tests for multiple comparisons (Tukey and Dunn tests, respectively). We analysed each hairiness component of each body part separately. Log (X + 1) and square-root transformations were applied to improve normality and homoscedasticity of model residuals if needed. Pollinator groups and bee taxa with three or fewer species (bee-flies, saw-flies, wasps, *Apis*, *Nomada*) were excluded from the analyses but their values are provided in the figures.

1.3- Results

1.3.1- Hairiness components: hair density and hair length

Hair density of all pollinators ranged from 0 to 5797.6 hairs/mm^2 (mean ± SE = 428.0 ± 32.3) and that of bees from 63.5 to 1052.2 (mean ± SE = 333.4 ± 11.6). Hair length of all pollinators ranged from 0.01 to 1.91 mm (mean ± SE = 0.48 ± 0.02) and that of bees from 0.09 to 1.58 mm (mean ± SE = 0.62 ± 0.03).

Dorsal thorax hair density and length were weakly and negatively correlated (all pollinators: r = -0.25, P < 0.01; bees: r = -0.48; P < 0.001; Fig. 1.2A-B). Ventral thorax and face hair density and length were also weakly and negatively correlated for bees (r = -0.38 and -0.39, respectively; P < 0.01), but not for all pollinators (P > 0.08).

1.3.2- Relationship between hairiness components and body size

Dorsal thorax hair density and body size were negatively correlated, weakly for all pollinators (r = -0.20, P < 0.05, Fig. 1.2C) and moderately for bees (r = -0.55, P < 0.001, Fig.1.2D). The analysis of ventral thorax and face hairiness yielded similar results (Table A2.2). Conversely, hair length and body size were positively and strongly correlated in all three body parts (all pollinators, r = 0.67 - 0.70, P < 0.001, Fig. 1.2E; bees, r = 0.89 - 0.93, P < 0.001, Fig. 1.2F).

1.3.3- Hairiness comparisons among body parts

Hairiness was positively correlated across body parts (all P < 0.001, Table A2.3). Correlation coefficients were higher for hair length (all pollinators: r = 0.91 - 0.95; bees: r = 0.96) than for hair density (all pollinators: P = 0.47 - 0.67; bees: r = 0.61 - 0.74). The hairiness index was also strongly correlated across body parts (all pollinators: r = 0.78 - 0.88; bees: r = 0.77 - 0.85).

1.3.4- Differences in hairiness across pollinator groups and bee taxa

Since both hairiness components and the hairiness index were correlated among body parts, hereafter we only show results of the dorsal region of the thorax (the analysis of the ventral region of the thorax and the face yielded similar results; see Tables A2.4 and A2.5, Figs. A2.3-A2.4).

The coefficient of variation of dorsal thorax hairiness components was much higher between species (all pollinators: 73.0 - 76.7%; bees: 53.4 - 60.7%) than within species (all pollinators: 17.1 - 18.7%; bees: 17.0 - 18.3%) (Table A2.4).

1.3.4.1- All pollinators

We found clear differences among pollinator groups in the two hairiness components and the hairiness index (Fig. 1.3, Fig. 1.4A). Butterflies and moths were the group with the highest hair density, followed by bees, hover-flies and beetles; other flies were the group with the lowest hair density (ANOVA, $F_{4,97} = 6.9$, $P < 0.001$, Fig. 1.3A). Butterflies and moths and bees had longer hair than any of the other pollinator groups ($F_{4,97} = 11.3$, $P < 0.001$, Fig. 1.3C). According to the hairiness index butterflies and moths were the hairiest group followed by bees, hover-flies, beetles and other flies ($F_{4,97} = 27.2$, $P < 0.001$, Fig. 1.3E).

1.3.4.2- Bees

Our measures of hairiness also yielded clear differences among bee taxa (Fig. 1.3, Fig. 1.4B). Halictini had the highest hair density, followed by *Bombus*, *Osmia* and *Andrena*, and Anthophorinae had the lowest density ($F_{4,45} = 16.25$, $P < 0.001$, Fig. 1.3B). This pattern changed completely for hair length. *Bombus* and Anthophorinae had the longest hair followed by *Osmia* and *Andrena*, and Halictini had the shortest hair ($F_{4,45} = 67.9$, $P < 0.001$, Fig. 1.3D). According to the hairiness index the hairiest taxa were *Bombus* and *Osmia*, followed by Anthophorinae, *Andrena* and Halictini ($F_{4,45} = 13.5$, $P < 0.001$, Fig. 1.3F).
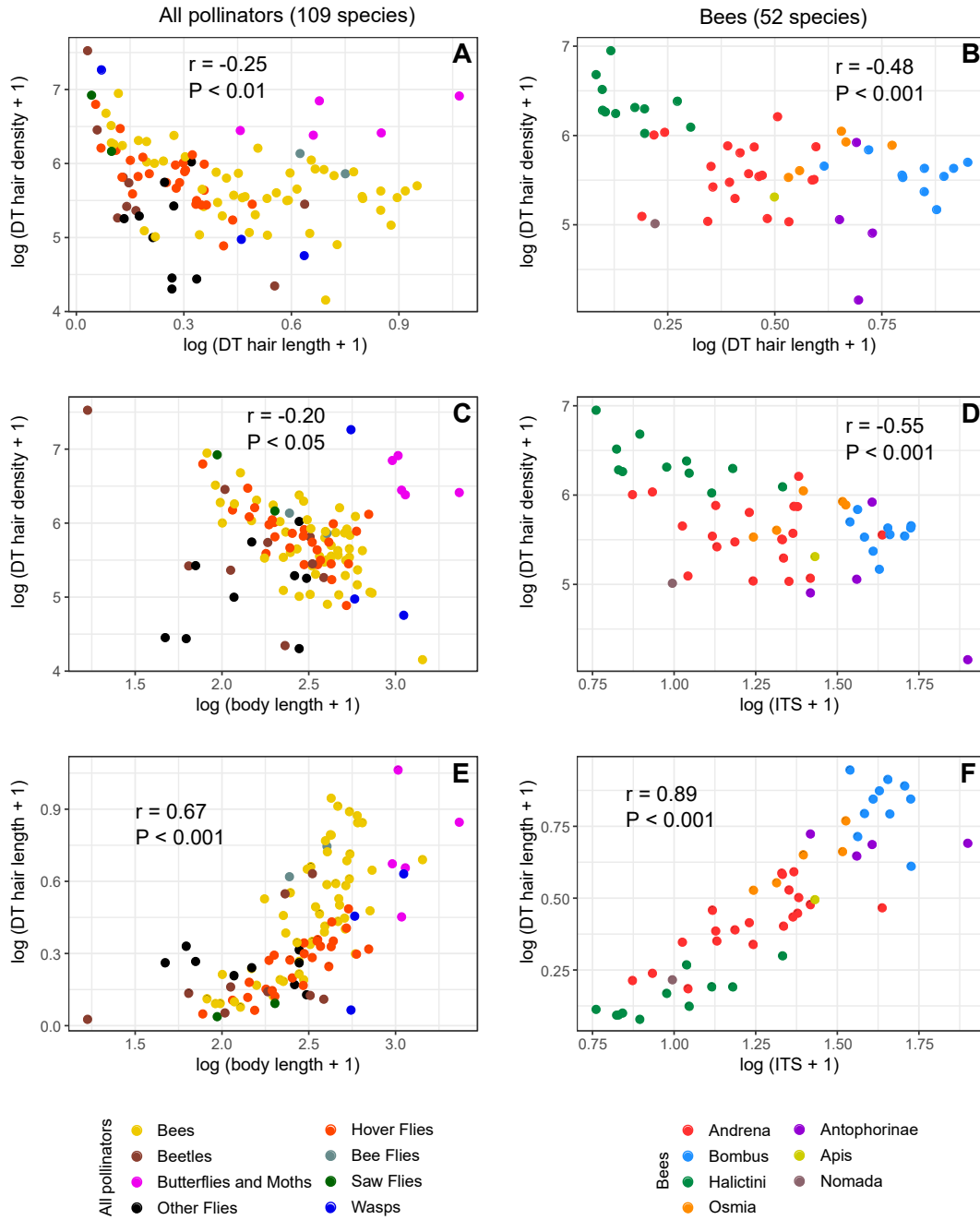
Figure 1.2: Scatter plots showing the relationship between hair density and hair length (A and B), between hair density and body size (C and D) and between hair length and body size (E and F); of the dorsal surface of the mesothorax for all pollinators (A, C, and E; 109 species) and for bees only (B, D, and F; 52 species). Each point corresponds to one species. See Table A2.2 for results of the ventral surface of the mesothorax and the face. DT, dorsal surface of the mesothorax; ITS, intertegular span
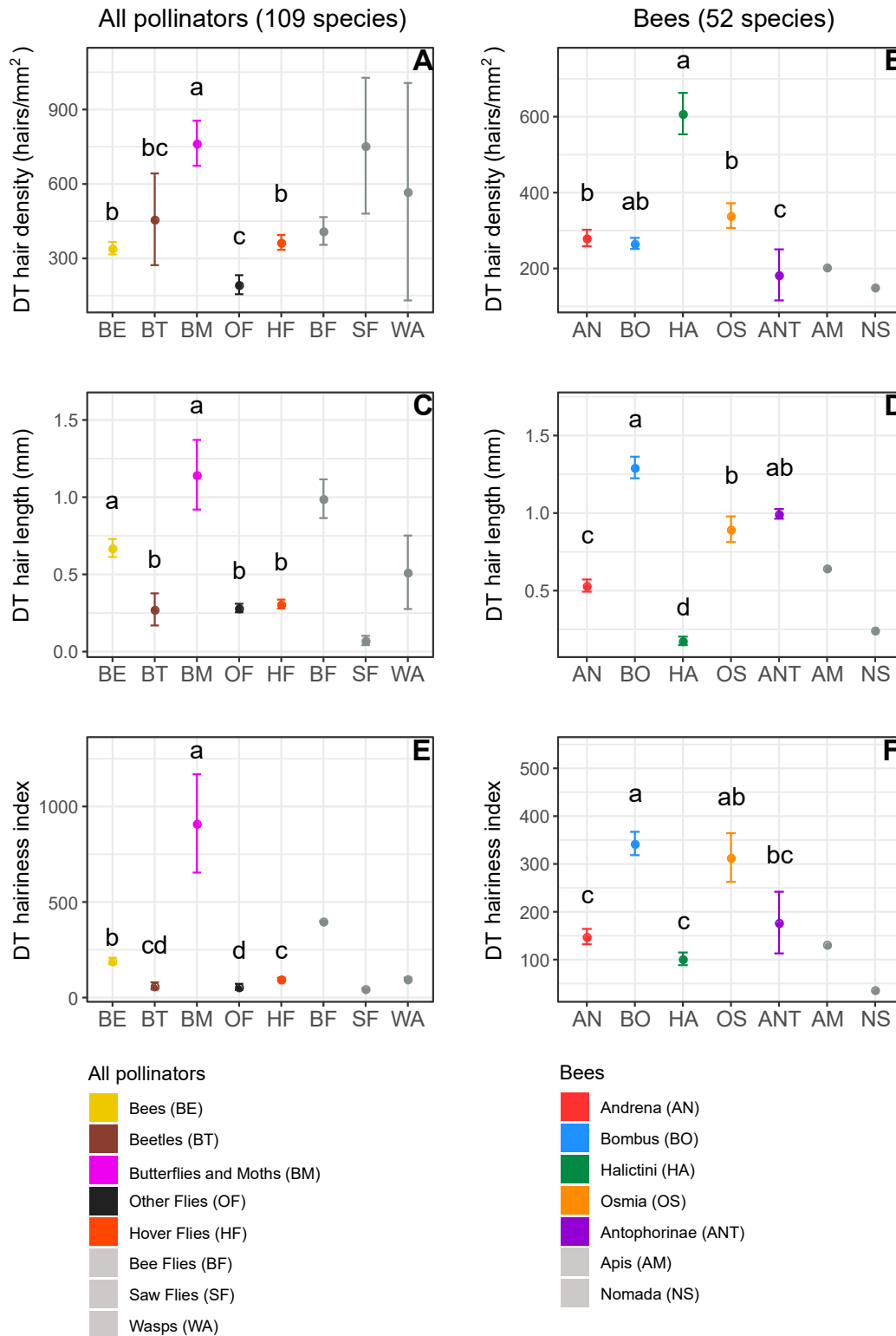
Figure 1.3: Mean ± SE hair density (A and B), hair length (C and D), and hairiness index (E and F) of the dorsal surface of the mesothorax (DT) of various pollinator groups and bee taxa. Different letters indicate significant differences among groups (post hoc Tukey's tests, $P < 0.05$). Groups with fewer than three species (in gray) were not included in the analyses
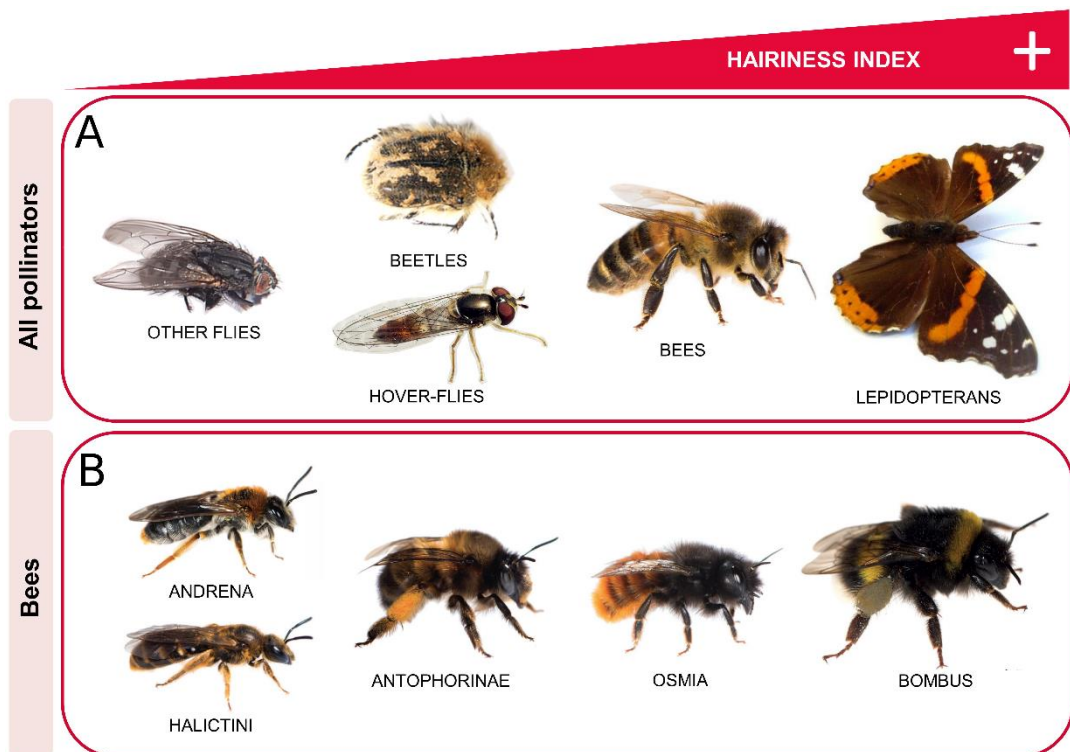
Figure 1.4: Pollinator groups (A) and bee taxa (B) ordered by increasing hairiness from left to right. (Photograph credits Nicolas J. Vereecken [all bees], Adrià Miralles [hoverflies] and Laura Roquer-Beni [other flies, beetles and lepidopterans]. All images used with permission.)

1.4- Discussion

The aim of our study was to establish a standard practical procedure to quantitatively measure the two components of hairiness and to promote the use of this important trait in pollinator studies.

1.4.1- Advantages of the method

The methodology we describe has several advantages. First, it provides a quantitative measure of hair density and length. Second, it is a non-invasive methodology; specimens remain undamaged. Therefore, our methodology can be applied not only to dead specimens, but also to live (anesthesized) insects. Third, it can be applied to specimens in which the hair cover has been altered due to manipulation. Tufts of clumped hair are common in specimens that have been exposed to high concentrations of ethyl acetate in killing jars and in specimens that have been kept in water or alcohol (e.g. specimens obtained from pan of malaise traps). Fourth, it accounts for hair loss due to aging or poor preservation. Certain pollinator groups, notably bee-flies, tend to lose hairs during capture and manipulation. Thus, if needed, it is possible to obtain a measure of original hair density (as opposed to actual hair density). Fifth, measurements are taken directly from the specimen rather than from photographs. For this reason, our method is not affected by shininess, a common feature of the cuticle of many pollinator insects. Sixth,

our method discriminates the two components of hairiness, thus allowing for a meaningful interpretation of the functional and evolutionary consequences of hairiness.

Although our method may appear to be time-consuming, a trained person can process a specimen (8-9 measures of hair length + 3 measures of hair density in 3 body parts) in just 15 minutes. This amount of time can be reduced if, depending on the objectives of the study, fewer body parts are considered.

1.4.2- Relationship between hair density, hair length and body size

We found a negative (albeit weak) correlation between hair length and density for all three measured body parts in bees and for the dorsal region of the thorax in all pollinators. Accounting for the two components of hairiness would be redundant if these two variables were highly correlated. Some groups such as beetles and Halictini had very short hair but very high hair density (Fig. 1.3). Other groups such as butterflies and moths and bees of the genera *Bombus* and *Osmia*, had long hair and high hair density.

Accounting for the two components of hairiness is also important because hair length and hair density may be differently related to body size. A positive relationship between hair length and body size is expected due to allometric and mechanical constraints (movement would be impared in a small animal with long hair). Previous studies have found a positive relationship between hair length and body size at the intraspecific level in bumblebees (Goulson *et al.* 2002; Peat *et al.* 2005). Our results show that this relationship holds at the interspecific level and when pollinators from different orders are considered. Positive relationships between body size and length of various appendages are common in insects (proboscis: Kunte 2007; Cariveau *et al.* 2016; legs: Kaspari & Weiser 1999; Teuscher *et al.* 2009; wings: Bullock 1999; Bosch & Vicens 2002).

The relationship between hair density and body size, on the other hand, is less straightforward. We cannot think of any a priori reason why hair density should differ between large and small animals. We found that the relationship between hair density and body size was weak and negative, especially in bees. Interestingly, studies on various groups of mammals have also found that small species tend to have denser (and shorter) fur (Schwartz & Rosenblum 1981; Steudel, Porter, & Sher 1994; Sandel 2013). We suggest that the negative relationship between hair length and hair density, rather than indicative of a direct trade-off, can be explained through the relationship between these two variables and body size. Given that small animals cannot have long hair due to the above-mentioned mechanical constraints, the evolutionary pathway to achieve high levels of hairiness in small animals is through increased hair density.

1.4.3- Hairiness as an effect trait

Our methodology and our results have important implications for studies on pollination effectiveness. The ability to incorporate, transport and deliver pollen is likely to be influenced by the two hairiness components. Longer hairs provide a greater surface for pollen grain adherence, and hair spacing (the inverse of hair density) may be important in relation to pollen grain size (Roberts & Vallespir 1978; Haider *et al.* 2014), which shows great variability among plant taxa (Willmer 2011).

A link between hairiness and pollination effectiveness has been found in some studies (Stavert *et al.* 2016; Phillips *et al.* 2018). Given the positive correlation between body size and hair length, studies exploring the relationship between hairiness and pollination effectiveness should account for body size, which, along with flower-handling behaviour and visit duration, has also been shown to affect pollination effectiveness (Kandori 2002; Willmer & Finlayson 2014; Jauker, Speckmann, & Wolters 2016; Phillips *et al.* 2018). Accordingly, in pollination studies hairiness measures should target the body parts involved in pollen transfer, which depend on flower morphology, pollinator body size and intra-floral foraging behaviour (Beattie, Breedlove, & Ehrlich 1973; Bosch 1992; Solís-Montero & Vallejo-Marín 2017; Araujo, Medina, & Gimenes 2018).

