Patterns of size variation in bees at a continental scale: does Bergmann's rule apply

Article

Accepted Version

Gérard, M., Vanderplanck, M., Franzen, M., Kuhlmann, M., Potts, S. G. ORCID: https://orcid.org/0000-0002-2045-980X, Rasmont, P., Schweiger, O. and Michez, D. (2018) Patterns of size variation in bees at a continental scale: does Bergmann's rule apply. Oikos, 27 (8). pp. 1095-1103. ISSN 0030-1299 doi: 10.1111/oik.05260 Available at https://centaur.reading.ac.uk/76127/

To link to this article DOI: http://dx.doi.org/10.1111/oik.05260

Publisher: Wiley

Patterns of size variation in bees at a continental scale: does Bergmann's rule apply?

Short running title: Bergmann's rule in bees

Gérard Maxence[1*], Vanderplanck Maryse[1], Franzen Markus[2, 3], Kuhlmann Michael[4, 5], Potts G. Simon[6], Rasmont Pierre[1], Schweiger Oliver[2], Michez Denis[1]

[1] Laboratory of Zoology, Research institute for Biosciences, University of Mons, Place du Parc 20, 7000 Mons, Belgium

[2] UFZ, Helmholtz Centre for Environmental Research, Department of Community Ecology, Theodor-Lieser-Straße 4, D-06120 Halle, Germany

[3] Ecology and Evolution in Microbial Model Systems, EEMIS, Department of Biology and Environmental Science, Linnaeus University, SE-391 82 Kalmar, Sweden

[4] Zoological Museum, Universiy of Kiel, Hegewischstraße 3, Kiel, Germany

[5] Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK

[6] Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, The University of Reading, Reading, RG6 6AR, UK.

Email addresses:

maxence.gerard@umons.ac.be; maryse.vanderplanck@umons.ac.be; markus.franzen@ufz.de; mkuhlmann@zoolmuseum.uni-kiel.de; s.g.potts@reading.ac.uk; pierre.rasmont@umons.ac.be; oliver.schweiger@ufz.de; denis.michez@umons.ac.be

*Corresponding author: maxence.gerard@umons.ac.be Orchid ID: 0000-0002-2485-0662

Abstract

Body size latitudinal clines have been widley explained by the Bergmann's rule in homeothermic vertebrates. However, there is no general consensus in poikilotherms organisms in particular in insects that represent the large majority of wildlife. Among them, bees are a highly diverse pollinators group with high economic and ecological value. Nevertheless, no comprehensive studies of species assemblages at a phylogenetically larger scale have been carried out even if they could identify the traits and the ecological conditions that generate different patterns of latitudinal size variation. We aimed to test Bergmann's rule for wild bees by assessing relationships between body size and latitude at continental and community levels. We tested our hypotheses for bees showing different life history traits (i.e. sociality and nesting behaviour). We used 142,008 distribution records of 615 bee species at 50 km x 50 km (CGRS) grids across the West Palearctic. We then applied Generalized Least Squares fitted linear model (GLS) to assess the relationship between latitude and mean body size of bees, taking into account spatial autocorrelation. For all bee species grouped, mean body size increased with higher latitudes, and so followed Bergmann's rule. However, considering bee genera separately, four~~ive~~ genera were consistent with Bergmann's rule, while three~~four~~ showed a converse trend, and three~~one~~ showed no significant cline. All life history traits used here (i.e. solitary, social and parasitic behaviour; ground and stem nesting behaviour) displayed a Bergmann's cline. In general there is a main trend for larger bees in colder habitats, which is likely to be related to their thermoregulatory abilities and partial endothermy, even if a "season length effect" (i.e. shorter foraging season) is a potential driver of the converse Bergmann's cline particularly in bumblebees.

Key Words – Bergmann's rule – Body size – Latitudinal clines – Life history traits – Thermoregulation – Wild bees

Introduction

In ecology, several general rules have been proposed to explain phenotypic variations (e.g. variability in colour, size appendages and body size) observed across species distributions and species assemblages (Millien, *et al.* 2006). Among them, the increase of mean body size in colder conditions has been widely reported in many organisms and is well known as the Bergmann’s rule (Bergmann, 1847; Mayr, 1956). Historically Bergmann’s intention was to describe a pattern related to variation in homoeothermic vertebrates (James, 1970; Shelomi, 2012). This rule is now widely tested (James, 1970; Blackburn, *et al*. 1999) from the population to the community level of vertebrates (Millien, *et al*. 2006; O’Gorman, *et al*. 2012). Several reviews have highlighted that the percentage of vertebrates conforming to this rule is relatively high, ranging from 62% to 83% (Ray, 1960; Atkinson, 1994; Millien, *et al.* 2006). Initially, the rule was suggested to derive from an adaptive response related to thermoregulation, as a smaller surface area to volume ratio improves heat conservation (Bergmann, 1847; Mayr, 1956). Alternative mechanisms, both adaptive (e.g., costs and benefits of life history traits and natural selection) and non-adaptive (e.g., effects of temperature on biochemical processes), have also been proposed to better explain Bergmann’s rule (Atkinson, 1994; Angilletta & Dunham, 2003). Angilletta, *et al.* (2004) suggested that no general mechanisms could describe these size variations, and that observed patterns are probably multifactorial in their origins. Despite this, “Bergmann’s rule” or “Bergmann’s rule *sensu lato*” (Shelomi, 2012), is now largely accepted by most authors as a name for the pattern of larger body size of homeothermic organisms in colder climates (Meiri, 2010). However, it is still debated for poikilothermic organisms (Atkinson, 1994; Angilletta & Dunham, 2003). Global studies are largely missing for many poikilothermic groups even though they constitute more than 99% of the global species diversity (Wilson, 1992; Atkinson & Sibly, 1997).

In arthropods, several studies have found patterns consistent with Bergmann's rule, for example some ants (Cushman, *et al.* 1993), antlions (Arnett & Gotelli, 1999), European butterflies (Nylin and Svärd, 1991), bumblebees (Peat, *et al.* 2005; Ramirez-Delgado, *et al.* 2016; Scriven, *et al.* 2016) and fruit flies (Azevedo, *et al.* 1998). In contrast, body size of some spiders (Entling, *et al.* 2010), and more generally larger arthropods (Blanckenhorn & Demont, 2004; Shelomi, 2012), often decreases in colder climates. Moreover no cline has been found in some groups of butterflies (Hawkins & Lawton, 1995; Garcia-Barros, 2000) and families of bees (i.e. Apidae, Colletidae and Halictidae) (Hawkins, 1995). Shelomi (2012) concluded that no global pattern could have been detected in insects, partly because of the huge differences among the study designs and the high diversity of species traits. Whereas most studies have investigated only one or few related species (e.g., Garcia-Barros, 2000; Radmacher & Strohm, 2010), comprehensive studies of species assemblages at a phylogenetically larger scale could identify the traits and the ecological conditions that generate different patterns of latitudinal size variation.

Bees are a highly diverse pollinator group (Michener, 2007) of more than 20,000 species worldwide (Ascher & Pickering, 2016) and ~2,000 species in Europe (Rasmont, *et al.* 2017). Three previous studies of bees have found contrasting responses, with a Bergmann's cline in American Andrenidae (Hawkins, 1995) but a converse Bergmann's cline in few European bumblebees and American Melittidae (Hawkins, 1995; Peat *et al.*, 2005; Ramirez-Delgado *et al.*, 2016). While Hawkins *et al.* (1995) assessed the relationship at the family level in eastern United-States; Peat *et al.* (2005) only assessed the relationship for 22 species of bumblebees in Great-Britain. Latitudinal clines in bees are generally understudied, and there is a need for a continental scale assessement focusing on a range of genera and life history traits to help us identify the potential drivers of observed trends. Bees display a wide range of life history traits which vary at different taxonomic levels (i.e., family-, genus-, or species-specific) and which may be important in order to determine whether bees follow the Bergmann's rule or not.

In this study, we used an extensive dataset of 615 bee species from 21 genera recorded in West-Palearctic, to establish the relationship among body size, life history traits (i.e. sociality and nesting behaviour) and latitude at the community level. This constitutes the largest single bee study of Bergmann's rule (Appendix S1 in Supporting information), and we test the following hypotheses. (1) Bishop & Armbruster (1999) argued that in bees, there would be an advantage to being larger in colder habitats because of a thermoregulatory advantage. In addition, social and solitary bees are known to display different degrees of endothermy, with greater endothermy found in social and/or larger species (Heinrich, 1993), thus we expect that the majority of bee genera will follow Bergmann's rule as an adaptation for heat conservation in cold climate. (2) In contrast, shorter season towards the poles can constrain food resources, development time and growth which result in smaller bee species being found in colder conditions. Large univoltine bees, such as bumblebees, which can live in arctic climates, are thus expected to show the converse cline because of those season length constraints. (3) Bee sociality ranges from solitary to highly eusocial and from cleptoparasitic to free-living behaviour (Michener, 2007). In most eusocial species, temporal and caste variability in body size could allow larger bees to forage in colder temperature, because of their greater thermoregulatory abilities which allow them to be active in colder conditions when solitary bees of the same size can not forage (Heinrich, 1993). Thus sociality may allow bees to be more independent from environmental temperature variations (i.e. neutral cline). (4) Moreover, bees also exhibit different nesting behaviour such as below-ground or inside dead plant stems (Michener, 2007), which could also affect the type of latitudinal cline seen. Depending on the location of the nest (below- or above-ground), bees may be buffered against temperature in different ways. Ground-nesting species could be better insulated from temperature variations than above-ground nesting species and so could be less likely to conform to Bergmann's rule.

Material and Methods

Bee distributional data were collected from a database hosted at the University of Mons (http://zoologie.umh.ac.be/hymenoptera) and from a database of M. Kuhlmann for bees of the genus *Colletes* (unpublished data) at a 50 km x 50 km (CGRS) grid across the West Palearctic region (i.e. 3,032 sampled squares; Fig. 1). Data on bee body size were collected from a database hosted by the University of Reading and contributed to by DM and MK. Female body size was estimated based on the intertegular distance (ITD), which is the distance in millimetres between the two insertion points (tegulae) of the wings. This distance is strongly correlated with the bee body size (Cane, 1987). We only considered females of solitary bees and of social halictids and queens of bumblebees because they almost always experience climatic conditions for a longer part of the year than males, and are crucial for founding the next generation. For each species, the same ITD value was attributed for each dot and was calculated as the mean of the ITD based on ten specimens. The total dataset contained 615 bee species of 21 genera (i.e. species for which we had available distributional and ITD data) recorded in the West Palearctic region (i.e. nearly 20% of the wild bee species pool of the area and 26% of the European wild bee species; Rasmont, *et al*. 2017) (Appendix S1 in Supporting Information). Unfortunately, phylogenetic distances among bee species could not be included in our analysis as they are largely unknown. Additionally, two life history traits were studied, namely sociality and nesting behaviour (Westrich, 1990; Richards, 1994; Schwarz *et al*. 2007). We assigned three categories of sociality according to Michener (2007): (i) social bees (i.e. from facultative cooperation to eusociality; n = 49 species), (ii) solitary bees (n = 553), and (iii) parasitic bees (n = 13); and two types of nesting behaviour of solitary bees: (i) ground-nesting (n = 532), including species nesting in pre-existing cavities and mining bees, and (ii) above-ground stem-nesting bees (n = 27). There is a potential bias in the dataset towards ground-nesting solitary bees since data of many stem-nesting solitary bee species did not allow performing the analysis.