1.4.4- Hairiness as a response trait

Our methodology can also be important for studies on thermal biology and studies exploring the geographical distribution of pollinator communities and populations and their response to climate change. Some pollinators generate heat endogenously by contracting their flight muscles (Heinrich 1993), and hairiness provides an insulation layer around the body surface that slows convective heat loss (May 1979). As with pollination effectiveness, both components of hairiness (length and density) are likely to contribute to the creation and maintenance of this insulation layer and therefore to influence thermoregulation (Wasserman & Nash 1979; Steudel, Porter, & Sher 1994). Consequently, we would expect pollinator species and populations to be hairier in colder climates. Again, given the correlation between hair length and body size, studies addressing the distribution of pollinators in relation to climate should account for body size. Body size is strongly related to the ability to generate heat and fly at low temperatures both at the intra- and inter-specific levels (Stone & Willmer 1989; Heinrich 1993; Stone 1993; Bishop & Armbruster 1999; Osorio-Canadas *et al.* 2016). Both body size and hair length of bumblebees have been shown to be greater in species from colder areas along latitudinal (Peat *et al.* 2005) and elevational gradients (Peters *et al.* 2016). Since most endogenous heat is produced by the flight muscles (Heinrich 1993), measures of hairiness in thermal biology studies should mainly target the thorax, although other body parts (head, abdomen) have also been shown to be involved in heat loss (Cooper 1985; Heinrich & Buchmann 1986; Roberts & Harrison 1998).

1.4.5- Hairiness in trait-based studies.

Functional diversity studies typically characterize species based on suites of traits. Ideally, these traits should be biologically meaningful, easy to measure and comparable across taxa. In principle, and until we have a better understanding of the mechanistic effects of hair length and hair density of different body regions on various ecological functions, we suggest keeping these two measures as separate traits in a multi-trait space. Otherwise, if a single measure is desirable, they can be combined into a single trait (hairiness index).

1.4.6- Concluding remarks

We have developed a standardized procedure to measure hairiness and explored the relationships between hairiness components and between hairiness and body size. Overall, these relationships were similar when analysing only bees and when analysing all pollinators. Importantly, in addition to insect pollinators, our methodology can be applied to other groups of terrestrial arthropods and can be used to explore the relationships between hairiness and other ecological functions besides those discussed above. Hairiness has been shown to act as a physical and sensory barrier against predators and parasites in caterpillars (Lindstedt, Lindström, & Mappes 2008; Castellanos *et al.* 2011; Sugiura & Yamazaki 2014) and moths (Shen *et al.* 2018). We hope our methodology will foster the inclusion of this important trait in insect data bases and will contribute to our understanding of the importance of hairiness in insect ecology.

2

What makes a good pollinator? Relationship between pollinator traits and pollination effectiveness in apple flowers

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Manuscript in preparation

ABSTRACT

Differences in pollination effectiveness (PE) among pollinators have been widely documented. By comparison, the morphological and behavioural pollinator traits underlying these differences have been less investigated. PE has been often associated with flower handling behaviour and body size. On the other hand, the relationship between PE and other traits such as tongue length, visit duration, hairiness and reward sought (pollen *vs.* nectar) is less consistent.

We used single-visit pollen deposition to previously unvisited apple flowers to explore the relationship between pollinator traits and PE. Our objectives were: 1) to determinate which traits promote PE in an actinomorphic bowl-shaped flower; 2) to compare apple pollinator species in terms of PE and to establish whether good pollinators share similar traits. For each single-visit flower we recorded visit duration, flower handling behaviour and resource sought (pollen *vs.* nectar). For each pollinator species we measured body size, tongue length, hair density and hair length.

We found that PE depended on flower handling behaviour (top visitors were more effective than side visitors), body size (larger pollinators were more effective) and visit duration (longer visits were more effective). Hairiness did not significantly affect PE. We found significant differences among 11 pollinator species in PE. Solitary bees (*Andrena* spp., *Osmia cornuta*, *Eucera nigrilabris*) tended to be more effective than bumblebees and especially honey bees. Some hoverflies (*Eristalis tenax*) and beetles (*Tropinota squalida*) were highly effective.

Our study demonstrates that PE in a disc-bowl shaped flower is dependent on a variety of traits. All effective pollinators were top-workers, but otherwise did not necessarily share similar traits. In other words, there are different ways to be a good pollinator.

Keywords: pollinating effectiveness, single-visit pollen deposition, stigma pollen load, legitimacy, apple pollination, actinomorphic flower

2.1- Introduction

Animal pollination is a first and crucial step towards seed and fruit production in many plants. About 85% of the angiosperm species worldwide (Ollerton, Winfree, & Tarrant 2011) and 75% of human crops (Klein *et al.* 2007) depend to a greater or lesser extent on pollination by animals, mostly insects, to set fruit. Most flower species are pollinator generalist, being visited by a wide array of bees, flies, beetles, moths, butterflies, wasps, and ants (Ollerton 2017). However, not all pollinators are equally effective as pollen vectors (Waser *et al.* 1996). Differences in pollination effectiveness among pollinator groups, species and even individuals have been widely documented (Motten *et al.* 1981; Herrera 1987; Olsen 1996; Thomson & Goodell 2001; Kandori 2002; Willmer & Finlayson 2014; Willmer, Cunnold, & Ballantyne 2017; Phillips *et al.* 2018). By comparison, the pollinator traits underlying these differences have been much less investigated.

Pollination effectiveness, usually measured as the amount of pollen delivered during a single visit (Inouye *et al.* 1994; Ne'Eman *et al.* 2010), has been associated with various pollinator behavioural and morphological traits. Flower handling behaviour, the way in which the pollinator positions itself and moves on the flower (e.g. top *vs.* side visitors) conditions visit legitimacy (contact between the body of the pollinator and the reproductive organs of the plant) and, consequently, pollinator effectiveness (Bosch & Blas 1994; Thomson & Goodell 2001; Park *et al.* 2016). Pollinator body size has also been associated with pollination effectiveness. Large pollinators have been found to deposit more pollen grains, again partly due to higher rates of visit legitimacy (Kandori 2002; Sahli & Conner 2007; Willmer & Finlayson 2014).

The relationship between other pollinator traits and pollinator effectiveness is less clear and/or consistent. Tongue length has been found to affect pollination effectiveness (Inouye 1980; Harder 1983), but this relationship seems to be highly dependent on the match between this trait and corolla depth (Inouye 1980; Alexandersson & Johnson 2002; Ibanez 2012; Barrios *et al.* 2016). More recently, some studies have found hairiness to be positively related to pollination effectiveness (Stavert *et al.* 2016), but others attach a greater importance to body size than to hairiness (Phillips *et al.* 2018). Similarly, visit duration has been positively related to pollen grain deposition (Conner, Davis, & Rush 1995; Phillips *et al.* 2018), but this relationship is not supported or even reversed in other studies (King, Ballantyne, & Willmer 2013; Zych *et al.* 2013). Finally, some authors have found pollen collectors to be more effective than nectar collectors (Monzón, Bosch, & Retana 2004; Tepedino, Arneson Horn, & Durham 2016) but others have found the opposite (Williams & Thomson 2003; Young, Dunning, & von Hasseln 2007).

Discrepancies among studies can be explained by differences in the number and identity of pollinator species investigated (especially whether they include only bees or also other pollinator groups), the number and identity of traits explored and the scale of measurement (individuals or species). Importantly, and often overlooked, some of the traits influencing pollination effectiveness are strongly correlated. Body size in particular is correlated to mouthparts length (Harder 1985; Peat, Tucker, & Goulson

2005; Cariveau *et al.* 2016) as well as hair length (Moretti *et al.* 2017; Roquer-Beni *et al.* 2020a), and visit duration may be related to flower handling behaviour (Thomson & Goodell 2001). Finally, pollination effectiveness may be dependent on combinations of traits, making it hard to establish the contribution of single traits by themselves (Brousseau, Gravel, & Handa 2018b). While most studies rank pollinators based on their effectiveness and then identifiy salient traits of the most effective pollinator species, studies directly measuring the relative importance of various traits are still lacking (but see Phillips *et al.*, 2018).

In addition to pollinator traits, pollination effectiveness may be strongly conditioned by flower morphology (Campbell 1989; Conner, Davis, & Rush 1995). Plant species with restrictive flowers (e.g., papilionaceous and narrowly-tubular corollas) are typically visited by a narrow array of pollinators (Herrera 1996; Fenster *et al.* 2004; Stang *et al.* 2006). In these specialized systems, pollination effectiveness is expected to be highly dependent on the match between flower morphology and particular pollinator traits such as proboscis length or adequate flower-handling skills (Inouye 1980; Laverty & Plowright 1988; Nilsson 1988; Ibanez 2012). In these cases, trait-matching may be a good predictor of pollinator effectiveness (Schleuning, Fründ, & García 2015). On the other hand, bowl-shaped open flowers are visited by a wide range of taxonomically and functionally diverse pollinator species (Kevan 2006; Willmer 2011). In these flowers, with exposed reproductive organs and easily accessible rewards, pollination effectiveness is likely to be affected by a wider range of pollinator traits.

Here we use apple flowers to explore the relationship between pollinator traits and pollinator effectiveness. Apples have open actinomorphic flowers and are visited by a wide array of pollinators (Vicens & Bosch 2000b; Garratt *et al.* 2014b; Miñarro & García 2018a, Roquer-Beni *et al.* 2020b). The two objectives of the study are: 1) to determinate which morphological and behavioural traits promote pollination effectiveness in an open bowl-shaped flower; 2) to compare apple pollinator species in terms of pollination effectiveness and to establish whether good pollinators share similar traits or not.

2.2- Materials and Methods

2.2.1- Study system

We worked in a 0.81-ha commercial organic apple orchard (Gala variety) in Girona, Catalonia, Spain (42.178506 X, 3.040833 Y). Apple flowers are actinomorphic, measure 3-4 cm in diameter and have 5 white-to-pink petals. The reproductive organs (about 20 stamens and a gynoecium with five stigmas) are located in the centre of the flower and are readily accessible. Five nectaries are located at the base of the petals.

2.2.2- Pollinator effectiveness

We measured single-visit pollen deposition to previously unvisited flowers as a proxy of pollinator effectiveness (Kearns & Inouye 1993; Ne'Eman *et al.* 2010).

On 5th April 2019, at the onset of apple bloom, we bagged 40 branches with screen enclosures (1-mm^2 mesh size) to prevent pollinator access. Over the following days, we collected newly opened flowers from the bagged branches and offered them to pollinators that were visiting apple flowers. When a pollinator landed on the flower offered, it was visually identified and left undisturbed until it flew off. Then, using a pair of forceps, we extracted the pistil and transferred it to a small Eppendorf tube containing fuchsine-stained gelatine (Kearns & Inouye 1993). To account for potential pollen self-deposition during flower manipulation, we also collected 12 non-visited flowers.

In the laboratory, single-visited pistils were mounted on glass slides and the pollen grains deposited on each of the five stigmas (hereafter, "stigmatic pollen load") were counted and identified under a microscope at 400 X. Stigmatic pollen load is positively related to seed set and fruit size in apples (Garratt *et al.* 2014a; Samnegård, Hambäck, & Smith 2019). We also recorded the number of stigmas with at least one apple pollen grain as a measure of pollination evenness. However, this variable was highly correlated to stigmatic pollen load (Pearson $r = 0.8$, $P < 0.001$).

Non-apple pollen grains were not considered because they represented a low proportion (4.3 %) of the pollen grains identified, and because total pollen load and apple pollen load were highly correlated ($r = 0.9$, $P < 0.001$). Stigmas of control flowers had very low pollen loads (mean ± SE = 11.4 ± 5.5) compared to visited flowers (504.1 ± 36.5).

2.2.3- Pollinator traits

Morphological traits

Some pollinator individuals were captured to confirm species identity and to measure morphological traits. We measured body length (as a proxy of body size), mouthparts length and hairiness. Body length was measured from the tip of the head to the tip of the abdomen, excluding body appendages (n = 5.3 ± 0.4 (mean ± SE) specimens per species). Mouthparts length was measured as the length of the extended mouth apparatus (extended glossa plus the prementum in bees) (n = 5.3 ± 0.4 specimens per species). We followed Roquer-Beni *et al.* (2020a) to measure two components of hairiness (hair density and hair length) (n = 3.9 ± 0.5 specimens per species). Both components were measured in the ventral surface of the thorax and the face, the two body parts that are more directly involved with stigma contact in apple and other open disc-bowl-shaped flowers. All bees recorded in the single-visit survey were females. For this reason, we only used female bee specimens to take morphological measurements.

Behavioural traits

For each single-visited flower we recorded three pollinator behavioural traits: visit duration (the time the pollinator spent on the flower), flower handling behaviour (whether the pollinator visited the flower from the top or from the side of the flower; Robinson 1979) and resource sought (pollen + nectar or only nectar). In addition, we noted whether the visit resulted in contact with the reproductive organs of the flower or not (visit legitimacy).

2.2.4- Statistical analysis

Traits affecting pollination effectiveness

To analyse which pollinator traits enhance pollination effectiveness, we performed linear mixed-effect models (GLMMs) with stigmatic pollen load as the response variable. We run these models twice, first including all recorded visits and then including only legitimate visits.

We first checked the correlation between pairs of quantitative explanatory variables and selected only one of them if correlation was greater than 0.7 (Fig. A3.1). Mouthparts length was strongly correlated to body length (Pearson r = 0.7, P < 0.001; Fig. A3.1). Thorax and face hair length were also strongly correlated (r = 0.9; P < 0.001), as well as thorax and face hair density (r = 0.7; P < 0.001; Fig. A3.1). We decided to retain body length, and to use hair density and hair length of the ventral surface of the thorax as measures of hairiness. Thus, initial models included body length, thorax hair density (hereafter hair density), thorax hair length (hereafter hair length), visit duration, and flower-handling behaviour (top *vs.* side) as fixed effects, and pollinator species as a random effect. Resource sought was not included because it was strongly related to flower handling behaviour (97.0% of side-working pollinators were collecting only nectar). In models including only legitimate visits, flower handling behaviour was not included because virtually all (96.6%) legitimate visits were top visits. We confirmed that VIF was < 5 in the two models.

Following a model selection procedure, all possible explanatory variable combinations were tested through a multi-model inference approach (Burnham & Anderson 2002) using the dredge function of MuMin package (Barton & Barton 2019) in R (R Core Team. 2016). We selected the best-fit models based on AICc values using maximum likelihood criteria. Models with ΔAICc < 2 were considered equal to the best model (Burnham & Anderson 2002). We considered significant those effects from explanatory variables with confidence intervals not overlapping with zero. We calculated a likelihood-ratio-based R^2 of the best models as a measure of explanatory power.

Species-level pollination effectiveness

We conducted ANOVA followed by post hoc Tukey tests to detect differences between pollinator species in pollination effectiveness. We also conducted a Principal Component Analysis (PCA) to order species according to their functional traits (body length, hair density, hair length, visit duration and flower handling behaviour). In this way, we could visually assess whether species with similar pollination effectiveness shared similar combinations of traits.

Only pollinator species with ten or more single-visit observations were included in these analyses. Model residuals were inspected to assess whether the normality assumption was met. The response variable (stigma pollen load) was log-transformed. Numerical explanatory variables were standardized (subtracting the mean and dividing by the standard deviation) to facilitate comparison across variables. To detect model outliers

we calculated Cooks' distance and excluded visits with a Cooks' distance > 4/N (Cook 1977; Fox 1991).

2.3-Results

We recorded 253 visits corresponding to 20 pollinator taxa (17 species and 3 morphospecies) (Fig. 2.1, Table A3.1). Most visits (71.5 %) were by bees, followed by hoverflies (10.7 %), other flies (8.3 %), beetles (7.9 %) and wasps (1.6 %).

2.3.1- Traits affecting pollination effectiveness

Considering all visits, two models best explained stigmatic pollen loads. The first model included, body length, flower-handling behaviour and visit duration (Table 2.1). The second model, included the same three variables plus hair density, although the effect of hair density was not significant (Table 2.1). Thus, body length, visit duration and percentage of top visits all had a positive effect on stigmatic pollen load (Fig. 2.2), and these traits explained between 22 % and 24 % of the variation in stigmatic pollen load (Table 2.1).

Results were very similar when considering only legitimate visits. The first selected model included body length and visit duration and the second included these same two variables plus hair density (Table A3.2), although the effect of this variable was again non-significant. As explained, flower handling behaviour was not included in these models because virtually all legitimate visits were by top-working pollinators. The exclusion of outliers provided better model adjustments but trends remained similar (see Table A3.3-A3.4 for results without outlier exclusion).

2.3.2- Species-level pollinator effectiveness

We found significant differences in pollination effectiveness among pollinator species (ANOVA, $F_{10,213}$ = 5.3, P < 0.001, R^2 = 0.19; Fig. 2.3). Five solitary bee species, *Andrena flavipes*, *Andrena limata*, *Andrena pilipes*, *Eucera nigrilabris* and *Osmia cornuta* and one hoverfly, *Eristalis tenax*, delivered greater pollen loads per visit than the honey bee, *Apis mellifera* (Tukey test; P < 0.05). Two Andrena species, *A. pilipes* and *A. flavipes*, were significantly more effective than the bumblebee *Bombus terrestris* (Tukey test; P < 0.05). Non-bee pollinators (hoverflies, other flies and beetles) tended to show intermediate pollination effectiveness (Fig. 2.3).

Figure 2.1: Flower handling behaviour of various apple pollinators. Top-working *Eucera nigrilabris* (A), *Andrena limata* (B), *Eristalis* sp. (C), *Tropinota squalida* (D), *Bombus terrestris* (E), *Osmia cornuta* (F) top-working *Apis mellifera* (G); and side-working *Apis mellifera* (H). Photo credits: Nicolas J. Vereecken [E,F,G], Marcos Miñarro [H] and Laura Roquer-Beni [A,B,C,D]. All images used with permission.

Table 2.1: Best fitting models (ΔAICc < 2) relating pollination effectiveness (stigma pollen load in single-visit apple flowers) to pollinator body length, hair density, hair length, visit duration and flower-handling behaviour. Estimated coefficients and their 95% intervals (in parentheses) are provided. Variables not appearing in the best models are indicated with "-". R^2m and R^2c are the marginal and conditional R^2 range values of the best-fitted models, respectively. Significant terms (with confidence intervals not overlapping with zero) are in bold.

Model *	Estimate	Body length	Hair density	Hair length	Visit duration	Flower handling behaviour**	df	logLik	AICc	ΔAICc	weight	R^2m	R^2c
1	**4.183** **(3.417, 4.980)**	**0.431** **(0.097, 0.790)**	-	-	**0.499** **(0.309, 0.689)**	**1.291** **(0.504, 2.070)**	6	-320.03	652.51	0.00	0.32	0.22	0.32
2	**4.209** **(3.454, 4.989)**	**0.353** **(0.016, 0.717)**	0.199 (-0.142, 0.527)	-	**0.518** **(0.326, 0.709)**	**1.265** **(0.484, 2.037)**	7	-319.31	653.22	0.71	0.23	0.24	0.31

* The response variable (pollination effectiveness) was log-transformed. The number of visits included in each model after outlier exclusion was 198. See Table A3.3 for results without outlier exclusion.
**Top is the reference level of flower handling behaviour.
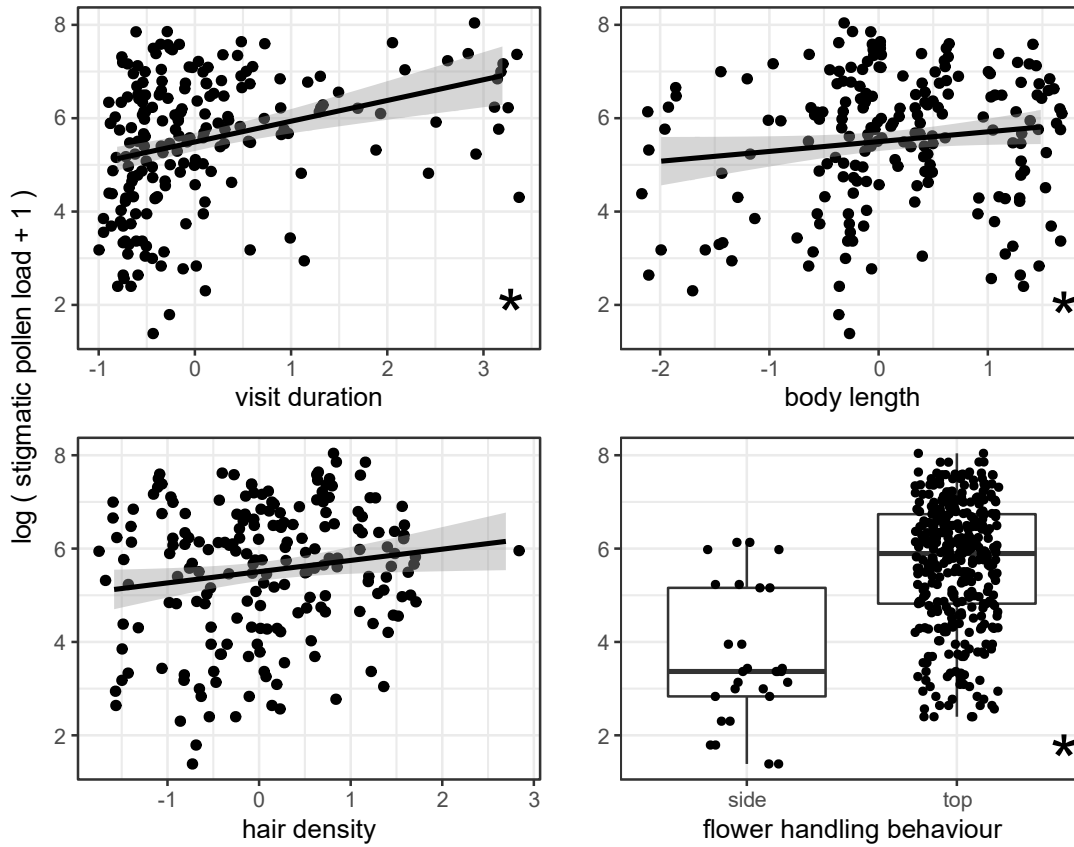
Figure 2.2: Effects of the pollinator traits selected in the best models (visit duration, body length, hair density and flower handling behaviour) on stigma pollen loads (log-transformed) in single-visit apple flowers. Quantitative explanatory variables are standardized. Regression lines from linear models are shown and grey bands indicate 95% confidence intervals. * indicates a significant effect.
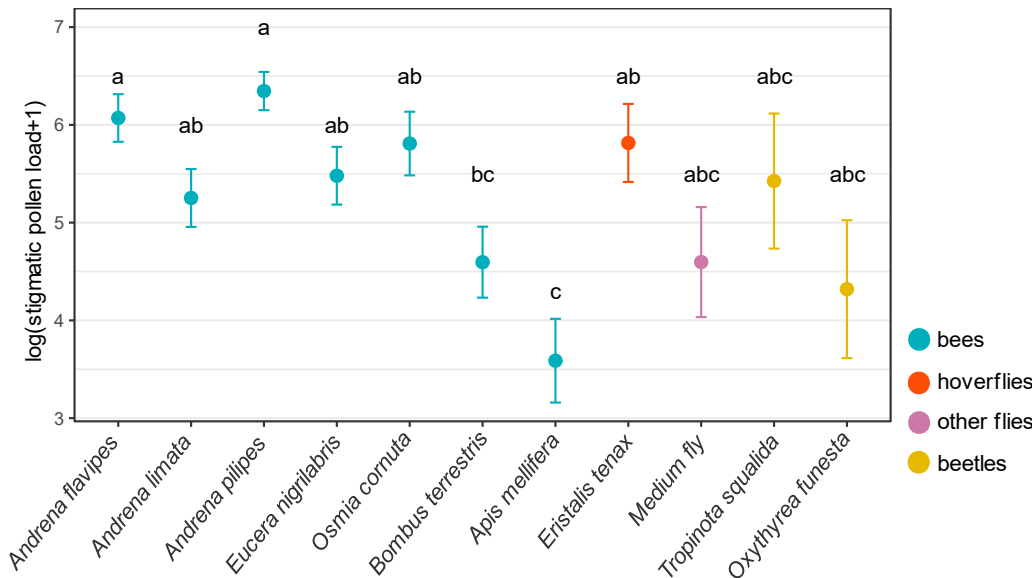
Figure 2.3: Mean ± SE pollination effectiveness (log-transformed stigma pollen load in single-visit flowers) of various apple pollinator species. Different letters indicate significant differences (post-hoc Tukey tests, $P < 0.05$).

The PCA ordering pollinator species based on their morphological and behavioural traits (Fig. 2.4) yielded a first axis (explaining a 47.4 % of the variability) with positive values associated with two morphological traits (body length, hair density) and one behavioural trait (visit duration), and a second axis (explaining 21.4%) associated with two behavioural traits (percentage of top visits, visit duration). Interestingly, species with similar pollination effectiveness did not necessarily share the same traits (Fig. 2.4). *A. pilipes, A. flavipes* and *E. tenax* were located in the centre of the biplot, indicating intermediate values for all traits. Another group of effective species, including *O. cornuta, A. limata*, *Eucera nigrilabris* and *Bombus terrestris* were associated with large body size and high hair density. Finally, two beetle species (*Tropinota squalida* and *Oxythyrea funesta)* were mostly associated with long visit duration. The only feature shared by all effective pollinators was a high proportion of top-working visits (Fig. 2.4). In fact, the least effective species, *A. mellifera* was, by far, the species with the lowest proportion of top-working visits.
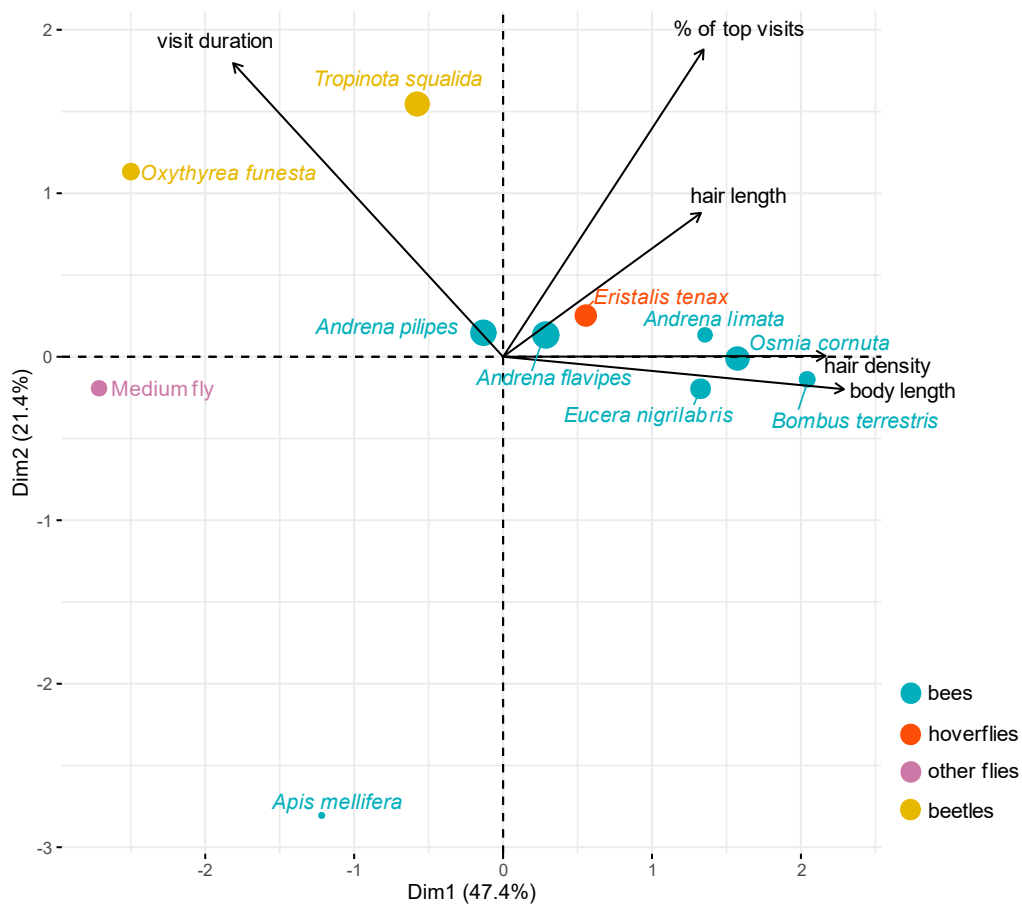
Figure 2.4: PCA ordering apple pollinator species based on morphological and behavioural traits potentially associated with pollination effectiveness. Dot size indicates pollination effectiveness (mean number of pollen grains deposited on the stigmas of single-visit flowers).

2.4-Discussion

The first objective of our study was to establish which pollinator traits were associated with pollination effectiveness in an open bowl-shaped flower.

Flower handling behaviour was the trait most strongly associated with pollination effectiveness. In fact, this was the only trait shared by all highly effective pollinators, which were all top-workers. This result is not surprising. Previous studies have shown that side-workers rarely contact the stigmas of fruit tree flowers, thus precluding pollen deposition (Bosch & Blas 1994; Thomson & Goodell 2001; Park *et al.* 2016). In honey bees, foragers that collect only nectar typically work the flowers from the side, whereas pollen collectors are top workers (Free 1960; Bosch & Blas 1994; Vicens & Bosch 2000a; Monzón, Bosch, & Retana 2004). However, this association between resource sought and flower handling behaviour does not apply to other pollinators, which consistently work the flowers from the top even when they only collect nectar (Bosch & Blas 1994; Vicens & Bosch 2000a; Thomson & Goodell 2001; Monzón, Bosch, & Retana 2004; Park *et al.* 2016). In fact, some studies have found no differences in pollination effectiveness between nectar and pollen foragers or even have found nectar foragers to be more effective (Wilson & Thomson 1991; Goodell & Thomson 2007)**.** Other flower types (e.g. smaller flowers), may allow less variability in flower handling behaviour thus precluding the relationship between this trait and pollination effectiveness (Thomson & Goodell 2001; Zych *et al.* 2013; Andrikopoulos & Cane 2018).

Visit duration was a second trait strongly associated with pollination effectiveness. Other studies have also found that visit duration enhances the probability of stigma contact and the amount of pollen transferred (Conner, Davis, & Rush 1995; Phillips *et al.* 2018). However, long visits do not result in higher pollination effectiveness unless contact with the reproductive organs of the flower is ensured (King, Ballantyne, & Willmer 2013; Zych *et al.* 2013). For example, *Bombus* spp. are able to extract nectar of *Brassica rapa* without contacting flower reproductive organs because their tongue is longer than the corolla tube, thus precluding any relationship between visit duration and pollen deposition (Goodell & Thomson 2007).

Body size was the third trait associated with pollination effectiveness. Large body size has been consistently associated with pollination effectiveness (Kandori 2002; Willmer & Finlayson 2014), and this relationship has again been attributed to a higher probability of contact with the flower reproductive organs (Thomson & Goodell 2001; Willmer & Finlayson 2014). However, as with visit duration, the effect of body size on pollen deposition is dependent on visit legitimacy (contact with the flower reproductive organs of the flower), as reported for protandrous flowers (Koski *et al.* 2018).

Hairiness did not emerge as a strong determinant of pollinator effectiveness in our study. In principle, hairier pollinators are likely to carry larger amounts of pollen on their body, and this relationship has been reported in some studies (Stavert *et al.* 2016; Phillips *et al.* 2018). However, the amount of pollen carried by a pollinator is not a direct measure of stigmatic pollen deposition (Herrera 1987; Inouye *et al.* 1994; Ne'Eman *et al.* 2010) and has been found not to be a reliable proxy of pollination effectiveness (Adler

& Irwin 2006; Zych *et al.* 2013). Nonetheless, two studies working on *Brassica napus* (Stavert *et al.* 2016; Phillips *et al.* 2018) did find a positive correlation between hairiness and pollination effectiveness, although body size had greater effect (Phillips *et al.* 2018). As with the above discussed traits, the effect of hairiness on pollen deposition may be modulated by other traits, such as flower handling behaviour and visit duration, and may be dependent on flower morphology. These results underscore the need to simultaneously analyse various morphological and behavioural traits and to account for potential correlation between traits (Young, Dunning, & von Hasseln 2007; Phillips *et al.* 2018; Roquer-Beni *et al.* 2020a).

Our second objective was to compare apple pollinator species in terms of pollination effectiveness and to establish whether good pollinators share similar traits or not. Solitary bees (*Andrena, Osmia, Eucera*) were amongst the most effective apple pollinators species. The high pollination effectiveness of various *Osmia* (Maeta & Kitamura 1981; Bosch & Blas 1994; Vicens & Bosch 2000a; Monzón, Bosch, & Retana 2004; Sheffield 2014; Eeraerts *et al.* 2020), and *Andrena* species (Larsson 2005; Zych *et al.* 2013; Mackenzie & Canada 2015; Park *et al.* 2016) on fruit trees has been well established. To our knowledge, information on *Eucera* species was hitherto missing.

By contrast, the honey bee *A. mellifera* was the most ineffective pollinator in our study. This species showed, by far, the lowest percentage of top-working visits (37.9 %; compared to 96.2 - 100 % in the rest of species investigated), resulting in a high proportion of illegitimate visits (30.5 %). Low pollination effectiveness by honey bees has been reported in various orchard crops including almonds (Bosch & Blas 1994), apples (Vicens & Bosch 2000a), pears (Monzón, Bosch, & Retana 2004), peaches (Zhang *et al.* 2015), and cherries (Eeraerts *et al.* 2020). As mentioned, top-working is associated with pollen collection in honey bees (Free 1960; Robinson 1979; Bosch & Blas 1994). For this reason, when introducing honey bee hives to improve orchard pollination, it is essential to use colonies with large amounts of brood so as to enhance pollen collection (Free 1993).

Another social bee species, the bumblebee *B. terrestris*, showed intermediate values of pollination effectiveness. Owing to their large size, one would expect bumblebees to be effective pollinators. However, bumblebees were also characterized by the short duration of their flower visits (mean ± SE: 3.4 ± 0.4 sec; compared to 12.8 ± 1.1 in solitary bee species). Other studies have also found *Bombus* spp. to conduct shorter visits (Martins, Gonzalez, & Lechowicz 2014; Park *et al.* 2016; Miñarro & García 2018a) and to be less effective pollinators than solitary bees (Javorek, Mackenzie, & Kloet 2002; Eeraerts *et al.* 2020).

Bee species have traditionally been considered the most effective pollinators of apple flowers. However, to our knowledge, ours is the first study measuring single-visit pollen deposition in apple by both bee and non-bee taxa. We found that the hoverfly *Eristalis tenax* and the beetle *Tropinota squalida* were more effective pollinators than some bees. With intermediate body size and visit duration, *E. tenax* shared similar traits with *Andrena* spp. *E. tenax* has been reported to be a good pollinator of other crops (Solomon & Kendall 1970; Rader *et al.* 2009). *T. squalida*, on the other hand was characterized by long visit duration (31.8 ± 6.8 sec), a feature common to other beetle pollinators (Ajerrar

et al. 2020). Scarab beetles have sometimes been found to damage flowers through consumption of anthers and other flower parts (Proctor *et al.* 1996). We did not observe this kind of behaviour in our study.

Our results demonstrate that pollination effectiveness in a disc-bowl shaped open flower is not dependent on a single trait but on a variety of behavioural and morphological traits (Phillips *et al.* 2018). All effective pollinators were top-workers, but otherwise did not necessarily share similar traits. Some pollinators were effective owing to their large body size, others to the long duration of their visits and others to intermediate values of both traits. In other words, there are different ways to be a good pollinator. Our results can be useful to predict the effectiveness of pollinators on wild or cultivated actinomorphic flowers. This predictive capacity can be used to improve the management of pollination services and to select candidate pollinator species for entomophilous crops.

3

Management-dependent effects of pollinator functional diversity on apple pollination services: a response-effect trait approach

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ABSTRACT

Functional traits mediate the response of communities to disturbances (response traits) and their contribution to ecosystem function (effect traits). Therefore, to predict how environmental disturbances influence ecosystem function requires a dual approach including both types of traits. Here, we use a response-effect trait framework to understand how local and landscape features affect pollination services in apple orchards. Our objectives are: 1) to establish whether pollination services are dependent on specific pollinator functional traits or rather on functional diversity; 2) to establish whether the relationship between pollinator functional composition and pollination service is dependent on orchard management; 3) to establish whether functional traits that affect pollination service overlap with traits that determine pollinator responses to changes in agricultural systems.

We worked in 110 apple orchards differing in management intensity (HI: high-input *vs.* LI: low-input), local factors (flower diversity, agri-environmental structures) and landscape features, including orchard cover and cover of pollinator-friendly habitats (henceforth PFH). We measured pollinator visitation rates and ten pollinator traits with which we calculated functional composition metrics. We also measured initial fruit set as a proxy of pollination service. We used a model selection approach.

Some pollinator traits (body size and hairiness) were negatively affected by orchard cover and positively by PFH cover. Bee functional diversity decreased with HI management and increased orchard cover. Pollination service was not associated to any particular trait. By contrast, pollination service increased with pollinator functional diversity, but only in LI orchards. As a result, LI orchards with high pollinator functional diversity reached levels of pollination service similar to those of HI orchards.

The relationship between response and effect traits (response-effect framework) is mediated by functional diversity rather than specific functional traits. Functional diversity enables pollinator communities to better respond to management and landscape intensity and to increase pollination function through complementarity. Our results have important implications for EU agricultural policies encouraging LI management. Enhancing pollinator functional diversity in LI orchards is a good strategy to promote biodiversity without compromising the provision of pollination services.

3.1- Introduction

The Earth is losing biodiversity at unprecedented rates (Dirzo *et al.* 2014; IPBES 2016) and there is a growing concern that these declines are threatening ecosystem functioning and services (Hooper *et al.* 2012; García *et al.* 2018). One endangered ecosystem service is animal pollination, crucial for fruit production and human nutrition (Klein *et al.* 2007; Brittain *et al.* 2014). At a time when the demand for food production is increasing (FAO 2017), bee diversity is experiencing strong declines in Europe and North America (e.g., Biesmeijer 2006; Bartomeus *et al.* 2013). These declines have been attributed to multiple causes, but there is a general consensus that agricultural intensification is one of the main drivers (IPBES 2016).

Environmental disturbances such as agricultural intensification can alter ecosystem function through changes in community functional composition (Larsen, Williams, & Kremen 2005; McGill *et al.* 2006). Species have traits that affect their ability to cope with environmental changes (response traits) and traits contributing to a specific function such as pollination (effect traits). The degree of overlap between response and effect traits will determine the magnitude of the effect of a disturbance on ecosystem functioning (Suding *et al.* 2008; Schleuning, Fründ, & García 2015). Thus, a response-effect trait framework is necessary to fully understand how specific drivers may affect specific ecosystem functions (Lavorel & Garnier 2002; Naeem & Wright 2003; Suding *et al.* 2008).

At the community level the response to environmental changes and the maintenance of ecosystem functioning, may depend on of the identity and abundance of specific functional traits (i.e. functional identity), trait diversity (i.e. functional diversity) or both (Leps *et al.* 2006; Moretti *et al.* 2009). While functional identity informs about the dominant traits in a community, functional diversity provides a measure of trait heterogeneity among species. A response-effect trait framework should therefore incorporate these two complementary measures (Ricotta & Moretti 2011).

Some studies have addressed the response of pollinator functional composition to agricultural intensification (Williams *et al.* 2010; Rader *et al.* 2014; De Palma *et al.* 2015; Forrest *et al.* 2015; Geslin *et al.* 2016) and others have addressed the effects of functional composition on pollination service (Hoehn *et al.* 2008; Gagic *et al.* 2015; Woodcock *et al.* 2019). However, studies analysing both processes simultaneously remain scarce (Klein *et al.* 2008; Bartomeus *et al.* 2018).