~~First we calculated Pearson correlation coefficients to explore the relationship between latitude and mean body size.~~ We ~~then~~ assessed the relationship between latitude and mean body size at three different levels. In each 50 km x 50 km grid cell, we estimated the mean body size (i) for all bee species taken together (i.e. mean body size at the community level), (ii) for each genus comprising at least 8 species (i.e. to display minimum variability; *Andrena*, *Bombus*, *Ceratina*, *Colletes*, *Dasypoda*, *Halictus*, *Lasioglossum*, *Melitta*, *Panurgus*, *Panurginus*) with available distributional data and body size information (i.e. mean body size at the genus level), and (iii) for each life history trait (i.e. sociality and nesting behaviour; mean body size for each level of each life history trait). We computed the analysis for each genus separately to explore the variability in the dataset, to be able to compare our results to previous studies (i.e. previous studies performed clades-based analysis) and because life history traits are highly conserved at the generic level (e.g. all the species of *Andrena* genus are solitary and ground-nesting bees). Using the 16 different size datasets (i.e the global dataset, ten genera and five life history traits), we performed separate~~a~~ Generalized Least Squares fitted linear model (GLS) with Bonferroni’s adjustment to assess the relationship between the average body size (i.e. dependent variable) and the latitude (i.e. independent variable), taking into account the spatial autocorrelation (gls function in the R-package “nlme”)~~.~~. This statistical model including latitude as fixed effect factor was compared to the intercept-only model. Since the former model provided the lowest Akaike Information Criterion (AIC), it has been selected for interpretations of the global analysis and each subset of trait-analysis (Akaike, 1974) (Table 1). The number of statistical individuals and the relative importance of the latitude are mentionned in Table 2. We also calculated the pseudo-R² statistics to assess the explanatory power of each model. An ANCOVA was used to compare the regression slopes of the GLS models assessing the relation between the latitude and either the nesting behaviour or the sociality and assess differences in the rate of size variation inside those two life history traits for the different levels (i.e. ground or above ground-stem nesting behaviour and social, solitary or parasitic bees). When the interaction was significant~~ly different from zero~~, we tested for the effet of latitude on body size in each level of categorical variable~~multiple pairwise comparisons~~ with Bonferroni's adjustment were performed for categorical variables with more than two levels. Statistical analyses were performed using the software R version 3.3.1 (2016, https://www.r-project.org/).

Results

Regardless of the genus and the life history trait, bee intertegular distance ranged from 0.63 mm to 7.52 mm with a mean at 2.44 mm. *Bombus* was the largest genus with a species mean of 5.63 mm and *Panurginus* was the smallest one with a mean of 1.31 mm. Stem-nesting solitary bees (mean of 2.4 mm) were not significantly larger than ground-nesting solitary bees (mean of 2.13 mm; t-test; $p = 0.45$). While the intertegular distance range was larger for stem-nesting solitary bees (from 0.74 mm for *Ceratina parvula* to 7.52 mm for *Xylocopa valga*), this range was narrower for ground-nesting solitary bees (from 0.65 mm for *Dufourea halictula* to 4.35 mm for *Habropoda tarsata*). Social bees were not significantly different (mean of 5.88 mm) than parasitic bees (mean of 4.69 mm) (t-test; $p = 0.3037$), but they were both significantly larger than solitary bees (mean of 2.15 mm) (t-test; $p < 0.001$).

The mean body size of bee assemblages followed the Bergmann's rule and the size significantly increased with higher latitudes (Fig. 2a; Table 2;; $R^2 = 0.525$; $p < 0.001$). Analyses per genus revealed contrasting patterns: (i) *Andrena*; $R^2 = 0.06$), *Dasypoda*; $R^2 = 0.1$), *Halictus* ($R^2 =$

0.02)~~, *Lasioglossum* ($R^2 = 0.01$)~~ and *Panurginus* ($R^2 = 0.73$) followed the Bergmann's rule (Fig. 2b; Table 2; $p < 0.001$); (ii) *Bombus* ($R^2 = 0.23$), ~~*Ceratina* ($R^2 = 0.02$),~~ *Colletes* ($R^2 = 0.02$) and *Melitta* ($R^2 = 0.22$) followed the converse to Bergmann's rule (Fig. 2c; Table 2; $p < 0.001$); and (iii) *Ceratina* ($R^2 = 0.01$), *Lasioglossum* ($R^2 = 0.01$) and *Panurgus* ($R^2 = 0.01$) did not display any significant relationship between mean body size and latitude (Table 2; $p > 0.05$). All social ($R^2 = 0.02$), solitary ($R^2 = 0.07$) and parasitic ($R^2 = 0.11$) species followed Bergmann's rule (Fig. 2d, e, f; Table 2; $p < 0.001$). However, the slopes of the three regression lines (one for social species, one for solitary species and one for parasitic species) were significantly different from each other ($p < 0.001$). Body size variation according to latitude was stronger in solitary species than in social ones ($p = 0.006$) and was highest for parasitic species (parasitic/solitary species, $p < 0.001$; parasitic/social species, $p < 0.001$). Similarly, both ground-nesting ($R^2 = 0.01$) and stem-nesting species ($R^2 = 0.03$) displayed a Bergmann's cline (Table 2) but the pattern was stronger in stem-nesting bees than in ground-nesting ones ($p < 0.001$).

Discussion

Our global dataset of 615 bee species conform to Bergmann's rule (i.e. larger body size in higher latitudes). At the generic level, five genera followed Bergmann's rule, four genera followed the converse Bergmann's rule, and only one did not show significant clines. However, while the pseudo-R^2 statistic reached 0.525 for the global analysis, we have to mention that most of the pseudo-R^2 statistics at genus level and in trait analyses were low (i.e. respectively six and five pseudo-R^2 statistics that are lower than 0.1). Thus even if the latitude seems to repeatedly impact body size cline, the results have to be taken carefully. Latitude is obviously far from being the only predictor of the body size trends, and probably not the major driver for most of the clades. Seven~~Nine~~ out of the ten genera significantly followed a latitudinal cline whether it was a Bergmann's cline or converse Bergmann's cline. Globally, no dominant drivers have been identified to explain body size patterns across literature. Moreover the observed differences among the genera cannot be readily explained by the nesting and sociality traits used in this analysis. Indeed, while *Melitta* and *Andrena* genera exhibit the same life history traits (i.e. solitary and ground nesting bees), their clines are different. Thus additional non-tested traits could impact strongly on the Bergmann's cline and generate those differences. For example, the level of floral specialization differs strongly among different genera. While *Melitta* species are all oligolectic (Michez & Eardley, 2007), *Andrena* species display a wide range of pollen diet (i.e. from monolectic to polylectic; Westrich, 1990). Most protein-rich pollens can produce larger adults (Roulston & Cane, 2002); consequently host plants could be a strong driver of the body size clines. Additionnal physiological mecanisms could strengthen this trend: higher temperatures imply a higher metabolic rate and an accelerated growth rate (i.e. often correlated with the number of generations), leading to smaller body size (Angilletta & Dunham, 2003; Kingsolver & Huey, 2008). Moreover a phylogenetic signal of the pattern of body size variation can also be found at interspecific level (Ashton, 2004). Latitudinal clines of the body size may be, at least, as much linked to a phylogenetic signal than to ecological factors. However, the current phylogeny of several bee families does not allow investigating deeply this hypothesis. Variation in selection gradients producing these clines could explain why there is a patterned variety of responses documented in the literature (i.e. from Bergmann's rule to converse Bergmann's rule with all intermediate clines; see Blanckenhorn and Demont, 2004).

There are very few studies as a benchmark for bees. Previously, only one study analyses the variation of bee body size at the continental scale (i.e. in United States), but size was only assessed at a family level (Hawkins, 1995). This study found that Andrenidae was the only family to follow the Bergmann's rule. This is consistent with our results that found that two out of three genera of the Andrenidae family also followed the Bergmann's rule (i.e. *Andrena* and

Panurginus). However, Hawkins (1995) focuses on Eastern United States between the 25th and the 50th parallel north. Thus it may have missed significant trends from northern populations that could exhibit a larger size as an adaptation to colder climates (e.g. Halictidae for which no significant relationship was found in his study). In the paper of Hawkins (1995), Melittidae was the only family to follow the converse Bergmann's rule. Of the two genera of the Melittidae in our study (*Dasypoda* and *Melitta*), only *Melitta* followed a converse Bergmann's rule. Conversely the results of a recent study contrast ours: Scriven *et al.* (2016) showed that at the scale of Great Britain, and in a complex of three cryptic bumblebee species, Bergmann's rule was followed. Similarly, Peat *et al*. (2005) showed that workers of bumblebees were larger in colder climates than in more temperate climates in Great Britain. They also assessed this relationship at a larger geographical scale, however they only selected five species from cold climates and five from hot (Mediterranean or tropical) climates. The framework and the sampling of these two previous studies particularly contrasts with ours, which studied the body size variation of queens belonging to 51 bumblebee species at the continental scale. Studies at inter-specific level with only a few species, and at a small geographical scale, can miss larger clines (Shelomi, 2012) and this is maybe the reason why our results differ from those studies. Indeed, in a recent study focused on bumblebees using a phylogenetic approach including 91 *Bombus* taxa, Ramirez-Delgado *et al*. (2016) found that bumblebees followed a converse Bergmann's rule.

Thermoregulation and Bergmann's rule in bees

Our results support the hypothesis that thermoregulation could be a notable driver of Bergmann's cline in bees. A larger size is associated with a higher mass of thoracic muscles and smaller surface/volume area, which improves the thermoregulation capabilities when associated with partial endothermy (Heinrich, 1993). Indeed, as heat loss and metabolic heat production are proportional to total body surface area and thoracic volume respectively, the production of metabolic heat cannot compensate for heat loss in smaller body sizes. This implies that smaller bees cannot elevate their thoracic temperatures above the operative environmental temperature (Bakken, 1976; 1980), which is crucial for flying, particularly at low temperatures. The result based on our global dataset (i.e. 615 species) corroborates this hypothesis: largest species assemblages are found in northern Europe. This mechanism could explain why bigger *Andrena* ~~, *Lasioglossum*~~ and *Halictus* are found in northern areas such as Scandinavia, and even in the Arctic Circle for some species (e.g. *Andrena barbilabris, A. lapponica, A. ruficrus*). ~~Similarly, several Halictidae species (genera of *Halictus* and *Lasioglossum*) can be found in colder habitats like Scandinavia.~~ Moreover, the strength of the Bergmann's cline in the global analysis could be driven to the presence of the bumblebees, which constitute most of the bee fauna at higher latitudes. Indeed, bumblebees are particularly well-adapted to sub-arctic and arctic climates, not only because of their greater body size and their better physiological thermoregulatory abilities (Bishop & Armbruster, 1999), but also because of their longer and denser fur (Heinrich, 1993; Peters *et al.*, 2016). However, we also found a significant Bergmann's cline when bumblebees were removed from the analysis ($p < 0.001$).

Season length and converse Bergmann's rule in bees

We corroborate this hypothesis, as it seems that for bumblebees (displaying one of the highest pseudo-R^2, i.e. 0.23), food rewards, and not thermoregulation advantages, are the major drivers of body size cline. Indeed in most univoltine species, a "season length effect" could occur. In wild bees, adult body size depends on the amount of food (e.g. Johnson, 1990). Consequently, a shorter foraging season in colder habitats limits the growth and thus the body size of the bees due to the shorter period of food availability (Adolf & Porter, 1996; White, 2008). Thus bees are not able to collect a large amount of food and reach large body size, or they have to spend a lot of energy in foraging at longer distances. These season and food restrictions could have a particularly strong effect on arctic bumblebees. Moreover, the largest bees tend to be found in the tropics, which support the hypothesis that season length and resource availability can be crucial constraints (Roubik, 1989). Even if a larger size can be unfavourable for flying in warmer habitats, some bee species have developed morphological (e.g. lighter-coloured insects in warmer conditions; Zeuss *et al*., 2014) and behavioural adaptations (Willmer & Stone, 2004). For instance, some species do not fly during the hotter parts of the day (Willmer & Stone, 2004) or increase their flight speed to favour thermoregulation (Heinrich, 1993). In contrast, some smaller solitary bees occur only in warmer microclimates or during the warmest part of the day in colder habitat (Willmer & Stone, 2004).