Agricultural intensification affects pollinators through landscape simplification, including loss of and isolation from natural and semi-natural habitats, leading to reductions of feeding resources (Roulston & Goodell 2011) and nesting substrates (Shuler, Roulston, & Farris 2005). In addition, the increased use of pesticides associated to intensive agriculture at local and landscape scales (Potts *et al.* 2010) has direct negative effects on pollinator fitness and survival (Woodcock *et al.* 2017; Sgolastra *et al.* 2018). Agri-environmental measures, both at the local and landscape scales, aiming to revert these effects and enhance on-farm biodiversity, have been promoted in the European Union since the late 1980s (Primdahl *et al.* 2003). These measures include

reducing pesticide use, preserving historical land-uses (e.g. unmanaged field margins, pastures and semi-natural grasslands) and promoting agri-environmental structures (hereafter AE structures) such as hedgerows and buffer strips to enhance non-cropping areas and to increase connectivity to natural and semi-natural habitats (Ekroos *et al.* 2016). The effects of agri-environmental measures on pollinator richness and abundance have been widely studied (Scheper *et al.* 2013; Marja *et al.* 2019) but much less is known about their effectiveness on the maintenance and promotion of pollinator functional composition.

Pollinators will respond to agricultural changes depending on their response traits. Species mobility, feeding and nesting requirements and physiological tolerance, among others, can explain pollinator sensitivity to disturbances (Rader *et al.* 2014; De Palma *et al.* 2015; Forrest *et al.* 2015). For example, large bee species may be better suited to find floral resources in disturbed habitats compared to small species (Klein *et al.* 2008; Jauker *et al.* 2013) but they may also have higher levels of exposure to pesticides (Brittain & Potts 2011). Although no general patterns have been found between single trait identity and responses to environmental changes (Bommarco *et al.* 2010; Bartomeus *et al.* 2018), there is evidence that disturbances such as landscape intensification act as filters of specific traits causing decreases in pollinator functional diversity (Forrest *et al.* 2015; Geslin *et al.* 2016). Functional trait diversity is crucial, as it allows for a variety of responses to disturbances over space and time (Mori, Furukawa, & Sasaki 2013).

As for effect traits, functional composition is suggested to better predict pollination function than taxonomic composition (Gagic *et al.* 2015). Some pollinator traits such as body size, flower-handling behaviour and hairiness have been associated with pollination success (Vicens & Bosch 2000a; Stavert *et al.* 2016; Phillips *et al.* 2018; Roquer-Beni *et al.* 2020c). In addition, according the complementarity hypothesis (Tilman 2001; Díaz & Cabido 2001; Fontaine *et al.* 2006), communities with high functional diversity, with low overlap in trait distribution across space and time, should be better suited to provide pollination services under a variety of environmental scenarios (Blüthgen & Klein 2011; Albrecht *et al.* 2012; Brittain, Kremen, & Klein 2013; Woodcock *et al.* 2019).

In this study we measure functional identity and diversity of apple pollinator assemblages in 110 orchards differing in management and in local and landscape features in four European apple growing regions. Apples (*Malus domestica* Borkh) are one of the most important crops in Europe covering 473,500 ha (EUROSTAT 2017) and are highly-dependent on pollination to achieve good levels of production and fruit quality (Martins, Gonzalez, & Lechowicz 2014; Garratt *et al.* 2014a). We then use a response-effect trait approach to determine how local and landscape features affect pollination service through changes in functional composition. Our objectives are: 1) to establish whether pollination services are dependent on specific pollinator functional traits or rather on functional diversity; 2) to establish whether the relationship between pollinator functional composition and pollination service is dependent on orchard management; 3) to establish whether functional traits that affect pollination service overlap with traits that determine pollinator responses to changes in agricultural systems.

3.2- Materials and Methods

3.2.1- Study sites

The study was conducted in 2015 in 110 commercial apple orchards from four European apple-growing regions: Skåne in Sweden (SWE), Baden-Württemberg in Germany (GER), and Asturias (AST) and Catalonia (CAT) in Spain (Fig. A4.1, see Happe *et al.* 2019, Samnegård *et al.* 2018, and Miñarro & García 2018b for details on the study orchards). Minimum distance between orchards was 0.3 km in Sweden, 2 km in Germany, 1.2 km in Asturias and 1 km in Catalonia (see Table A4.1 for orchard characteristics).

In each region, orchards were selected to encompass a range of local and landscape features (Table A4.1). In SWE, GER and CAT half of the orchards followed IOBC guidelines (Cross 2002) for integrated pest management (IPM) (see Happe *et al.* 2019). These orchards were considered high-input (henceforth HI) orchards. The rest of orchards in SWE, GER and CAT and all orchards in AST were either certified organic or followed close-to-organic guidelines (with very low levels of synthetic inputs) and were grouped into a low-input orchard category (LI).

3.2.2- Local features

In each orchard, we established two 20-m transects in which we conducted pollinator counts (see below). To assess local features, we used aerial photographs combined with on-site inspection to measure the area occupied by AE structures within a 20 m-buffer from the first transect trees. AE structures included hedgerows (trees and shrubs), forests (forest edges, riparian forests, tree plantations), fallow lands, orchard meadows, and semi-natural grasslands (including terraced field margins and embankments) (Table A4.1). During apple bloom, we estimated flower cover and diversity of entomophilous plant species within and around each orchard. These measures were taken using 12-14 gridded quadrats (1 m^2 in SWE, GER and CAT; 0.25 m^2 in AST) equally distributed between the inside and the surroundings of the orchard. Flower diversity in each orchard was calculated with the Shannon Diversity Index using mean cover of each flower species from all the quadrats.

3.2.3- Landscape features

We used ArcView 10.3.1, MiraMon v8.2e and R 3.2.3 (R Core Team. 2016) together with digital databases and maps (see Table A4.1) to measure the area covered by different habitat types within 1-km-buffer from the pollinator survey trees. From these measures we calculated two landscape variables. First, the percent area of "pollinator-friendly-habitat", defined as habitats free of pesticides and hosting abundant floral resources and potential nesting substrates for bees. These habitats (henceforth PFH) included shrublands, orchard meadows, semi-natural grasslands, abandoned orchards and hedgerows. Second, the area occupied by orchards, as a proxy of agricultural landscape homogenization (Table A4.1).

3.2.4- Pollinator surveys

Pollinator surveys were conducted during apple bloom (April-May). In SWE, GER and CAT, observers walked along two 20-m transects (mean ± SE: 35 ± 1.3 trees per row) starting at one end of the orchard and recorded all apple visitors contacting reproductive parts of the apple flowers. Transect walks lasted five minutes and were repeated three times during the day, amounting to 30 minutes of pollinator survey per orchard. In AST, observers surveyed a canopy area of ca. 1-m diameter during 5 minutes in 5 trees per orchard three times during the day for a total of 75 minutes of survey per orchard. Pollinators were visually identified in the field. Some specimens were captured for later identification in the laboratory.

From these surveys, we calculated abundance of each pollinator species (number of observed individuals visiting flowers) and total pollinator visitation rate per orchard (number of visits observed per 100 flowers in 5 minutes).

3.2.5. Pollination service

At the onset of bloom, we marked 2 branches per tree on each of 6-7 trees per orchard and counted the number of flower buds (1200-1300 flower buds per orchard). A few weeks after petal fall (apple phenological stage 71 BBCH; Meier 1997) we assessed initial fruit set as the percentage of marked flowers that developed into a fruitlet. Initial fruit set is a better measure of pollination service than fruit set at harvest because it is not influenced by post-pollination factors such as natural and/or artificially-induced fruit abortion. Initial fruit set data were not available for GER.

3.2.6- Pollinator traits

We selected pollinator traits that, based on our knowledge and/or previous studies (Table 3.1), could either influence the response to environmental conditions (response traits, hereafter R) and/or pollination service (effect traits, hereafter E), or both (hereafter R-E). All pollinator species recorded in the surveys (99 species, Table A4.2) were characterized with three functional traits: body length (R-E), hairiness (R-E) and larval diet (R-E). Because bees are the most frequent and effective apple pollinators (Vicens & Bosch 2000b; Garratt *et al.* 2016, Roquer-Beni *et al.* 2020c), we measured eight traits in this group (45 species): intertegular-span (ITS, a proxy of body size; R-E), hairiness (R-E), proboscis length (E), forewing aspect ratio (WAR, ratio between maximum length and width; R), sociality (R), voltinism (R), nesting substrate (R) and pollen transportation structure (E) (see Table 3.1 for details on each functional trait).

Quantitative traits were measured on pinned specimens and categorical traits were based on literature records and author's expert knowledge (see Table 3.1 for methods and sample sizes). We worked with a single mean value per trait and species. We tested Pearson correlations between each pair of numerical functional traits (Table A4.3). In bees, proboscis length was highly correlated with ITS ($r > 0.7$). Thus, we only used ITS in the analyses (Table A4.3).

3.2.7- Functional composition metrics

For each orchard, we calculated two complementary measures of community functional composition. First, the "community-weighted mean" (CWM) of each trait, as a measure of functional identity (Garnier *et al.* 2004). CWM of numerical traits was calculated as the mean value of each species trait weighted by the relative abundance of each species in the orchard (Ricotta & Moretti 2011). CWM of categorical traits was calculated as the proportion of pollinator individuals in the community within each trait category. Second, the Rao quadratic diversity index (RaoQ) of all traits combined as a measure of trait dissimilarity and functional diversity (Rao 1982; Ricotta 2005; Leps *et al.* 2006). RaoQ measures the dissimilarity between two randomly selected individuals and calculates the sum of weighted abundance dissimilarity between each pair of species. RaoQ can be used to compute functional diversity for numerical or categorical traits and is relatively unaffected by species richness (Leps *et al.* 2006; Arnan *et al.* 2013; Fornoff *et al.* 2017).

All indexes were calculated separately for all pollinators and only for bees. To overcome potential effects of highly correlated traits in the RaoQ calculations, we initially conducted principal coordinate analyses (PCoA) on the standardized trait data (Devictor *et al.* 2010; Arnan, Cerdá, & Retana 2017). The axes obtained in the PCoA were used to build an Euclidean distance matrix that we used for the RaoQ calculations.

Honey bees were excluded in response trait analyses because their presence was mostly (or solely) attributable to managed colonies in all four regions. Conversely, honey bees were included in effect trait analyses because they affect apple pollination (Vicens & Bosch 2000a; Garratt *et al.* 2016; Russo *et al.* 2017). Measures of functional composition were conducted with the dbFD and functomp functions from FD library (Laliberté *et al.* 2010) with R .

3.2.8- Statistical analysis

All statistical analyses were conducted with R 3.2.3.

Response traits

To assess the response of pollinator functional composition to local and landscape features, we performed separate linear mixed-effect models (LMMs) for each functional composition metric (CWM of each trait, and RaoQ of all traits combined). This was done for all pollinator species (body length, hairiness, larval diet) and for bee species only (ITS, hairiness, WAR, sociality, voltinism, nesting substrate and pollen transportation structure). Full models included three local variables (orchard management, AE structure cover, flower diversity) and two landscape variables (orchard cover, PFH cover) as fixed effects, and region as a random effect. Numerical explanatory variables were not highly correlated ($r < 0.7$, Table A4.4) and the full model VIF was < 5.

Effect traits

To analyze the effect of functional traits on pollination service, we conducted two LMMs with initial fruit set as the response variable and functional composition metrics (CWM of hairiness and pollinivorous larvae or RaoQ) as predictor variables. We also included

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two other variables that could affect initial fruit set: overall pollinator visitation rate and orchard management. To distinguish between trait identity and trait diversity effects, CWM and RaoQ were tested in two separate models. To establish whether the relationship between functional composition and pollination services can be mediated by management, models also included the interaction between management and the above-mentioned functional composition metrics as fixed effects. Apple variety was included as a random effect because different varieties may be differently dependent on pollination service for fruit set (Garratt *et al.* 2016). Region was again included as a random effect. We checked for correlation between pairs of predictors. Because some predictors were correlated, we excluded one variable of the pair with the strongest correlation in the full model until VIF was < 5. This procedure excluded the CWM of body length and of proportion of insectivorous larvae (Table A4.5). Because all pollinators potentially contribute to fruit set, these analyses included the managed honey bee and were not conducted with only bee species.

We conducted a model selection procedure, testing all possible explanatory variable combinations through a multi-model inference approach (Anderson & Burnham 2004) with the dredge function of MuMin package (Barton & Barton 2019). We selected the best models based on AICc values using maximum likelihood criteria. Models with ΔAICc< 2 were considered equal to the best model. When the null model was one of the selected models, no variable was considered to be a good predictor of the response variable. Following model selection, we used a model averaging approach (with averaged variable coefficients) based on AICc to assign a relative importance to each variable (hereafter, *Σwi*). Relative importance of a variable (ranging from 0 to 1) was calculated as the sum of the Akaike weights of this variable over all the selected models including this variable (Anderson & Burnham 2004). To be conservative, explanatory variables were only considered important if their confidence intervals did not overlap with zero and their relative importance was greater than 0.50. Finally, we calculated a likelihood-ratio-based R^2 of the best models as a measure of explanatory power.

The normality and homoscedasticity assumptions of all models was tested by visually analyzing the distribution of residuals of each model. Response variables were transformed (square root or log-transformed) as needed. Numerical explanatory variables were standardized to facilitate comparison across variables. To detect model outliers we calculated Cooks' distance and excluded sites with a Cooks' distance > 4/N (Cook 1977; Fox 1991) The exclusion of outliers provided better model adjustments but trends remained similar (see Table A4.6-A4.7 for results without outlier exclusion).

Table 3.1: Description of the functional traits studied.

Trait	Trait Type (Q: quantitative; C: categorical; R: response; E: effect)		Units/ Categories (n species)	Trait Function	Procedure/Source (sample size: mean±SE specimens per species)
Body length	Q	R-E	mm	Body length is strongly correlated to body mass in various insect taxa (Rogers, Hinds, & Buschbom 1976). Body size has been associated with foraging range (Greenleaf *et al.* 2007; Klein *et al.* 2008), thermoregulation (Stone & Willmer 1989), ability to fly at low temperatures (Stone 1993), phenology (Osorio-Canadas *et al.* 2016) and pollination effectiveness (Willmer & Finlayson 2014; Roquer-Beni *et al.* 2020c) , among other functions.	Body length was measured from the tip of the head to the tip of the abdomen, excluding body appendages (legs, wings, antennae) (5.94 ± 0.46).
Hairiness	Q	R-E	index	Hairiness is associated with thermoregulation (Heinrich 1993), ability to fly at low temperatures (Peters *et al.* 2016), pollen collection (Thorp 2000) and pollination effectiveness (Stavert *et al.* 2016; Phillips *et al.* 2018).	We measured hair density and length of the dorsal part of the mesothorax using a stereomicroscope with a micrometer at 20-80X. Hairiness is correlated across various body parts (Roquer-Beni *et al.* 2020a). We calculated a hairiness index: hair density x hair length (Roquer-Beni *et al.* 2020a) (3.04 ± 0.12) (all bee specimens were females).
Larval diet	C	R-E	Pollinivorous (45), insectivorous (21), aquatic-saprophagous (12) saprophagous (8), phytophagous (13)	In addition to pollen and nectar, pollinators require appropriate larval food resources. Larval diet differs among pollinator groups, including pollinivorous (bees); insectivorous (predatory hoverflies and wasps); saprophagous (flies); aquatic-saprophagous (some hoverflies); and phytophagous (lepidopterans). Environmental disturbances can alter food availability (Holzschuh, Steffan-Dewenter, & Tscharntke 2010). Pollinators with pollinivorous larvae show a greater level of dependency on flowers, with consequences on visitation rates and pollination service.	Author's expert knowledge
Intertegular span (ITS)	Q	R-E	mm	ITS is a good proxy of dry weight across bee genera (Cane 1987).	We measured the distance between the two tegulae using a stereomicroscope with a micrometer at 35X. (7.66 ± 0.85 female specimens).

Trait	Trait Type (Q: quantitative; C: categorical; R: response; E: effect)		Units/ Categories (n species)	Trait Function	Procedure/Source (sample size: mean±SE specimens per species)
Wing aspect ratio (WAR)	Q	R	index	Wing aspect ratio (maximum wing length / maximum wing width), a measure of wing shape. It has been associated with flying performance (speed and acceleration capacity) in insects (Berwaerts, Van Dyck, & Aerts 2002; Hassall 2015).	We measured length and width of the forewing using a stereomicroscope with a micrometer at 35 X. (6.80 ± 0.79 female specimens).
Proboscis length	Q	E	mm	Proboscis length has been associated with flower choice (Peat, Tucker, & Goulson 2005; Goulson, Lye, & Darvill 2008) and pollination effectiveness (Inouye 1980; Harder 1983; Stout, Allen, & Goulson 2000).	We measured the length of the extended glossa plus the prementum using a stereomicroscope with a micrometer at 35 X. (3.18 ± 0.45 female specimens).
Pollen transportation structure	C	E	leg scopa (32), ventral scopa (4), corbicula (8), crop (1)	Pollen transportation structures may influence pollen collecting behaviour, flower specialization and pollen transfer (Parker *et al.* 2015; Portman, Orr, & Griswold 2019).	Author's expert knowledge, Michener (2000)
Nesting substrate	C	R	above ground (9), below ground (36)	Landscape intensification may alter the availability of nesting sites and substrates, with negative consequences for ground nesters (Williams *et al.* 2010) as well as above-ground nesters (Forrest *et al.* 2015).	Bees, Wasps & Ants Recording Society (BWARS, www.bwars.com), Westrich (1989), Westrich (2018); Michez, D.; Rasmont, P.; Terzo, M.; Vereecken (2019)
Voltinism	C	R	univoltine (25), multivoltine (20)	Univoltine species have been suggested to be particularly vulnerable to disturbances (Brittain & Potts 2011). Multivoltine species require flower resources for longer periods, and thus may be more vulnerable in agricultural landscapes with intense but short flowering periods (Roulston & Goodell 2011).	Bees, Wasps & Ants Recording Society (BWARS, www.bwars.com), Westrich (1989), Westrich (2018); Michez, D.; Rasmont, P.; Terzo, M.; Vereecken (2019)
Sociality (SO)	C	R	social (15), solitary (30)	Solitary bees have more restrictive habitat requirements, smaller foraging ranges and lower reproductive capacity. Consequently, they have been found to be more susceptible to landscape intensification (Klein *et al.* 2008; De Palma *et al.* 2015). On the other hand, social bees need resources for continuous brood production, which may be scarce in agricultural landscapes (Williams *et al.* 2010).	Bees, Wasps & Ants Recording Society (BWARS, www.bwars.com), Westrich (1989), Westrich (2018); Michez, D.; Rasmont, P.; Terzo, M.; Vereecken (2019) Cleptoparasitic species were classified as their hosts.

3.3- Results

We recorded 8,246 pollinator individuals visiting apple flowers. Most pollinators were honey bees (77.7 %) followed by wild bees (9.1 %), hoverflies (5.8 %), other flies (6.1 %), beetles (1 %) and others (0.4 %) (Table A4.2). Honey bee visitation rate was similar in LI and HI orchards (LMM, estimate β = 0.08, P = 0.24), but overall pollinator visitation rate was higher in LI orchards (β = 0.15, P < 0.05) (Table A4.8).

3.3.1- Response traits

At the local scale, AE structure cover favoured pollinators with insectivorous larvae (Table 3.2). There were no significant effects of local features, landscape features or their interactions on pollinator functional diversity (RaoQ). Landscape orchard cover was negatively associated with the CWM of body length and hairiness (Table 3.2). On the other hand, PFH cover was positively associated with these same traits, and additionally with the proportion of pollinators with pollinivorous larvae.

When considering only bees, the best-fitted models for all CWM variables included the null model. Thus, we could not attribute any effect of local or landscape features to any specific bee trait (Table 3.2). By contrast, local and landscape features had important effects on the RaoQ, being negatively affected by landscape orchard cover (Fig. 3.1A) and enhanced by LI management (Fig. 3.1B).

3.3.2- Effect traits

Management was a good predictor of initial fruit set (Table 3.3). Models including CWM metrics showed that initial fruit was enhanced by HI management but was not affected by any CWM (Table 3.3). By contrast, models including RaoQ metrics revealed an interaction effect between functional diversity and management on initial fruit set (Fig. 3.2). This interaction arose because there was a positive effect of functional diversity on initial fruit set in LI orchards but not in HI orchards. In orchards with low functional diversity, initial fruit set was lower in LI, but in orchards with high functional diversity, initial fruit set was similar in the two types of management (Table 3.3). In other words, differences between LI and HI orchards in initial fruit set disappeared as pollinator functional diversity increased (Fig. 3.2).