Sociality and nesting behaviour

Those two life history traits do not seem to be the main drivers of the discrepancy between Bergmann’s and converse Bergmann’s rule. Indeed, all the life history traits of our study produced a Bergmann’s cline. However, the slopes between the different traits were significantly different which means that the intensity of the Bergmann’s cline differed depending on the traits. Ground-nesting solitary bees seemed to be buffered against this latitudinal cline and respond less strongly than the stem-nesting solitary bees. Indeed, ground-nesting bees may be better isolated from the climatic variations and so be less likely to conform to Bergmann’s rule. When we assessed the impact of the different types of sociality and included social *Halictus* and *Lasioglossum* species with the bumblebees, we found that social bees followed the Bergmann’s cline. However, this could reflect our dataset composition, as social Halictidae are smaller than bumblebees and mainly live in lower latitudes, which leads to this Bergmann’s cline. Even if we only add six species of social Halictidae in the sociality analysis, their southern distribution compared to the distribution of bumblebees induced a Bergmann’s cline. Similarly, smaller parasitic bees of solitary bees mostly inhabit latitudes below 55°, while parasitic bumblebees of the sub-genus *Psythirus* can live at latitude up to 70°, which again leads to a Bergmann’s cline. Moreover, social bees may respond less strongly to latitude than solitary bees. For instance, bumblebee workers are able to cool the entrance of the nest and buffer against hotter climates. Nevertheless this may only be part of the explantion since those mechanisms of cooling are not known in others wild social bees. Additionaly, analysis on solitary bees together could be biased by *Andrena* genus since *Andrena* species represent more than the half of the solitary bee species in our data set. *Andrena* genus is also the bee genus including the largest number of species in Europe and the Bergmann’s cline in solitary bee analysis could be largely explained by them.

Conclusion

Our results suggest that bees at full community level follow the Bergmann’s rule but analysis at generic level revealed different clines. Nonetheless there is a major trend for bees being larger in colder habitat. Indeed (1) it is very likely that their thermoregulatory abilities and partial endothermy are strong drivers of this latitudinal cline as reported in most genera of solitary bees. However, (2) shorter season length in higher latitudes could be a major driver of the converse Bergmann’s cline, notably in bumblebees which have longer phenology and face arctic conditions. In agreement with our hypotheses, while all sociality (3) and nesting behaviours (4) produced Bergmann’s cline, both social and ground-nesting bees seemed to be buffered against latitudinal clines. We suggest that further studies should focus on unexplored drivers of the body size latitudinal clines (e.g. floral ressources and pollen nutritional quality) and complete the distributional and ITD dataset of European bees with missing genera (e.g. *Megachile*, *Nomada* and *Osmia*) and have a better representation of the European bee fauna.

Acknowledgments

This research project was funded by the Belgian *Fonds pour la Recherche Scientifique* (FRS-FNRS; FRFC 2.4613.10). We acknowledge the support of the European Commission Framework Programme (FP) 7 via the Integrated Project STEP (grant no. 244290, Potts *et al*. 2011). MG is supported by a grant from the Belgian *Fonds pour la Recherche dans l'Industrie et l'Agriculture* (FRIA) and MV is FNRS grant fellowship "Chargé de recherches". The authors declare that there is no conflict of interest regarding the publication of this article.

Authors' Contributions

MV, DM and VD conceived the ideas and designed methodology; MG and OS collected the data; MG and MV analysed the data; MG led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

All body size data are available in Supporting Information. Distributional data will be available on the Dryad database as an excel file once the paper will be accepted.

References

Adolf, S.C. & Porter, W.G. (1996) Growth, Seasonality and Lizard life histories: age and size at maturity. - Oikos 77: 267-378.

Akaike, H. (1974) A new look at the statistical model identification. - IEEE Trans.Autom. Control 19: 716-723.

Angilletta, M.J. & Dunham, A.E. (2003) The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. - Am. Nat. 162: 333-342.

Angilletta, M.J., Steury, T.D. & Sears, M.W. (2004) Temperature, Growth Rate, and Body Size in Ectotherms: Fitting Pieces of a Life-History Puzzle. - Integr. Comp. Biol. 44: 498-509.

Arnett, A.E. & Gotelli, N.J. (1999) Bergmann's rule in the ant lion Myrmeleon immaculatus (Neuroptera: Myrmeleontidae): geographic variation in body size and heterozygosity. - J. Biogeogr., 26: 275-283.

Ascher, J.S. & Pickering, J. (2016) Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Available online at http://www.discoverlife.org/mp/20q?guide=Apoidea_species&flags=HAS.

Ashton, K.G. (2004) Comparing phylogenetic signal in intraspecific and interspecific body size datasets. - J. Evolution. Biol. 17: 1157-1161.

Atkinson, D. (1994) Temperature and organism size – a biological law for ectotherms? - Adv. Ecol. Res., 25: 1-58.

Atkinson, D. & Sibly, R. (1997) Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. - Trends Ecol. Evol., 12: 235-239.

Azevedo, R.B.R, James, A.C., McCabe, J. & Partridge, L. (1998) Latitudinal variation of wing: thorax size ratio and wing-aspect ratio in *Drosophila melanogaster*. - Evolution, 52: 1353-1362.

Bakken, G.S. (1976) A heat transfer analysis of animals: uniflying concepts and the application of metabolism chamber data to field ecology. - J. Theor. Biol., 60: 337-384.

Bakken, G.S. (1980) The use of standard operative temperature in the study of the thermal energetics of birds. - Physiol. Zool. 53: 108-119.

Bergmann, C. (1847) Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. - Göttinger Studien 1: 595-708.

Bishop, J.A. & Armbruster, W.S. (1999) Thermoregulatory abilities of Alaskan bees: effects of size, phylogeny and ecology. - Funct. Ecol. 13: 711-724.

Blackburn, T.M., Gaston, K.J. & Loder, N. (1999) Geographic gradients in body size: a clarification of Bergmann's rule. - Divers. Distrib. 5: 165-174.

Blanckenhorn, W.U. & Demont, M. (2004) Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? - Integr. Comp. Biol. 44, 413-424.

Cane, J.H. (1987) Estimation of bee size using intertegular span (Apoidea). - J. Kans. Entomol. Soc. 60: 145-147.

Cushman, J.H., Lawton, J.H. & Manly, B.F.J. (1993) Latitudinal patterns in European ant assemblages: variation in species richness and body size. - Oecologia 95: 30-37.

Entling, W., Schmidt, M.H., Bacher, S., Brandl, R. & Nentwig, W. (2007) Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. - Glob. Ecol. Biogeogr. 16: 440-448.

Garcia-Barros, E. (2000) Body size, egg size, and their interspecific relationships with ecological and life history traits in butterflies (Lepidoptera: Papilionoidea, Hesperioidea). - Biol. J. Linn. Soc. 70: 251-284.

Hawkins, B.A. (1995) Latitudinal body-size gradients for the bees of the eastern United States. - Ecol. Entomol. 20: 195-198.

Hawkins, B.A. & Lawton, J.H. (1995) Latitudinal gradients in butterfly body sizes: is there a general pattern? - Oecologia, 102: 31-36.

Heinrich, B. (1993) The Hot-blooded Insects: Strategies and mechanisms of Thermoregulation. Harvard University Press, Cambridge, MA: 1993.

IPCC (2007) Climate Change 2007: Synthesis Report. Contributions of working groups I, II, and III to the fourth assessment report of the Intergovernmental Panel on Climate Change. (eds R Pachauri & A Reisinger). IPCC, Geneva, Switzerland.

James, F.C. (1970) Geographic size variation in birds and its relationship to climate. - Ecology. 51: 385-390.

Johnson, M.D. (1990) Female size and fecundity in small carpenter bee, Ceratina calcarata (Robertson) (Hymenoptera Anthophoridae). - J. Kans. Entomol. Soc. 63: 414-419.

Kingsolver, J.G. & Huey, R.B. (2008) Size, temperature, and fitness. - Evol. Ecol. Res. 10: 251-268.

Kuhlmann, M., Ascher, J.S., Dathe, H.H., et al. (2014). Checklist of the Western Palaearctic bees. Available at: westpalbees.myspecies.info.

Mayr, E. (1956) Geographical character gradients and climatic adaptation. - Evolution, 10: 105-108.

Meiri, S. (2010) Bergmann’s Rule – what’s in a name. - Glob. Ecol. Biogeogr. 20, 203-207.

Michener, C.D. (2007) The bees of the world. Baltimore, MD: Johns Hopkins University Press.

Michez, D. & Eardley, C. (2007) Monographic revision of the bee genus *Melitta* Kirby 1802 (Hymenoptera: Apoidea: Melittidae). - Ann. Soc. Entomolo. Fr. 43: 379-440.

Millien, V., Lyons, S., Olson, L., Smith, F., Wilson, A.L. & Yom-Tov, Y. (2006) Ecotypic variation in the context of global climate change: revisiting the rules. - Ecol. Lett. 9: 853-869.

Nylin, S. & Svärd, L. (1991) Latitudinal patterns in the size of European butterflies. - Holarctic Ecol. 14: 192-202.

O'Gorman, E.J., Pichler, D.E., Adams, G. & Benstead, J.P. (2012). Impacts of warming on the structure and functioning of aquatic communities: individual- to ecosystem-level responses. - Adv. Ecol. Res. 47: 81-176.

Peat, J., Darvill, B., Ellis, J. & Goulson, D. (2005) Effects of climate on intra- and interspecific size variation in bumble-bees. - Funct. Ecol. 19: 145-151.

Peters, M.K., Peisker, J., Steffan-Dewenter, I. & Hoiss, B. (2016) Morphological traits are linked to the cold performance and distribution of bees along elevational gradients. J. Biogeogr. 43: 2040-2049.

R Development Core Team (2016) R: A language and environment for statistical computing, version 3.3.1, ISBN 3-900051-07-0. R Foundation for Statistical Computing. Vienna. Austria.

Radmacher, S. & Strohm, E. (2010) Factors affecting offspring body size in the solitary bee *Osmia bicornis* (Hymenoptera, Megachilidae). - Apidologie, 41: 169-177.

Ramírez-Delgado V.H., Sanabria-Urbán S., Serrano-Meneses M.A., Cueva Del Castillo R. (2016) The converse to Bergmann's rule in bumblebees, a phylogenetic approach. - Ecol. Evol. 6: 6160-6169.

Rasmont, P., Devalez, J., Pauly, A., Michez, D., Radchenko, V.G. 2017. Addition to the checklist of IUCN European wild bees (Hymenoptera: Apoidea). - Ann. Soc. Entomol. Fr. 53: 17-32.

Ray, C. (1960) The application of Bergmann's and Allen's rules to the poikilotherms. - J. Morphol. 106: 85-108.

Richards, M.H. (1994) Social evolution in the genus *Halictus*: a phylogenetic approach. Insect. Soc. 41: 315-325.

Roubik, D.W. (1989) Ecology and Natural History of Tropical Bees. Cambridge University Press, Cambridge, UK.

Roulston, T.A. & Cane J. H. (2002) The effect of pollen protein concentration on body size in the sweat bee *Lasioglossum zephyrum* (Hymenoptera: Apiformes). - Evol. Ecol. 16: 49-65.

Schwarz, M.P., Richards, M.H., Danforth, B.N. (2007) Changing paradigms in insect social evolution: insights from halictine and allodapine bees. - Annu. Rev. Entomol. 52: 127-150.

Scriven, J.J., Whitehorn, P.R., Goulson, D. & Tinsley, M.C. (2016) Bergmann's Body Size Rule Operates in Facultatively Endothermic Insects: Evidence from a Complex of Cryptic Bumblebee Species. - Plos One, doi:10.1371/journal.pone.0163307.

Shelomi, M. (2012) Where are we now? Bergmann's Rule Sensu Lato in Insects. - Am. Nat. 180: 511-519.

Westrich, P. (1990) Die Wildbienen Baden-Württembergs. Stuttgart, E. Ulmer.

White, T.C.R. (2008) The role of food, weather and climate in limiting the abundance of animals. - Biol. Rev. 83: 227-248.

Willmer, P.G. & Stone, G.N. (2004) Behavioural, ecological and physiological determinants of the activity patterns of bees. - Adv. Stud. Behav. 34: 347-466.

Wilson, E.O. (1992) The Diversity of Life. Harvard University Press, Cambridge.

Zeuss, D., Brunzel, S. & Brandl, R. (2017) Environental drivers of voltinism and body size in insect assemblages across Europe. - Glob. Ecol. Biogeogr. 26: 154-165.

Table 1. Selection of the model providing the lowest Akaike Information Criterion (AIC) for the global analysis. In bold italic, the selected model.

Models	Degrees of freedom	AIC
ITD ~ 1	df = 3032	8617.141
ITD ~ latitude	df = 3032	6879.03

Table 2. Results from 16 gls models analysing body-size distribution of bee assemblages at generic level and in regard of different life history traits in relation to latitude (n = number of species). The models with the lowest AIC values are shown. N = number of statistical individuals. Significant p-value are in bold.