Table 3.2: Statistical outputs of model averaging (average of best-fitted models; ΔAICc < 2) relating wild pollinator and wild bee functional composition descriptors (response variables) to local and landscape features (predictor variables). Response variables of models in which a null model was selected among the best-fitted model are not shown. Estimated coefficients, their 95% intervals (in parentheses) and relative importance (in brackets) are provided. Variables not appearing in the model average are indicated with "-". R^2m and R^2c are the range values of marginal and conditional R^2 of the best-fitted models, respectively. "Sites" indicates the number of orchards included in the model after removing outliers (see Table A4.6 for results without outlier exclusion). Significant terms (with confidence intervals not overlapping with zero) are in bold.

Response variable	Management*	Flower diversity	AE structure cover	% orchard cover	% Pollinator friendly habitat cover	R^2m	R^2c	Sites
ALL POLLINATORS								
CWM Body length	-	0.145 [0.31] (-0.201, 0.491)	-	**-0.683 [1] (-0.108, -0.288)**	**0.986 [1] (0.423,1.550)**	0.3	0.3	98
CWM Hairiness [a]	-	-	-0.397 [0.44] (-0.889, 0.095)	**-1.046 [1] (-1.627, -0.465)**	**0.676 [0.83] (0.054, 1.299)**	0.16-0.23	0.28-0.35	99
CWM Pollinivorous larvae	0.0264 [0.18] (-0.076, 0.129)	-	-	-0.031 [0.33] (-0.083, 0.021)	**0.154 [1] (0.073, 0.235)**	0.11-0.14	0.56-0.57	94
CWM Insectivorous larvae [a]	-0.026 [0.14] (-0.099, 0.047)	0.033 [0.84] (-0.000, 0.066)	**0.075 [1] (0.040, 0.110)**	0.023 [0.20] (-0.018, 0.063)	-0.017 [0.17] (-0.050, 0.017)	0.14-0.17	0.36-0.39	99
BEES								
RaoQ	**4.946 [1] (0.655, 9.236)**	-	-	**-3.478 [1] (-5.704, -1.252)**	1.657 [0.36] (-1.488, 4.802)	0.18-0.20	0.24-0.26	105

Data transformations: [a] Square-root; [b] Log (X+1)
*Low-Input is the reference level of management

Table 3.3: Statistical outputs of model averaging (average of best-fitted models; ΔAICc < 2) relating initial fruit set to management (low-input vs high-input), functional composition metrics, the interaction between management and functional composition metrics and pollinator visitation rate. The first model includes single-trait metrics (CWM: hairiness, pollinivorous larvae) and the second models includes functional diversity (multi-trait RaoQ). Estimated coefficients, their 95% intervals (in parentheses) and relative importance (in brackets) are provided. Variables not appearing in the model average are indicated with "-". R^2m and R^2c are the marginal and conditional R^2 range values of the best-fitted model, respectively. "Sites" indicates the number of orchards included in the model after removing outliers (see Table A4.7 for results without outlier exclusion). Significant terms (with confidence intervals not overlapping with zero) are in bold.

	ALL POLLINATORS								
Response variable	Management*	CWM hairiness	CWM pollinivorous	CWM hairiness $_x$ management	CWM pollinivorous $_x$ management	Visitation rate	R^2m	R^2c	Sites
Initial fruit set [a]	**-1.617 [1]** **(-2.304, -0.930)**	0.113 [0.20] (-0.251, 0.477)	-	-	-	0.154 [0.25] (-0.193, 0.500)	0.24-0.25	0.24-0.25	76
Response variable	Management*	RaoQ	RaoQ $_x$ management			Visitation rate	R^2m	R^2c	Sites
Initial fruit set [a]	**-1.580 [1]** **(-2.193, -0.966)**	-0.301 [0.64] (-0.821, 0.219)	**0.750 [0.64]** **(0.089, 1.409)**			-	0.27-0.32	0.27-0.32	76

Data transformations: [a] Square-root
*Low-Input is the reference level of management
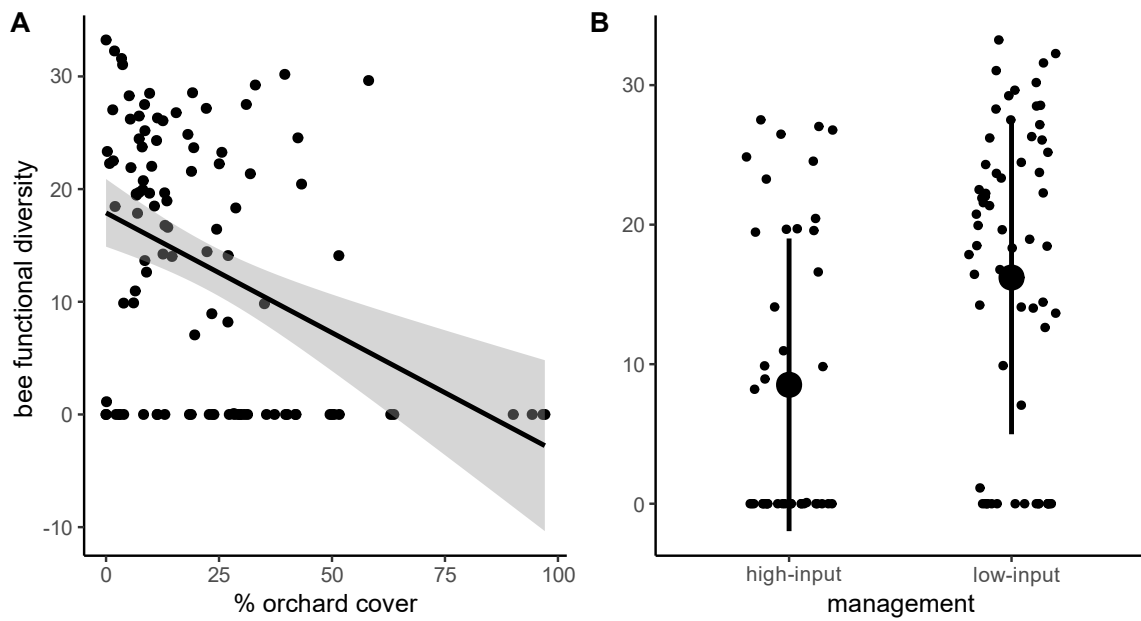
Figure 3.1: Effects of landscape orchard cover (A) and orchard management (high-input versus low-input) (B) on bee multi-trait functional diversity. Grey bands indicate 95% confidence intervals. Vertical bars indicate standard deviations.
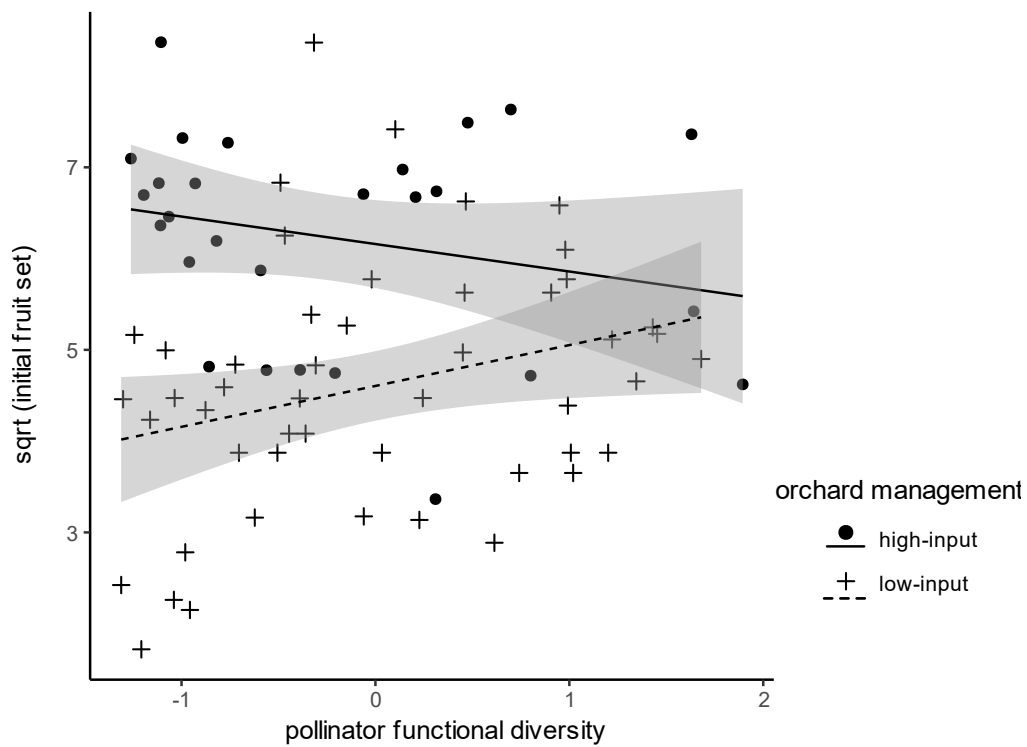
Figure 3.2: Effects of pollinator multi-trait diversity (including wild and managed pollinators) on initial fruit set (square-root transformed) in low-input and high-input apple orchards. Grey bands indicate 95% confidence intervals.

3.4- Discussion

The general aim of our study was to determine how local and landscape features affect pollination service through changes in functional composition in apple orchards. Our results show that bee functional diversity was enhanced by LI management and negatively affected by increased orchard cover at the landscape level. At the same time, pollinator functional diversity enhanced pollination service in LI (but not in HI) orchards. Our results suggest that pollinator functional complementarity is an important mechanism linking responses to agricultural intensification and contribution to pollination services in agricultural systems.

Local factors were important determinants of pollinator functional composition. AE structures enhanced the abundance of pollinators with insectivorous larval diet. AE structures provide insect prey for larvae of aphidophagous hoverflies and predatory wasps (Miñarro & Prida 2013; Gurr *et al.* 2017; Rodríguez-Gasol *et al.* 2019) Other studies have reported AE structures to benefit bees (Hannon & Sisk 2009; Carvalheiro *et al.* 2012; Blaauw & Isaacs 2014), which are pollinivorous larvae feeders. However, we found no effects on pollinivorous larvae suggesting that during apple bloom floral resources are not limiting for them.

LI management enhanced bee functional diversity. Various studies have shown positive effects of organic farming on bee abundance and taxonomic diversity, particularly in homogeneous landscapes, and these results were attributed to a reduced use of chemical inputs at a local scale (Holzschuh *et al.* 2007; Rundlöf, Nilsson, & Smith 2008; Carvalheiro *et al.* 2012; Kennedy *et al.* 2013; Forrest *et al.* 2015). However, as far as we know, effects of agricultural management on bee functional diversity have not been previously reported.

Landscape features also affected pollinator functional composition. Large pollinators were negatively affected by landscapes with high orchard cover but enhanced by increased PFH cover. The response of body size and other species traits to landscape intensification is controversial and appears to be context-dependent. Some studies have found smaller bee species to be more sensitive to landscape intensity and isolation from natural habitats (Klein *et al.* 2008; De Palma *et al.* 2015). However, other studies have found opposite trends (Larsen, Williams, & Kremen 2005; Bartomeus *et al.* 2013; Rader *et al.* 2014) or no clear patterns (Williams *et al.* 2010; Forrest *et al.* 2015; Bartomeus *et al.* 2018). Hairiness was affected by landscape features similarly to body size. We cannot think of any clear reason why hairier pollinators should be more abundant in natural and semi-natural habitats than in agricultural areas.

We also found that landscapes with high levels of PFH promoted the relative abundance of pollinators with pollinivorous larvae (bees). Natural and semi-natural habitats provide spatio-temporal stability to flower visitors (Klein 2009), through a widespread and continued accessibility to flower resources, especially before and after crop flowering period. These habitats also provide nesting resources and agrochemical-free refuge areas (Potts *et al.* 2005; Holzschuh, Steffan-Dewenter, & Tscharntke 2010). For these reasons, PFH promote the colonization and establishment of bee communities in

agricultural areas (Kremen *et al.* 2004; Klein *et al.* 2012). Bee functional diversity was not affected by PFH in our study, but we found that landscapes with high orchard cover negatively affected bee functional diversity. Bee functional diversity is known to be lower in farmland compared to natural habitats (Forrest *et al.* 2015, Hass *et al.* 2018). In addition to being exposed to higher levels of agrochemical inputs, orchard-dominated landscapes are characterized by landscape homogenisation and isolation from natural and semi natural habitats, thus hindering consistent spatio-temporal availability to flower and nesting resources (Marini *et al.* 2012). Landscape level initiatives supporting complementary resources are needed to promote pollinators in agroecosystems (Cole *et al.* 2020).

HI orchards had higher initial fruit set than LI orchards. Because overall pollinator visitation rates were higher in LI orchards and honey bee visitation rates were similar in the two types of orchards, the higher initial fruit set in HI orchards is best explained by non-pollinator factors. First, early fruit retention may be higher in HI orchards due to the use of chemical fertilizers and to a lower impact of pests and diseases compared to LI orchards (Ferree & Warrington 2003; Kirchmann *et al.* 2008; Samnegård *et al.* 2018). Second, to enhance the production of large fruits, apple crop load is often artificially reduced. In HI orchards, this reduction is accomplished through synthetic chemical thinning of young fruits (Ferree & Warrington 2003; Fallahi & Greene 2010). By contrast, because this practice is not allowed in organic management, LI orchards usually implement bloom thinning (either mechanical or with organic chemicals) (McArtney *et al.* 2006; Kon & Schupp 2018).

No specific traits emerged as significant determinants of pollination service. On the other hand, we found that pollinator functional diversity enhanced initial fruit set but, importantly, only in LI orchards. The positive effect of functional diversity on pollination services has been previously recognized (Hoehn *et al.* 2008; Martins, Gonzalez, & Lechowicz 2014; Woodcock *et al.* 2019), but ours is, as far as we know, the first study showing interactive effects between functional diversity and agricultural management on pollination services. Functionally-diverse pollinator communities may enhance pollination function through various complementarity mechanisms such as temporal variability (foraging at different times of the day or under different weather conditions) and spatial variability (foraging on different parts of the tree) (Blüthgen & Klein 2011). Our results show that, through the enhancement of pollinator functional diversity, LI orchards may reach levels of initial fruit set similar to those of HI orchards. Importantly, the positive effect of bee functional diversity on initial fruit set in LI orchards was detected despite a very strong background of honey bee visitation (see also Garibaldi *et al.* 2013; Pérez-Méndez *et al.* 2020).

Some pollinator traits responded to local and/or landscape factors but, as mentioned no specific traits influenced pollination services. In other words, pollination service could not be explained by sampling effects of dominant traits (Mokany, Ash, & Roxburgh 2008). However, pollinator functional diversity enhanced initial fruit set in LI orchards and bee functional diversity responded negatively to two important features linked to agricultural intensification, HI management and increased orchard cover. These results suggest that the response-effect framework applies better to integrative measures (multi-trait functional diversity) than to single traits (Peña et al. 2020). In sum, trait

diversity not only enables pollinator communities to respond better to landscape and management intensification but also leads to increased pollination function through complementarity. One of the main challenges of modern agriculture is to feed an increasing human population while protecting biodiversity (Godfray *et al.* 2010), and the preservation of landscapes and biodiversity is one of the specific objectives of the new European Common Agricultural Policy to be implemented in 2020 (European Comission 2019). Our results have important implications in this so-called post-CAP 2020 scenario. We show that high levels of ecosystem services can be reached in low-input farms so long as we maintain high levels of functional diversity. Consequently, efforts to promote biodiversity should target low-input rather than high-input farms. Ensuring high levels of productivity through the provision of ecosystem services such as pollination and biological control would be a good strategy to encourage the conversion of high-input into low-input farms.

Conclusions

Chapter 1

- We developed a standardized methodology to measure hairiness in pollinators. Our method has several advantages: 1) it provides a quantitative measure of hair length and hair density; 2) it is a non-invasive; 3) it can be applied to dead and live (anesthesized); 4) it accounts for hair loss due to aging or poor preservation; 5) measurements can be taken directly from the specimens rather than photographs and 6) it discriminates between two components of hairiness, which allows for a meaningful interpretation of the functional and evolutionary consequences of hairiness.
- Body size and hair length are positively correlated. Therefore, body size must be accounted for in studies measuring hairiness.
- Hair length and hair density are negatively (albeit weakly) correlated. Rather than indicative of a direct trade-off, this correlation can be explained through the relationship between these two variables and body size.
- We provide a standardized protocol that we hope will foster the inclusion of this important trait in insect data bases.
- Our methodology can be applied to studies on thermoregulation, responses to climate change and pollination effectiveness among others.

Chapter 2

- Pollinator effectiveness depended on flower handling behaviour (top visitors were more effective than side visitors), body size (larger pollinators were more effective) and visit duration (longer visits were more effective).
- Solitary bees (Andrena, Osmia, Eucera) were the most effective apple pollinators. By contrast, the honey bee *Apis mellifera* was the most ineffective pollinator.
- Pollination effectiveness in a disc-bowl shaped open flower is not dependent on a single trait but on a variety of behavioural and morphological traits.
- All effective pollinators were top-workers, but otherwise did not necessarily share similar traits. In other words, there are different ways to be a good pollinator.
- Our results can be useful to predict the effectiveness of pollinators, to improve the management of pollination services and to select candidate pollinator species for entomophilous crops.

Chapter 3

- Local and landscape features were important determinants of pollinator functional identity in apple orchards. Agri-environmental structures enhanced

pollinators with insectivorous larvae. Large and hairy pollinators were negatively affected by landscapes with high orchard cover and positively affected by landscapes with high pollinator-friendly habitat cover.

- Two important features linked to agriculture intensification, high-input management and percentage of orchard cover, negatively affected bee functional diversity.

- Pollination service was not associated to any particular trait. By contrast, pollination service increased with pollinator functional diversity, but only in low-input orchards. As a result, low-input orchards with high pollinator functional diversity reached levels of pollination service similar to those of high-input orchards.

- The relationship between response and effect traits (response-effect framework) was mediated by functional diversity rather than specific functional traits.

- Functional diversity enabled pollinator communities to better respond to management and landscape intensity and to increase pollination function through complementarity.

- Future EU agricultural policies should enhance pollinator functional diversity in low-input managed orchards to promote biodiversity without compromising the provision of pollination services.

Appendix 1

Protocol to measure hairiness in bees and other

insect pollinators

Protocol to measure hairiness in bees and other insect pollinators

This protocol follows the structure of the "Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits" (Moretti *et al.* 2017). We focus on insect pollinators, but our methodology can also be applied to other groups of arthropods.

Definition and relevance

Insect hairiness (pilosity) is the collective presence of hairs, scales, seta or bristles growing from the cuticle (Moretti *et al.* 2017). Hairiness creates an insulation layer that mitigates the convective loss of heat generated by the vibration of thoracic muscles, thus playing an essential role in thermoregulation (May 1979; Heinrich 1993). Some studies have found a negative relationship between bee hair length and ambient temperature (Peat *et al.* 2005; Peters *et al.* 2016), suggesting that hairiness acts as a response trait to climate. Hairiness can also be considered an effect trait involved in pollen collection and transfer (Müller 1995; Thorp 2000; Amador *et al.* 2017), potentially affecting pollination effectiveness (Stavert *et al.* 2016; Phillips *et al.* 2018; Woodcock *et al.* 2019). Hairiness may also be involved in antipredator strategies. In caterpillars and moths, hairs have been shown to provide mechanical and sensory defence against predators and parasites (Lindstedt, Lindström, & Mappes 2008; Castellanos *et al.* 2011; Sugiura & Yamazaki 2014; Shen *et al.* 2018).

Technical support

Measurements should be taken with a stereomicroscope with a magnification range of 20-80x and a camera connected to a computer equipped with a software module that allows taking length and surface measurements directly on live images in real units. We used a LEICA M165C and the live measurement module from Leica Microsystems. Alternatively, other stereomicroscopes and software packages could be used (e.g. free software *ImageJ*). Measurements can also be taken from microscope pictures (instead of live images) but this is a more time-consuming alternative. If real units are not provided by the software, then the level of magnification must be accounted for.