	Coefficient	**Std. Error**	**t value**	**p-value**	**N**	**Pseudo-R^2**
Bees (n = 615)					3032	0.525
(Intercept)	-0.386	0.074	-5.184	**<0.001**		
Latitude	0.072	0.001	48.699	**<0.001**		
Andrena						
(Andrenidae; n = 310)					2830	0.06
(Intercept)	2.014	0.02	100.33	**<0.001**		
Latitude	0.004	<0.001	10.723	**<0.001**		
Bombus						
(Apidae; n = 51)					2488	0.23
(Intercept)	6.547	0.035	185.808	**<0.001**		
Latitude	-0.017	<0.001	-24.32	**<0.001**		
Ceratina						
(Apidae; n = 22)					852	0.01

(Intercept)	1.848	0.075	24.707	**<0.001**		
Latitude	-0.003	0.002	-3.41	0.052~~**<0.001**~~		
Colletes						
(Colletidae; n = 53)					1070	0.02
(Intercept)	2.94	0.053	55.344	**<0.001**		
Latitude	-0.004	0.001	-4.07	**<0.001**		
Dasypoda						
(Melittidae; n = 14)					715	0.10
(Intercept)	3.151	0.04	78.878	**<0.001**		
Latitude	0.004	<0.001	5.25	**<0.001**		
Halictus						
(Halictidae; n = 34)					1477	0.02
(Intercept)	1.523	0.06	25.175	**<0.001**		
Latitude	0.006	0.001	4.874	**<0.001**		
Lasioglossum						
(Halictidae; n = 65)					1028	0.01
(Intercept)	1.414	0.053	26.799	**<0.001**		
Latitude	0.002	0.001	1.31	0.32~~**0.02**~~		
Melitta						
(Melittidae; n = 8)					704	0.22
(Intercept)	3.463	0.085	40.892	**<0.001**		
Latitude	-0.016	0.002	-9.11	**<0.001**		
Panurginus						
(Andrenidae; n = 11)					163	0.73

(Intercept)	0.242	0.058	4.206	**<0.001**		
Latitude	0.023	0.001	19.549	**<0.001**		
Panurgus						
(Andrenidae; n = 11)					687	0.01
(Intercept)	1.883	0.066	28.354	**<0.001**		
Latitude	<0.001	0.001	0.4	0.686		
Nesting Behaviour						
Ground-nesting bees (n = 532)					2872	0.03
(Intercept)	2.03	0.022	92.062	**<0.001**		
Latitude	0.003	<0.001	7.601	**<0.001**		
Stem-nesting bees (n = 27)					1040	0.03
(Intercept)	1.829	0.05	36.522	**<0.001**		
Latitude	0.005	0.001	4.433	**<0.001**		
Sociality						
Parasitic bees (n = 12)					1595	0.11
(Intercept)	2.49	0.17	14.64	**<0.001**		
Latitude	0.055	0.003	16.82	**<0.001**		
Social bees (n = 43)					2537	0.02
(Intercept)	4.964	0.08	61.905	**<0.001**		
Latitude	0.01	0.002	5.857	**<0.001**		
Solitary bees (n = 560)					2878	0.07
(Intercept)	1.917	0.022	87.34	**<0.001**		
Latitude	0.006	<0.001	12.724	**<0.001**		

Figure legends

Figure 1. Map of the geographic framework and the full data set. Each dot represents a 50 km x 50 km (CGRS) echantillonated square.

Figure 2. Relationship between latitude (°) and intertegular distance (ITD): (a) in the global analysis, bees follow the Bergmann's rule, (b) Andrena follows the Bergmann's rule, (c) Bumblebees (*Bombus*) follow the converse Bergmann's rule, (d) Solitary bees, (e) Social bees and (f) Parasitic bees all follow the Bergmann's rule, but the intensity of the slope was higher for solitary bees than for social bees and the highest for parasitic bees.