Pre-treatment of the specimens

The method can only be applied to dry specimens. Apart from this, no special pre-treatment is necessary. The method works well even with specimens that have lost hair due to aging or poor manipulation, as well as with specimens with clumps of hair (e.g. specimens initially kept in alcohol that have not been properly dried). The method can also be applied to anesthesized live specimens.

Body parts

Hairiness is best measured in body parts with flat surfaces, but the method can be applied to any body part. Hairiness may strongly differ among body parts. The target body part(s) should be decided based on the objectives of the study. A study on pollination effectiveness should target body parts directly involved with the uptake and transfer of pollen. A study on thermoregulation should emphasize body parts involved in heat generation (thorax) and dissipation (abdomen, head, appendages).

We found hairiness to be correlated across the face, the dorsal surface of the thorax and the ventral surface of the thorax.

Measurement of hairiness components

Hairiness can be decomposed in hair density and hair length (Moretti et al. 2017).

Hair density

Counting all hairs in an entire body part is unpractical. We found that averaging hair counts of three areas of ca. 0.1 mm² each provides a good measure of hair density for a given body part. The area sampled (and if needed the area of the entire body part) can be measured with the appropriate tool in the software.

Counting hairs can be complicated when hair density is high and when hairs are long and form clumps due to manipulation during capture and/or preservation. In these cases, it is easier to count the micropores of the cuticle in which hairs are inserted (Fig. A1.1). Because insect cuticles may display a large variety of microsculpture patterns, including several types of punctuations, it is very important to spend some time to identify the correct type of micropores before starting the counts. Counting micropores has the added advantage that it provides a measure of original hairiness even in specimens that have lost hair due to aging or poor manipulation (e.g. bee-flies typically lose a lot of hair during manipulation). In some cases, it may be practical to rub the cuticle of the insect with an insect pin to detach hairs, thus facilitating micropore counts. If instead of original hairiness a measure of actual hairiness is desirable, then only micropores with standing hairs should be counted.

Sometimes hairiness patterns are distinctly non-uniform across a body part, notably in the face. In these cases, the area occupied by each hairiness pattern can be sampled separately. The percentage of surface occupied by each different density should be reported and the overall mean of hair density for that body part should be weighted by the area occupied by each hairiness pattern.
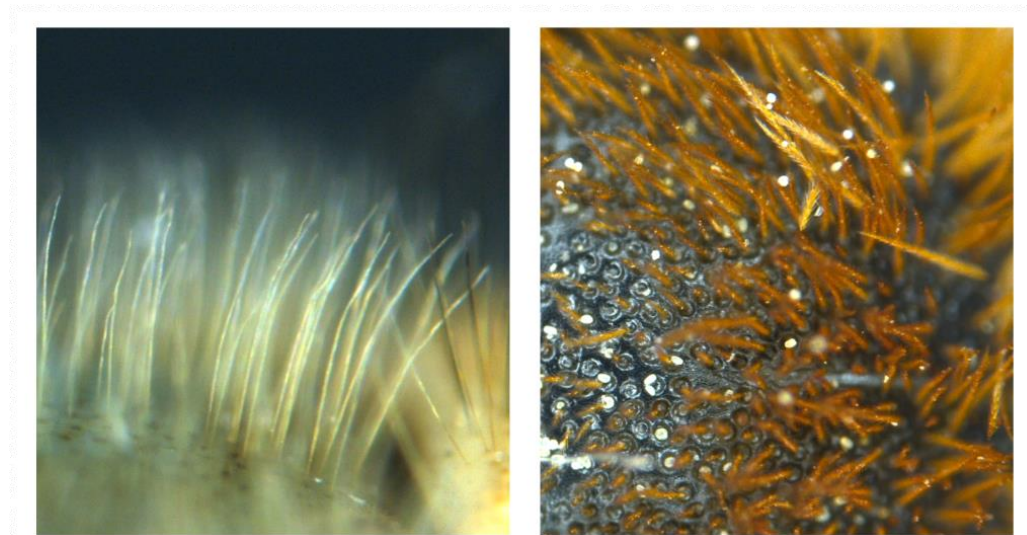
Figure A1.1: Hair micropores in the dorsal thorax region of *Scaeva albomaculata* (left) and of *Andrena haemorrhoa* (right).

Hair length

The length of a hair can be measured using the length measuring tool of the software (Fig. A1.2). Hair length is best measured from a side view. We recommend measuring 5-10 hairs in each focal body part.
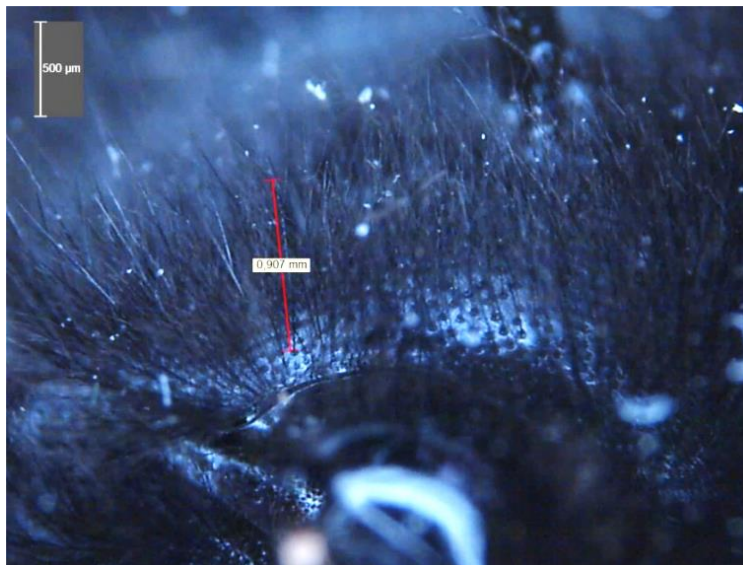
Figure A1.2. Measurement of hair length on the dorsal thorax region of *Xylocopa violacea*.

Duration of the measurements

Following the above-mentioned recommendations, a trained person can measure hair density and hair length of a body part in 5 minutes.

Hairiness index

We found hair length and hair density to be only weakly (and negatively) correlated. For this reason, we recommend reporting measures of the two components of hairiness (hair density and hair length) separately. However, in studies in which the two components are suspected to have a similar effect on function, we propose a hairiness index combining the two hairiness components (hair density x hair length).

Body size

We found that body size was positively correlated to hair length and, to a lesser extent, negatively correlated to hair density. Body size is strongly related to heat generation and dissipation and the ability to fly at low temperatures (e.g.: Stone & Willmer 1989a; Heinrich 1993; Bishop & Armbruster 1999; Peat *et al.* 2005; Osorio-Canadas *et al.* 2016; Peters *et al.* 2016), and may influence pollination effectiveness (Kandori 2002; Willmer & Finlayson 2014; Jauker, Speckmann, & Wolters 2016; Phillips *et al.* 2018). For these reasons, we recommend accounting for body size in studies measuring hairiness. Appropriate measures of body size for bees include intertegular span (interspecific level, Cane 1987), head width and forewing length (intraspecific level, Bosch & Vicens 2002). Forewing length and wingspan are appropriate measures for butterflies (Miller 1991; Nylin *et al.* 1993; García-Barros 2000, 2015; Beck & Kitching 2007). When comparing species from different insect orders, body length is probably the most suitable measure.

Other considerations

We found that measuring three specimens per species allowed us to discriminate between pollinator groups and bee genera. Sample sizes should be increased in studies addressing intra-specific variability.

Because many pollinator species (notably bees) show marked sexual dimorphism, males and females should be measured separately.

Measures of hairiness on the thorax dorsal region and body size of 109 pollinator species from Spain, Germany and Sweden are provided in Table S1.

Appendix 2

Supplementary material - Chapter 1

Table A2.1: List of pollinator species and mean values of hair length and density of the dorsal surface of the mesothorax (DT), body length and intertegular span (ITS).

	Species name	Pollinator group	Bee taxa	DT hair length (mm)	DT hair density (hairs/mm²)	Body length (mm)	ITS (mm)
1	*Bombylius major*	bee-flies	-	0.9	466.4	9.9	-
2	*Bombylius medius*	bee-flies	-	1.1	354.6	12.5	-
3	*Andrena bicolor*	bees	*Andrena*	0.6	256.3	9.5	2.1
4	*Andrena cineraria*	bees	*Andrena*	0.8	358.3	13.2	2.9
5	*Andrena dorsata*	bees	*Andrena*	0.4	227.7	11.4	2.1
6	*Andrena flavipes*	bees	*Andrena*	0.5	334.4	12.3	2.4
7	*Andrena fulva*	bees	*Andrena*	0.6	264.7	13.4	2.9
8	*Andrena haemorrhoa*	bees	*Andrena*	0.4	154.9	11.3	2.5
9	*Andrena helvola*	bees	*Andrena*	0.5	361.9	9.7	2.1
10	*Andrena humilis*	bees	*Andrena*	0.5	240.1	12.3	2.3
11	*Andrena jacobi*	bees	*Andrena*	0.7	154.1	13.5	2.9
12	*Andrena lathyri*	bees	*Andrena*	0.6	260.1	11.9	4.1
13	*Andrena leptopyga*	bees	*Andrena*	0.2	163.6	9.5	1.8
14	*Andrena limata*	bees	*Andrena*	0.7	501.5	13.5	3.0
15	*Andrena minutula*	bees	*Andrena*	0.3	421.0	7.7	1.5
16	*Andrena nigroaenea*	bees	*Andrena*	0.8	247.7	12.5	2.8
17	*Andrena nitida*	bees	*Andrena*	0.6	357.3	13.9	3.0
18	*Andrena pilipes*	bees	*Andrena*	0.6	159.8	16.3	3.1
19	*Andrena* sp. 1	bees	*Andrena*	0.5	200.4	14.0	2.8
20	*Andrena* sp.2	bees	*Andrena*	0.4	287.3	10.4	1.8
21	*Andrena subopaca*	bees	*Andrena*	0.2	408.6	6.4	1.4
22	*Andrena vaga*	bees	*Andrena*	0.8	246.3	14.0	2.8
23	*Anthophora acervorum*	bees	Antophorinae	1.0	375.7	14.1	4.0
24	*Eucera collaris*	bees	Antophorinae	1.1	135.5	12.5	3.1
25	*Eucera nigrilabris*	bees	Antophorinae	0.9	157.9	16.5	3.8
26	*Xylocopa violacea*	bees	Antophorinae	1.0	63.5	22.4	5.7
27	*Apis mellifera*	bees	*Apis*	0.7	203.6	11.6	3.2
28	*Bombus bohemicus*	bees	*Bombus*	1.4	176.6	15.1	4.1
29	*Bombus hortorum*	bees	*Bombus*	1.6	301.1	12.8	3.7
30	*Bombus humilis*	bees	*Bombus*	1.2	260.6	12.8	4.3
31	*Bombus hypnorum*	bees	*Bombus*	1.5	281.0	13.4	4.2
32	*Bombus lapidarius*	bees	*Bombus*	1.4	256.8	14.4	4.5
33	*Bombus lucorum*	bees	*Bombus*	0.9	288.2	14.4	4.6
34	*Bombus pascuorum*	bees	*Bombus*	1.3	216.4	15.1	4.0
35	*Bombus pratorum*	bees	*Bombus*	1.1	345.7	14.4	3.8
36	*Bombus sylvarum*	bees	*Bombus*	1.2	253.6	12.8	3.9
37	*Bombus terrestris*	bees	*Bombus*	1.3	280.9	15.6	4.6

	Species name	Pollinator group	Bee taxa	DT hair length (mm)	DT hair density (hairs/mm²)	Body length (mm)	ITS (mm)
38	*Halictus crenicornis*	bees	Halictini	0.2	548.4	10.8	2.3
39	*Halictus scabiosae*	bees	Halictini	0.4	446.6	14.9	2.8
40	*Halictus tumulorum*	bees	Halictini	0.1	804.8	7.2	1.4
41	*Lasioglossum calceatum*	bees	Halictini	0.1	520.3	8.9	1.8
42	*Lasioglossum fulvicorne*	bees	Halictini	0.1	539.3	6.3	1.3
43	*Lasioglossum morio*	bees	Halictini	0.1	1052.2	5.8	1.1
44	*Lasioglossum pallens*	bees	Halictini	0.2	556.3	8.0	1.7
45	*Lasioglossum pauxillum*	bees	Halictini	0.1	529.0	6.9	1.3
46	*Lasioglossum punctatissimum*	bees	Halictini	0.1	681.4	6.1	1.3
47	*Lasioglossum* sp.	bees	Halictini	0.3	596.3	10.5	1.8
48	*Lasioglossum zonulum*	bees	Halictini	0.2	416.0	9.3	2.1
49	*Nomada succincta*	bees	*Nomada*	0.3	150.8	10.5	1.7
50	*Osmia aurulenta*	bees	*Osmia*	0.7	253.8	8.4	2.5
51	*Osmia bicolor*	bees	*Osmia*	0.8	274.0	9.9	2.7
52	*Osmia bicornis*	bees	*Osmia*	0.9	426.5	11.1	3.0
53	*Osmia cornuta*	bees	*Osmia*	1.2	363.9	12.4	3.6
54	*Osmia tricornis*	bees	*Osmia*	0.9	378.2	11.3	3.6
55	*Agrypnus murinus*	beetles	-	0.1	194.8	12.3	-
56	*Cantharis* sp.	beetles	-	0.1	337.7	11.3	-
57	*Cantharis livida*	beetles	-	0.2	215.2	6.8	-
58	Curculionidae	beetles	-	0.2	227.9	5.1	-
59	*Meligethes* sp.	beetles	-	0.0	1875.6	2.4	-
60	*Oedemera nobilis*	beetles	-	0.2	313.6	8.6	-
61	*Oxythyrea funesta*	beetles	-	0.7	77.1	9.6	-
62	*Ragonycha* sp.	beetles	-	0.1	642.7	6.5	-
63	*Tropinota squalida*	beetles	-	0.9	234.7	11.4	-
64	*Macroglossum stellatarum*	butterflies & moths	-	1.3	616.7	27.9	-
65	*Pieris brassicae*	butterflies & moths	-	0.9	597.8	20.2	-
66	*Pieris napi*	butterflies & moths	-	1.0	951.2	18.7	-
67	*Vanessa atalanta*	butterflies & moths	-	1.9	1016.8	19.3	-
68	*Vanessa cardui*	butterflies & moths	-	0.6	636.6	19.8	-
69	*Cheilosia pagana*	hover-flies	-	0.1	487.2	6.8	-
70	*Episyrphus balteatus*	hover-flies	-	0.2	355.0	10.1	-
71	*Eristalinus aeneus*	hover-flies	-	0.4	373.2	10.8	-
72	*Eristalinus* sp.	hover-flies	-	0.4	283.6	11.8	-
73	*Eristalis arbustorum*	hover-flies	-	0.4	232.2	10.8	-
74	*Eristalis interrupta*	hover-flies	-	0.4	246.4	12.0	-
75	*Eristalis pertinax*	hover-flies	-	0.6	189.2	12.9	-

	Species name	Pollinator group	Bee taxa	DT hair length (mm)	DT hair density (hairs/mm²)	Body length (mm)	ITS (mm)
76	*Eristalis similis*	hover-flies	-	0.5	133.1	14.1	-
77	*Eristalis tenax*	hover-flies	-	0.6	234.6	14.3	-
78	*Eupeodes corollae*	hover-flies	-	0.4	410.8	9.0	-
79	*Helophilus hybridus*	hover-flies	-	0.4	365.3	15.0	-
80	*Helophilus pendulus*	hover-flies	-	0.3	314.9	12.6	-
81	*Helophilus trivitattus*	hover-flies	-	0.4	458.8	16.2	-
82	*Melanostoma mellinum*	hover-flies	-	0.1	653.8	7.6	-
83	*Melanostoma scalare*	hover-flies	-	0.2	443.7	7.6	-
84	*Meliscaeva auricollis*	hover-flies	-	0.2	269.9	8.5	-
85	*Myathropa florea*	hover-flies	-	0.4	232.2	11.8	-
86	*Neoascia podagrica*	hover-flies	-	0.1	908.0	5.6	-
87	*Platycheirus albimanus*	hover-flies	-	0.1	502.2	7.9	-
88	*Platycheirus peltatus*	hover-flies	-	0.2	426.0	8.9	-
89	*Rhingia campestris*	hover-flies	-	0.3	399.4	8.7	-
90	*Scaeva albomaculata*	hover-flies	-	0.4	404.0	13.0	-
91	*Scaeva pyrastri*	hover-flies	-	0.4	234.5	12.8	-
92	*Sphaerophoria scripta*	hover-flies	-	0.1	338.7	9.0	-
93	*Syrphus ribesii*	hover-flies	-	0.3	314.7	11.4	-
94	*Syrphus vitripennis*	hover-flies	-	0.3	291.7	9.9	-
95	*Xanthandrus comtus*	hover-flies	-	0.2	341.8	10.8	-
96	Anthomyiidae	other flies	-	0.3	85.9	4.3	-
97	*Bibio hortulanus*	other flies	-	0.1	192.9	11.0	-
98	*Dilophus* sp.	other flies	-	0.3	229.0	5.3	-
99	*Empis* sp.	other flies	-	0.2	199.8	10.2	-
100	Large fly	other flies	-	0.4	416.7	10.5	-
101	Medium-sized fly	other flies	-	0.3	315.5	7.8	-
102	*Neomyia cornicina*	other flies	-	0.2	149.1	6.9	-
103	*Sarcophaga carnaria*	other flies	-	0.3	73.9	10.5	-
104	Small fly	other flies	-	0.4	84.7	5.0	-
105	*Hoplocampa testudinea*	saw-flies	-	0.0	1027.3	6.2	-
106	*Tenthredo koehleri*	saw-flies	-	0.1	480.6	9.0	-
107	*Polistes dominulus*	wasps	-	0.1	1444.4	14.5	-
108	*Vespula germanica*	wasps	-	0.6	145.5	14.8	-
109	*Vespula vulgaris*	wasps	-	0.9	116.6	20.0	-

Table A2.2: Correlations (Pearson *r* or Spearman *ρ*) of body size (body length (BL) for all pollinators, intertegular span (ITS) for bees) with hair density and hair length in each body part (dorsal thorax: DT, ventral thorax: VT; face: FA).

All pollinators			Bees		
BL[a]	Body Part	*r/ρ*	ITS[a]	Body Part	*r /ρ*
	DT[a]	*r* = -0.20*		DT[a]	*r* = -0.55***
Hair density	VT	*ρ* = 0.06 n.s.	Hair density	VT[a]	*r* = -0.50***
	FA	*ρ* = 0.12 n.s.		FA[a]	*r* = -0.48***
	DT[a]	*r* = 0.67***		DT[a]	*r* = 0.89***
Hair length	VT[b]	*r* = 0.70***	Hair length	VT[b]	*r* = 0.93***
	FA[b]	*r* = 0.70***		FA[b]	*r* = 0.91***

n.s.: non-significant; *: $P \leq 0.05$;** : $P \leq 0.01$ and *** : $P \leq 0.001$
Data transformations: [a] Log (X + 1) and [b] Square root.

Table A2.3: Correlation coefficients (Pearson *r* and Spearman *ρ*) of hair density, hair length and hairiness index among body parts (dorsal thorax: DT, ventral thorax: VT; face: FA).

	All pollinators		Bees	
	Body part (A-B)	*r/ρ*	Body part (A-B)	*r/ρ*
Hair density	DT - VT	*ρ* = 0.47***	DT[a] - VT[a]	*r* = 0.68***
	DT - FA	*ρ* = 0.48***	DT[a] - FA[a]	*r* = 0.61***
	VT - FA	*ρ* = 0.67***	VT[a] - FA[a]	*r* = 0.74***
Hair length	DT[a] - VT[b]	*r* = 0.95***	DT[b] - VT[b]	*r* = 0.96***
	DT[a] - FA[b]	*r* = 0.90***	DT[b] - FA[b]	*r* = 0.96***
	VT[b] - FA[b]	*r* = 0.91***	VT[b] - FA[b]	*r* = 0.96***
Hairiness index	DT[a] - VT[a]	*r* = 0.80***	DT[a] - VT[a]	*r* = 0.80***
	DT[a] - FA[a]	*r* = 0.78***	DT[a] - FA[a]	*r* = 0.77***
	VT[a] - FA[a]	*r* = 0.88***	VT[a] - FA[a]	*r* = 0.85***

*: $P \leq 0.05$;** : $P \leq 0.01$ and *** : $P \leq 0.001$
Data transformations: a Log (X + 1) and b Square root.