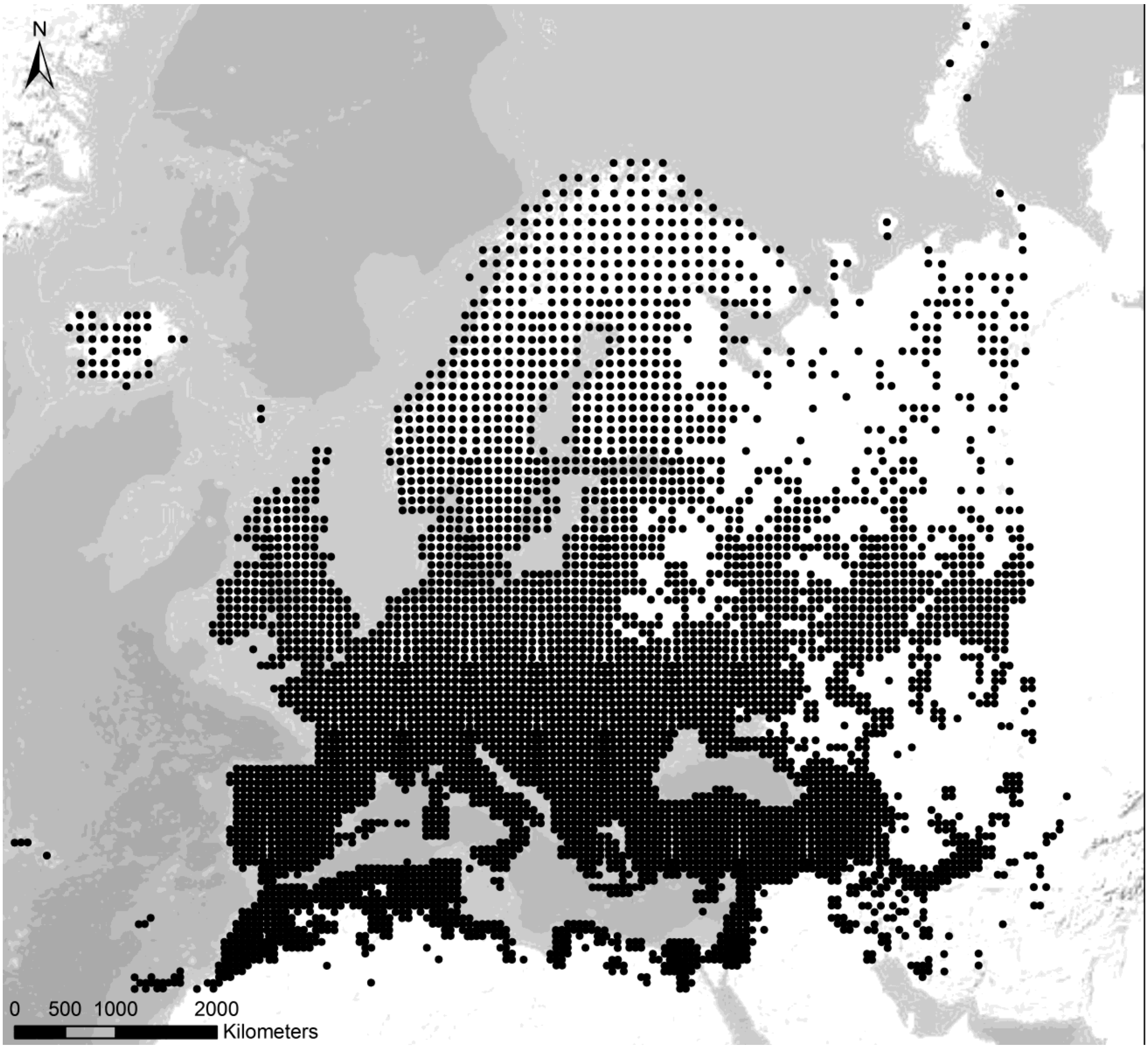

Figure 1.

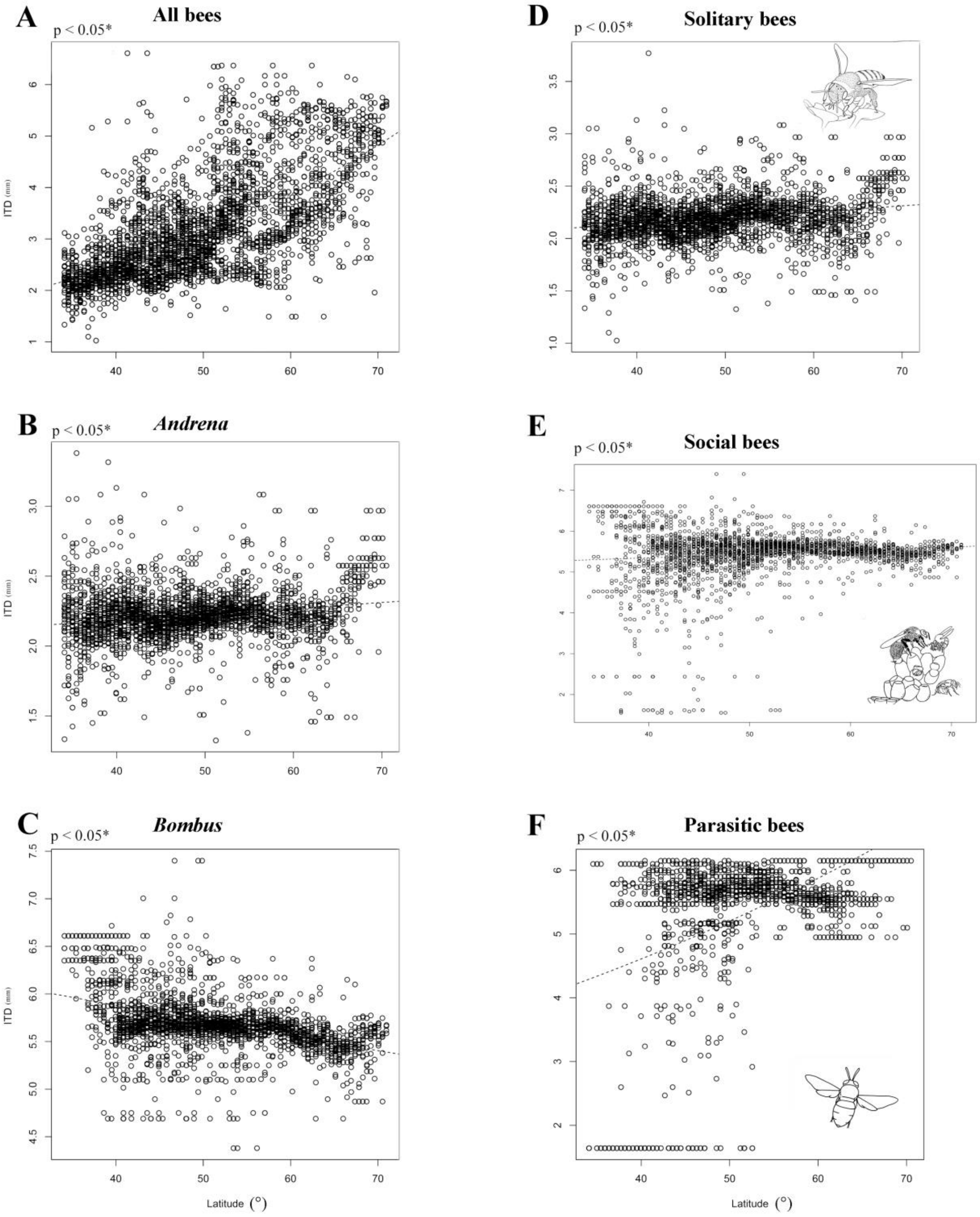
A
All bees
p < 0.05*
ITD (mm)
1
2
3
4
5
6
40
50
60
70
B
Andrena
p < 0.05*
ITD (mm)
1.5
2.0
2.5
3.0
40
50
60
70
C
Bombus
p < 0.05*
ITD (mm)
4.5
5.0
5.5
6.0
6.5
7.0
7.5
40
50
60
70
Latitude (°)
D
Solitary bees
p < 0.05*
1.0
1.5
2.0
2.5
3.0
3.5
40
50
60
70
E
Social bees
p < 0.05*
2
3
4
5
6
7
40
50
60
70
F
Parasitic bees
p < 0.05*
2
3
4
5
6
40
50
60
70
Latitude (°)

Figure 2.