Table A2.4: Within and between species coefficients of variation (CV, %) of hair density and hair length of three body parts (dorsal thorax: DT, ventral thorax: VT; face: FA) for all pollinators and for bees.

		All pollinators		Bees	
	Body Part	CV within	CV between	CV within	CV between
Hair density	DT	18.7	73.0	18.3	53.4
Hair length		17.1	76.7	17.0	60.7
Hair density	VT	23.6	103.0	21.7	38.3
Hair length		18.5	65.9	17.0	48.5
Hair density	FA	22.1	145.3	20.0	38.6
Hair length		18.3	67.9	17.0	50.3

Table A2.5: Statistical outputs of ANOVA (F-value) and Kruskal Wallis (H-statistic) tests analyzing differences in hair length, hair density and hairiness index between pollinator (n=109 species) and bee groups (n=52 species) of three body parts (dorsal thorax: DT, ventral thorax: VT; face: FA).

	df	DT		VT			FA		
			F		F/H			F/H	
All pollinators	4	Hair density[a]	6.92***	Hair density	H	32.50***	Hair density	H	44.68***
	4	Hair length[a]	11.34***	Hair length[b]	F	17.14***	Hair length[b]	F	16.08***
	4	Hairiness index[a]	27.21***	Hairiness index[a]	F	39.87***	Hairiness index[a]	F	15.89***
Bees	4	Hair density[a]	16.25***	Hair density[a]	F	4.06**	Hair density[a]	F	2.62*
	4	Hair length[a]	67.90***	Hair length[b]	F	40.09***	Hair length[a]	F	54.20***
	4	Hairiness index[a]	13.52***	Hairiness index[a]	F	22.53***	Hairiness index[a]	F	19.96***

*: $P \leq 0.05$;** : $P \leq 0.01$ and *** : $P \leq 0.001$
Data transformations: [a] Log (X + 1) and [b] Square root.

Figure A2.1: Lateral view of hairs from the dorsal surface of the mesothorax of six non-bee pollinators.

Figure A2.2: Lateral view of hairs from the dorsal surface of the mesothorax of six bee species.
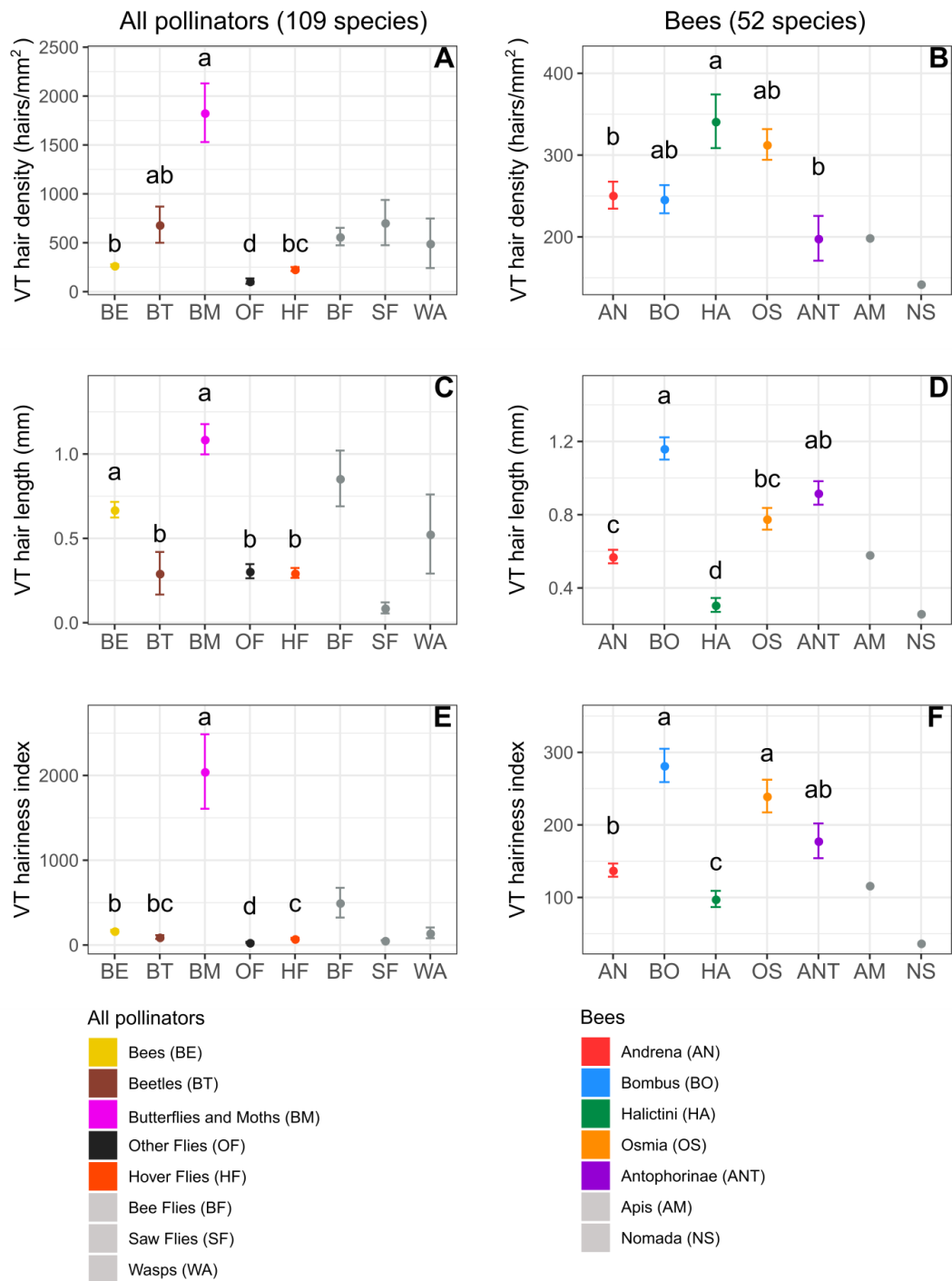
Figure A2.3. Mean ± SE hair density (A, B), hair length (C, D) and hairiness index (E, F) of the ventral surface of the mesothorax (VT) of various pollinator groups and bee taxa. Different letters indicate significant differences among groups (post-hoc Tukey tests, $P < 0.05$). Grey bars correspond to groups with fewer than three species that were not included in the analyses.
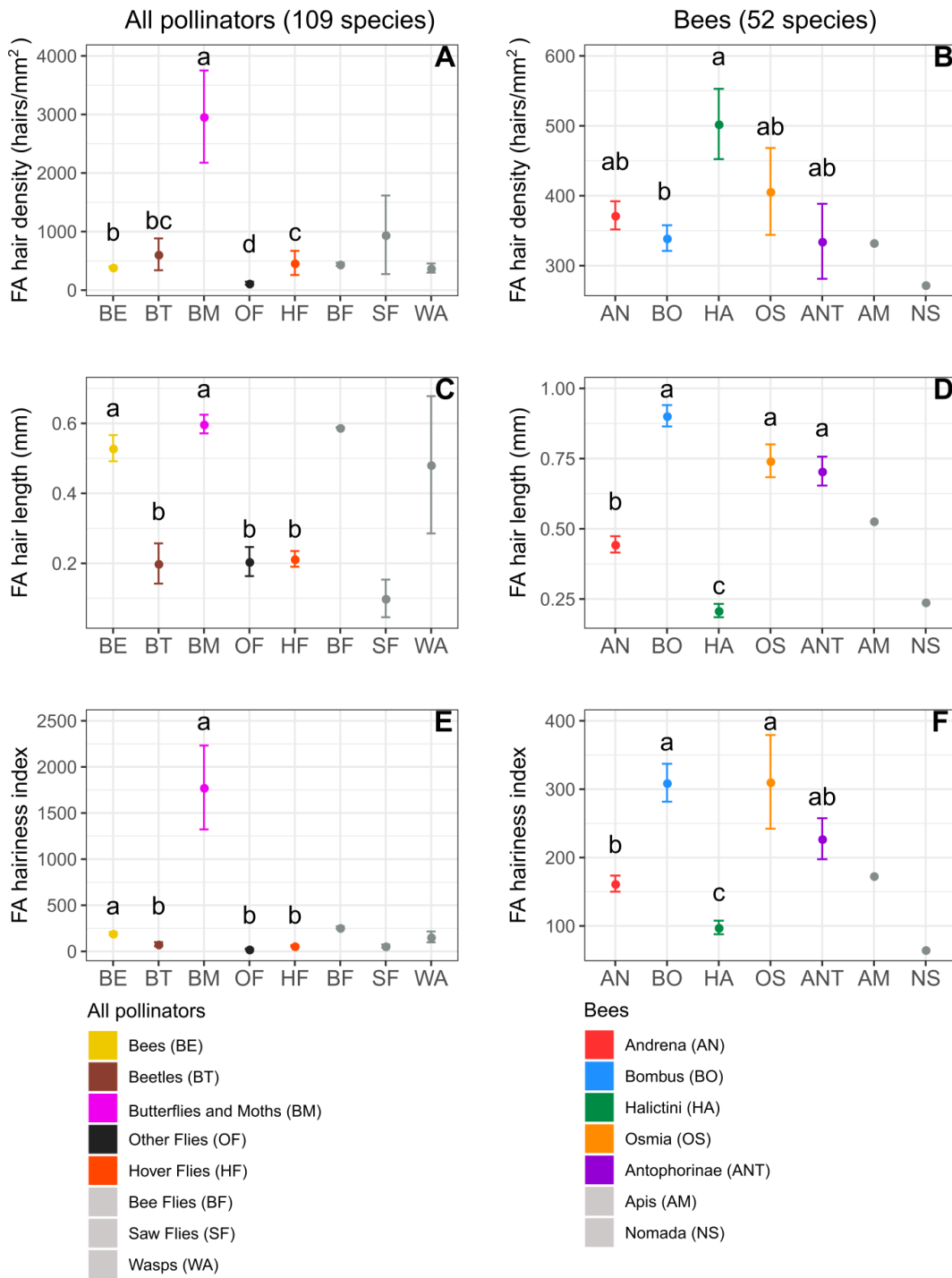
Figure A2.4: Mean ± SE hair density (A, B), hair length (C, D) and hairiness index (E, F) of the face (FA) of various pollinator groups and bee taxa. Different letters indicate significant differences among groups (post-hoc Tukey tests, $P < 0.05$). Grey bars correspond to groups with fewer than three species that were not included in the analyses.

Appendix 3

Supplementary material - Chapter 2

Table A3.1: Number of single-visit observations recorded for each apple pollinator species or morphospecies.

Species name	visits
Andrena flavipes	33
Andrena limata	20
Apis mellifera	29
Large fly	3
Andrena pilipes	19
Bombus terrestris	31
Episyrphus balteatus	4
Eristalis tenax	11
Eucera nigrilabris	26
Helophilus sp.	5
Lasioglossum sp.	1
Medium fly	16
Nomada succincta	3
Osmia cornuta	19
Oxythyrea funesta	10
Platycheirus albimanus	2
Polistes dominula	4
Small fly	2
Melanostoma sp.	5
Tropinota squalida	10

Table A3.2: Best fitting models (ΔAICc < 2) relating pollination effectiveness (stigma pollen load in single-visit apple flowers) to pollinator body length, hair density, hair length, visit duration and flower-handling behaviour considering only legitimate visits after outlier exclusion. Estimated coefficients, their 95% intervals (in parentheses) are provided. Variables not appearing in the best models are indicated with "-". R^2m and R^2c are the marginal and conditional R^2 range values of the best-fitted models, respectively. Significant terms (with confidence intervals not overlapping with zero) are in bold.

Model *	Estimate	Body length	Hair density	Hair length	Visit duration	df	logLik	AICc	ΔAICc	weight	R^2m	R^2c
1	**5.508** **(5.110, 5.883)**	**0.588** **(0.218, 0.979)**	-	-	**0.416** **(0.223, 0.609)**	5	-260.79	531.93	0.00	0.45	0.19	0.36
2	**5.526** **(5.143, 5.881)**	**0.512** **(0.118, 0.938)**	0.175 (-0.278, 0.589)	-	**0.425** **(0.230, 0.620)**	6	-260.43	533.37	1.43	0.22	0.19	0.33

* Response variable was log (X+1) transformed. The number of visits included in each model after outlier exclusion was 171. See Table A3.4 for results without outlier exclusion.

Table A3.3: Best fitting models (ΔAICc < 2) relating pollination effectiveness (stigma pollen load in single-visit apple flowers) to pollinator body length, hair density, hair length, visit duration and flower-handling behaviour without excluding outliers. Estimated coefficients and their 95% intervals (in parentheses) are provided. Variables not appearing in the best models are indicated with "-". R^2m and R^2c are the marginal and conditional R^2 range values of the best-fitted models, respectively. Significant terms (with confidence intervals not overlapping with zero) are in bold.

Model *	Estimate	Body length	Hair density	Hair length	Visit duration	Flower handling behaviour**	df	logLik	AICc	ΔAICc	weight	R^2m	R^2c
1	**4.173** **(3.401, 4.966)**	-	-	-	**0.44** **(0.185, 0.697)**	**1.019** **(0.235, 1.801)**	5	-489.73	989.71	0	0.21	0.09	0.20
2	**4.235** **(3.476, 5.022)**	0.259 (-0.133, 0.631)	-	-	**0.461** **(0.206, 0.715)**	**1.005** **(0.225, 1.780)**	6	-488.82	989.99	0.29	0.18	0.10	0.19
3	**4.178** **(3.424, 4.956)**	-	0.239 (-0.120, 0.590)	-	**0.463** **(0.208, 0.719)**	**1.033** **(0.253, 1.809)**	6	-488.82	990	0.29	0.18	0.10	0.20
4	**4.214** **(3.461, 4.995)**	0.171 (-0.302, 0.609)	0.155 (-0.261, 0.572)	-	**0.471** **(0.215, 0.725)**	**1.022** **(0.242, 1.795)**	7	-488.52	991.52	1.81	0.08	0.11	0.19
5	**4.202** **(3.417, 5.012)**	-	-	0.085 (-0.340, 0.538)	**0.439** **(0.184, 0.695)**	**1.001** **(0.219, 1.789)**	6	-489.64	991.64	1.94	0.08	0.09	0.21

* The response variable (pollination effectiveness) was log-transformed. The number of visits included in each model was 242.

Table A3.4: Best fitting models (ΔAICc < 2) relating pollination effectiveness (stigma pollen load in single-visit apple flowers) to pollinator body length, hair density, hair length, visit duration and flower-handling behavior considering only legitimate visits without excluding outliers. Estimated coefficients, their 95% intervals (in parentheses) are provided. Variables not appearing in the best models are indicated with "-". R^2m and R^2c are the marginal and conditional R^2 range values of the best-fitted models, respectively. Significant terms (with confidence intervals not overlapping with zero) are in bold.

Model *	Estimate	Body length	Hair density	Hair length	Visit duration	df	logLik	AICc	ΔAICc	weight	R^2m	R^2c
1	**5.012 (4.439, 5.521)**	-	-	-	**0.485 (0.233, 0.738)**	4	-409.83	827.86	0	0.28	0.06	0.27
2	**5.111 (4.552, 5.584)**	0.264 (-0.215, 0.672)	-	-	**0.498 (0.246, 0.749)**	5	-409.17	828.63	0.76	0.19	0.08	0.23
3	**5.079 (4.521, 5.602)**	-	-	0.253 (-0.217, 0.752)	**0.481 (0.230, 0.732)**	5	-409.24	828.77	0.9	0.18	0.08	0.27
4	**5.033 (4.462, 5.533)**	-	0.113 (-0.334, 0.529)	-	**0.492 (0.239, 0.745)**	5	-409.69	829.68	1.82	0.11	0.06	0.26

* The response variable (pollination effectiveness) was log-transformed. The number of visits included in each model was 209.
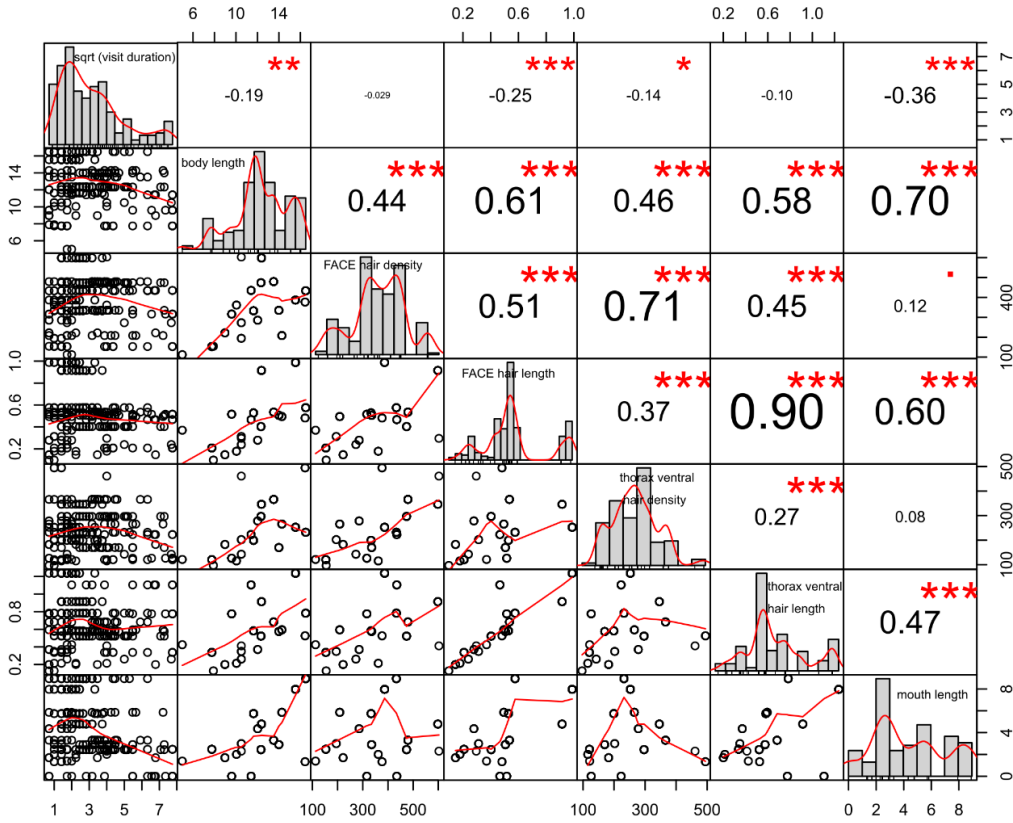
Figure A3.1: Correlation between each pair of numerical explanatory variables. Pearson *r* and level of significance (*: *P* ≤ 0.05; ** : *P* ≤ 0.01 and *** : *P* ≤ 0.001) are indicated.

Appendix 4

Supplementary material - Chapter 3

Table A4.1: Cultivars and local and landscape (% cover in 1 km radius) features in low–input (LI) and high-input (HI) apple orchards in Sweden (SWE), Germany (GER) and Spain (AST and CAT). Means followed by ± SD.

	Sweden (SWE)		Germany (GER)		Asturias (AST)		Catalonia (CAT)	
Management (n)	HI	LI	HI	LI	HI	LI	HI	LI
	14	14	14	15	0	25	14	14
Cultivars	Aroma, Amorosa, Ingrid Marie, Rubinola		Braeburn		Regona		Gala, Golden	
Local variables								
Flower diversity (Shannon's index)	1.6±0.5	1.7±0.5	2.1±0.5	2.1±0.5	2.1±0.5		1.9±0.4	2.0± 0.4
AE- structure cover (m^2)	182.1±188.5	359.7±285.0	144.2±174.7	163.3±152.5	99.8±79.2		211.4±252.8	234.3±184.7
*Landscape variables**								
% Orchard cover	15.4±12.2	11.2±12.8	34.1±16.4	27.0±11.1	8.42±3.8		41.6±30.5	32.5±31.1
% Pollinator-friendly habitat cover**	7.0±6.3	10.5±10.1	2.9±2.0	4.0±2.9	9.1±4.4		1.4±3.4	7.4±14.5
% Forest cover	14.3±14.1	19.7±14.2	19.3±17.3	19.5±15.6	12.56±10.51		1.0±2.0	2.6±3.3
% Arable land cover	40.9±32.7	29.6±19.3	20.9±12.8	27.2±15.8	0.94±0.7		51.8±29.2	51.0±34.0
% Grassland cover	4.97±5.89	8.65±9.79	11.9±5.6	14.0±6.2	41.05±11.1		0.62±0.93	1.26±2.71

* We used official digital maps of habitat types for GER (LGL, 2016. ATKIS Digitales Landschaftsmodell, Baden-Württemberg, Basis-DLM Version 6.0. Landesamt für Geoinformation und Landentwicklung, Stuttgart) and CAT (Carreras, J., Diego, F., 2009. Catalan Habitats Cartography, 1:50,000. Departament de Medi Ambient i Habitatge, Generalitat de Catalunya, Barcelona), spatially explicit data from the Swedish Board of Agriculture (Integrated Administrative Control System, IACS) from year 2014, complemented with "Swedish ground covering data raster" from 2000 from the Swedish environmental protection agency (SvenskMarktäckeData, Naturvårdsverket) for SWE, and a Geographic Information System created ad hoc for AST, based on the digitalization of habitat patches from 1:5000-scale ortophotographs (2014).

** Pollinator-friendly habitats were defined based on expert knowledge, and included semi-natural grasslands in SWE, orchard meadows in GER, hedgerows in AST and shrubland and dryland/abandoned almond orchards in CAT.

Table A4.2: List of pollinator species and morphospecies and their abundances (total number of individuals surveyed per orchard, decimal numbers correspond to corrected relative abundances to specific species in AST) in each region (SWE = Sweden, GER = Germany, AST = Asturias, CAT= Catalonia).

	Species	Pollinator group	SWE	GER	AST	CAT	Total
1	*Agrypnus murinus*	beetles	0.0	0.0	1.0	0.0	1.0
2	*Andrena bicolor*	bees	0.0	0.0	5.4	0.0	5.4
3	*Andrena cineraria*	bees	0.0	16.0	0.0	0.0	16.0
4	*Andrena dorsata*	bees	0.0	0.0	10.3	0.0	10.3
5	*Andrena flavipes*	bees	0.0	1.0	10.0	1.0	12.0
6	*Andrena fulva*	bees	20.0	3.0	1.0	0.0	24.0
7	*Andrena haemorrhoa*	bees	50.0	12.0	3.5	0.0	65.5
8	*Andrena helvola*	bees	4.0	0.0	0.0	0.0	4.0
9	*Andrena humilis*	bees	0.0	0.0	1.0	0.0	1.0
10	*Andrena jacobi*	bees	0.0	3.0	0.0	0.0	3.0
11	*Andrena lathyri*	bees	0.0	0.0	0.1	0.0	0.1
12	*Andrena leptopyga*	bees	0.0	0.0	0.1	0.0	0.1
13	*Andrena limata*	bees	0.0	0.0	0.0	2.0	2.0
14	*Andrena minutula*	bees	0.0	0.0	4.2	0.0	4.2
15	*Andrena nigroaenea*	bees	17.0	0.0	15.2	2.0	34.2
16	*Andrena nitida*	bees	0.0	3.0	0.8	0.0	3.8
17	*Andrena pilipes*	bees	0.0	0.0	8.4	0.0	8.4
18	*Andrena* sp.	bees	26.0	36.0	1.0	13.0	76.0
19	*Anthophora plumipes*	bees	0.0	0.0	0.0	8.0	8.0
20	*Apis mellifera*	bees	1004.0	1418.0	1247.0	2733.0	6402.0
21	*Bibio hortulanus*	other flies	0.0	0.0	0.0	4.0	4.0
22	Big-sized fly	other flies	5.0	10.0	3.0	102.0	120.0
23	*Bombus hortorum*	bees	0.0	1.0	0.0	0.0	1.0
24	*Bombus hypnorum*	bees	4.0	0.0	0.0	0.0	4.0
25	*Bombus lapidarius*	bees	6.0	15.0	0.0	0.0	21.0
26	*Bombus pascuorum*	bees	3.0	19.0	12.0	2.0	36.0
27	*Bombus pratorum*	bees	2.0	6.0	14.2	0.0	22.2
28	*Bombus* sp.	bees	11.0	7.0	2.0	0.0	20.0
29	*Bombus terrestris*	bees	88.0	60.0	89.8	40.0	277.8
30	*Bombylius major*	other flies	0.0	1.0	0.1	0.0	1.1
31	*Bombylius* sp.	other flies	0.0	17.0	0.0	2.0	19.0
32	*Cantharis* sp.	beetles	0.0	0.0	2.0	28.0	30.0
33	*Cheilosia pagana*	hoverflies	0.0	0.0	0.1	0.0	0.1
34	Curculionidae	beetles	6.0	0.0	0.0	0.0	6.0
35	*Dilophus* sp.	other flies	0.0	0.0	0.0	2.0	2.0
36	Muscidae	other flies	47.0	119.0	0.0	0.0	166.0
37	*Empis* sp.	other flies	12.0	0.0	1.0	0.0	13.0
38	*Episyrphus balteatus*	hoverflies	0.0	1.0	9.2	7.0	17.2
39	*Eristalinus aeneus*	hoverflies	0.0	0.0	0.0	1.0	1.0
40	*Eristalis arbustorum*	hoverflies	0.0	0.0	1.5	0.0	1.5
41	*Eristalis interrupta*	hoverflies	0.0	0.0	1.0	0.0	1.0

42	*Eristalis pertinax*	hoverflies	15.0	0.0	0.0	0.0	15.0
43	*Eristalis similis*	hoverflies	0.0	0.0	15.1	0.0	15.1
44	*Eristalis* sp.	hoverflies	0.0	0.0	110.0	1.0	111.0
45	*Eristalis tenax*	hoverflies	0.0	0.0	142.9	71.0	213.9
46	*Eucera nigrilabris*	bees	0.0	0.0	1.0	7.0	8.0
47	*Eupeodes corollae*	hoverflies	0.0	0.0	9.4	2.0	11.4
48	*Halictus crenicornis*	bees	0.0	0.0	0.9	0.0	0.9
49	*Halictus scabiosae*	bees	0.0	0.0	2.0	0.0	2.0
50	*Halictus* sp.	bees	0.0	0.0	2.3	0.0	2.3
51	*Halictus tumulorum*	bees	0.0	0.0	13.5	0.0	13.5
52	*Helophilus hybridus*	hoverflies	0.0	0.0	0.0	2.0	2.0
53	*Helophilus pendulus*	hoverflies	0.0	0.0	1.0	0.0	1.0
54	*Helophilus* sp.	hoverflies	0.0	0.0	0.1	2.0	2.1
55	*Helophilus trivitattus*	hoverflies	0.0	0.0	0.0	2.0	2.0
56	*Lasioglossum calceatum*	bees	0.0	0.0	1.7	0.0	1.7
57	*Lasioglossum fulvicorne*	bees	0.0	0.0	1.2	0.0	1.2
58	*Lasioglossum morio*	bees	0.0	0.0	0.7	0.0	0.7
59	*Lasioglossum pallens*	bees	0.0	0.0	4.7	0.0	4.7
60	*Lasioglossum pauxillum*	bees	0.0	0.0	8.3	0.0	8.3
61	*Lasioglossum punctatissimum*	bees	0.0	0.0	3.0	0.0	3.0
62	*Lasioglossum* sp.	bees	0.0	5.0	0.0	0.0	5.0
63	*Lasioglossum zonulum*	bees	0.0	0.0	0.5	0.0	0.5
64	*Macroglossum stellatarum*	others	0.0	0.0	0.0	2.0	2.0
65	Medium-sized fly	other flies	14.0	0.0	0.0	76.0	90.0
66	*Melanostoma mellinum*	hoverflies	4.0	0.0	5.7	0.0	9.7
67	*Melanostoma scalare*	hoverflies	1.0	0.0	0.0	24.0	25.0
68	*Meligethes* sp.	beetles	0.0	0.0	0.0	1.0	1.0
69	*Meliscaeva auricollis*	hoverflies	0.0	0.0	10.3	0.0	10.3
70	*Neoascia podagrica*	hoverflies	0.0	0.0	0.1	0.0	0.1
71	*Nomada succincta*	bees	0.0	0.0	1.0	0.0	1.0
72	*Oedemera nobilis*	beetles	0.0	0.0	1.0	0.0	1.0
73	*Osmia aurulenta*	bees	0.0	1.0	0.0	0.0	1.0
74	*Osmia bicolor*	bees	0.0	1.0	1.8	0.0	2.8
75	*Osmia bicornis*	bees	0.0	2.0	0.0	18.0	20.0
76	*Osmia* sp.	bees	0.0	1.0	0.0	0.0	1.0
77	*Oxythyrea funesta*	beetles	0.0	0.0	12.0	18.0	30.0
78	*Pieris brassicae*	others	0.0	0.0	0.0	3.0	3.0
79	*Pieris napi*	others	0.0	0.0	0.0	1.0	1.0
80	*Pieris* sp.	others	0.0	1.0	0.0	0.0	1.0
81	*Platycheirus albimanus*	hoverflies	0.0	0.0	1.0	0.0	1.0
82	*Platycheirus peltatus*	hoverflies	3.0	0.0	0.0	0.0	3.0
83	*Polistes dominulus*	others	0.0	0.0	0.0	4.0	4.0
84	*Ragonycha fulva*	beetles	0.0	0.0	1.0	0.0	1.0
85	*Rhingia campestris*	hoverflies	3.0	4.0	0.0	0.0	7.0
86	*Sarcophaga carnaria*	other flies	0.0	4.0	0.0	0.0	4.0
87	*Scaeva albomaculata*	hoverflies	0.0	0.0	0.0	1.0	1.0
88	Small sized-fly	other flies	0.0	0.0	0.0	84.0	84.0
89	*Sphaerophoria scripta*	hoverflies	0.0	0.0	11.2	1.0	12.2
90	*Syrphus ribesii*	hoverflies	0.0	0.0	3.7	0.0	3.7
91	*Syrphus vitripennis*	hoverflies	1.0	0.0	9.0	0.0	10.0
92	*Tenthredo koehleri*	others	0.0	0.0	1.0	0.0	1.0
93	*Tropinota squalida*	beetles	0.0	0.0	0.0	11.0	11.0

94	*Vanessa cardui*	others	14.0	0.0	0.0	5.0	19.0
95	*Vespula* sp.	others	1.0	0.0	0.0	0.0	1.0
96	*Vespula germanica*	others	0.0	0.0	0.0	1.0	1.0
97	*Vespula vulgaris*	others	0.0	1.0	0.0	0.0	1.0
98	*Xanthandrus comtus*	hoverflies	0.0	0.0	3.0	0.0	3.0
99	*Xylocopa violacea*	bees	0.0	0.0	0.0	8.0	8.0
	Total		1361.0	1768.0	1824.8	3292.0	8245.8

Table A4.3: Pearson's correlation between numerical functional traits. Correlation coefficient (r) and number of observations (n) are indicated. Significant relationships are in bold ($P < 0.05$).

ALL POLLINATORS		r	n	P
Body length	Hairiness [a]	**0.57**	98	**<0.001**
BEES				
Intertegular span [a]	Mouthparts length	**0.79**	44	**<0.001**
	Hairiness [a]	**0.67**	44	**<0.001**
	Wing aspect ratio	0.16	44	0.291
Mouthparts length	Hairiness [a]	**0.60**	44	**<0.001**
	Wing aspect ratio	-0.02	44	0.882
Hairiness [a]	Wing aspect ratio	0.05	44	0.749

Data transformation: [a] Log(X+1)

Table A4.4: Pearson's correlation between pairs of local (Management, Agri-environmental structure cover, Flower diversity) and landscape (%Orchard cover, % Pollinator-friendly habitat cover) explanatory variables. Correlation coefficient (r) and number of observations (n) are indicated. Significant relationships are in bold ($P < 0.05$).

variable 1	variable 2	r	n	P
Agri-environmental structure cover [a]	Flower diversity	0.030	110	0.767
	% Orchard cover [b]	0.120	110	0.206
	% Pollinator-friendly habitat cover [b]	**0.200**	**110**	**0.035**
Flower diversity	% Orchards [b]	0.070	110	0.454
	% Pollinator-friendly habitat cover [b]	0.080	110	0.380
% Orchard cover [b]	% Pollinator-friendly habitat cover [b]	-0.180	110	0.055

Data transformation: [a] Square-root, [b] Log(X+1).

Table A4.5: Pearson's or Spearman's rank correlations between pairs of numerical predictors of initial fruit set (CWM of single traits, multiple-trait RaoQ, pollinator visitation rate). Correlation coefficients (Pearson's r and Spearman's ρ) and number of observations (n) are indicated. Significant relationships are in bold ($P < 0.05$).

variable 1	variable 2	r	ρ	n	P
CWM hairiness	CWM body length	**0.82**		81	**<0.001**
	CWM pollinivorous larvae		**0.37**	81	**<0.001**
	CWM insectivorous larvae		**-0.36**	81	**<0.001**
	Pollinator visitation rate		**0.36**	81	**<0.010**
CWM body length	CWM pollinivorous larvae		**0.42**	81	**<0.001**
	CWM insectivorous larvae		**-0.31**	81	**<0.010**
	Pollinator visitation rate		**0.47**	81	**<0.001**
CWM pollinivorous larvae	CWM insectivorous larvae		**-0.54**	81	**<0.001**
	Pollinator visitation rate		0.06	81	0.607
CWM insectivorous larvae	Pollinator visitation rate		-0.082	81	0.466

Table A4.6: Statistical outputs of model averaging (average of best-fitted models; ΔAICc< 2) relating wild pollinator and wild bee functional composition descriptors (response variables) to local and landscape features (predictor variables) without outlier exclusion. Response variables of models in which a null model was selected among the best-fitted model are not shown. Estimated coefficients, their 95% intervals (in parentheses) and relative importance (in brackets) are provided. Variables not appearing in the model average are indicated with "-". R^2m and R^2c are the range values of marginal and conditional R^2 of the best-fitted models, respectively. "Sites" indicates the number of orchards included in the model. Significant terms (with confidence intervals not overlapping with zero) are in bold.

Response variable	Management*	Flower diversity	AE structure cover	% orchard cover	% Pollinator friendly habitats cover	R^2m	R^2c	Sites
ALL POLLINATORS								
CWM Body length	0.404 [0.21] (-0.444, 1.252)	0.103 [0.16] (-0.288, 0.494)	-	**-0.454 [0.81] (-0.872, -0.035)**	**0.585 [1] (0.190, 0.981)**	0.08-0.16	0.18-0.19	109
CWM Hairiness [a]	-	-	-0.451 [0.56] (-1.034, 0.1314)	**-0.641 [0.84] (-1.259, -0.024)**	0.552 [0.69] (-0.022, 1.125)	0.06-0.11	0.12-0.17	109
CWM Pollenivorous larvae	-	-	-	-0.037 [0.41] (-0.010, 0.030)	**0.114 [1] (0.060, 0.167)**	0.12-0.14	0.38-0.39	109
CWM Insectivorous larvae [a]	-	0.037 [0.66] (-0.005, 0.079)	**0.070 [1] (0.028, 0.112)**	-	-0.011 [0.18] (-0.053, 0.032)	0.09-0.11	0.22-0.24	109
BEES								
RaoQ	**6.805 [1] (1.303, 12.308)**	-	-	**-2.885 [1] (-5.552, -0.217)**	1.672 [0.41] (-0.980, 4.325)	0.13-0.14	0.13-0.14	110

Data transformations: [a] Square-root
*Low-Input is the reference level of management

Table A4.7: Statistical outputs of model averaging (average of best-fitted models; ΔAICc < 2) relating initial fruit set to management (low-input vs high-input), functional composition metrics, the interaction between management and functional composition metrics and pollinator visitation rate. The first model includes single-trait metrics (CWM: hairiness, pollinivorous larvae) and the second models includes functional diversity (multi-trait RaoQ) without excluding outliers. Estimated coefficients, their 95% intervals (in parentheses) and relative importance (in brackets) are provided. Variables not appearing in the model average are indicated with "-". R^2m and R^2c are the marginal and conditional R^2 range values of the best-fitted model, respectively. "Sites" indicates the number of orchards included in the model. Significant terms (with confidence intervals not overlapping with zero) are in bold.

	ALL POLLINATORS								
Response variable	Management*	CWM hairiness	CWM pollinivorous	CWM hairiness $_x$ management	CWM pollinivorous $_x$ management	Visitation rate	R^2m	R^2c	Sites
Inital fruit set [a]	**-1.399 [1]** **(-2.072, -0.726)**	-	-0.012 [0.62] (-0.532, 0.495)	-0.572 [0.37] (-1.209, 0.065)	-	-	0.17-0.22	0.17-0.22	81
	Management*	RaoQ	RaoQ $_x$ management			Visitation rate	R^2m	R^2c	Sites
Inital fruit set [a] **	**-1.412** **(-2.047, -0.776)**	-0.177 (-0.680, 0.327)	**0.838** **(0.207, 1.470)**			-	0.27	0.27	81

Data transformations: [a] Square-root
*Low-Input is the reference level of management
** only one model selected

Table A4.8: Linear mixed models (with region as random effect) testing visitation rates and abundance of honey bees and of all pollinators between management types: low–input (LI) and high-input orchards (HI). Estimate, standard error, t statistics, degrees of freedom (df) and *P*-values are indicated.

Response variable	Fixed effect	estimate	SE	t	df	*P*
Honey bee visitation rate [a]	Intercept	0.93	0.48	1.93	3.04	0.148
	Management (LI)	0.08	0.07	1.18	104.2	0.239
Honey bee abundance [a]	Intercept	**6.87**	**0.75**	**9.12**	**5.85**	**<0.001**
	Management (LI)	0.10	0.66	0.15	104.9	0.879
All pollinators visitation rate [a]	Intercept	1.16	0.65	1.81	3.01	0.168
	Management (LI)	**0.15**	**0.59**	**2.53**	**105.1**	**<0.05**
All pollinators abundance [a]	Intercept	**8.18**	**0.81**	**10.14**	**4.99**	**<0.001**
	Management (LI)	0.38	0.64	0.60	107.5	0.552

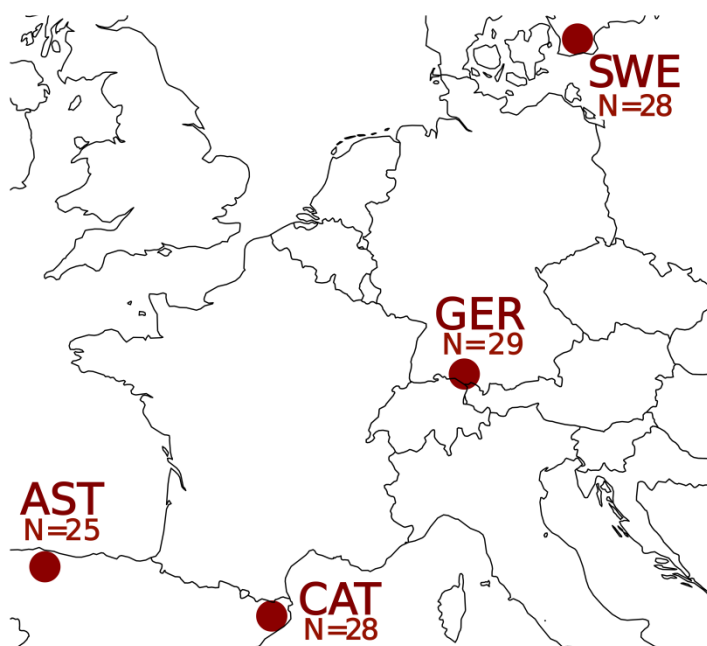Data transformations: [a] Square-root

Figure A4.1. Location of the study regions in Sweden (SWE), Germany (GER) and Spain (Catalonia, CAT; Asturias, AST) (N=number of orchards).

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