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Global patterns and drivers of buzzing bees and poricidal plants

Highlights

- Distributional patterns differed for buzzing species compared with all bee species
- Drivers of species richness differed for buzzing species compared with all bees
- Poricidal species richness was a major predictor of buzzing species distributions
- Poricidal species richness was highest in areas with low wind and high aridity

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In brief

Russell et al. find that distributional patterns and drivers of species richness differ for buzzing bee species compared with all bee species and within each major family. They also find that poricidal plant species richness (highest in areas with low wind and high aridity) was a major predictor of buzzing species distributions for 4 of 5 bee families.

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Global patterns and drivers of buzzing bees and poricidal plants

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SUMMARY

Foraging behavior frequently plays a major role in driving the geographic distribution of animals. Buzzing to extract protein-rich pollen from flowers is a key foraging behavior used by bee species across at least 83 genera (these genera comprise ∼58% of all bee species). Although buzzing is widely recognized to affect the ecology and evolution of bees and flowering plants (e.g., buzz-pollinated flowers), global patterns and drivers of buzzing bee biogeography remain unexplored. Here, we investigate the global species distribution patterns within each bee family and how patterns and drivers differ with respect to buzzing bee species. We found that both distributional patterns and drivers of richness typically differed for buzzing species compared with hotspots for all bee species and when grouped by family. A major predictor of the distribution, but not species richness overall for buzzing members of four of the five major bee families included in analyses (Andrenidae, Halictidae, Colletidae, and to a lesser extent, Apidae), was the richness of poricidal flowering plant species, which depend on buzzing bees for pollination. Because poricidal plant richness was highest in areas with low wind and high aridity, we discuss how global hotspots of buzzing bee biodiversity are likely influenced by both biogeographic factors and plant host availability. Although we explored global patterns with state-level data, higher-resolution work is needed to explore local-level drivers of patterns. From a global perspective, buzz-pollinated plants clearly play a greater role in the ecology and evolution of buzzing bees than previously predicted.

INTRODUCTION

Bees are one of the most important pollinator groups in both natural and agricultural systems.[1,2] Yet in recent decades, there has been fervent discussion of potential bee declines and their causes.[3–7] Accordingly, understanding the dimensions of bee distribution is fundamental to targeting conservation efforts and to developing strategies to respond effectively to anthropogenic threats, including climate change, agricultural intensification, habitat loss, and urbanization. Furthermore, species vulnerability to environmental change is non-random and is linked to species-specific traits,[8] yet for the majority of species the relationship between traits, habitat breadth, and distribution is only poorly understood.[9–11]

Bees are very diverse, comprising over 20,000 described species, spread among 508 genera and seven families.[12] However, similar to most invertebrates, bees generally lack the data required for high-resolution, global analysis (barring extensive modeling efforts[2,13]), and we have yet to explore how patterns of richness vary among families or how certain traits and their distribution over evolutionary time may influence these patterns. Current efforts to map large-scale patterns and drivers of bee distribution have focused strongly on the broadest phylogenetic patterns and abiotic drivers but without substantial consideration of bee foraging behavior.[2,14,15] This represents a fundamental gap in our understanding of the mechanisms underlying bee richness because how and which flowering plant species bees interact with depends fundamentally on foraging behavior, which should, in turn, influence the geographic distributions of bees. One especially well-studied bee behavior that likely influences global patterns of bee distributions is the ability of many bees to vibrate flowers to extract their pollen (“floral buzzing,”

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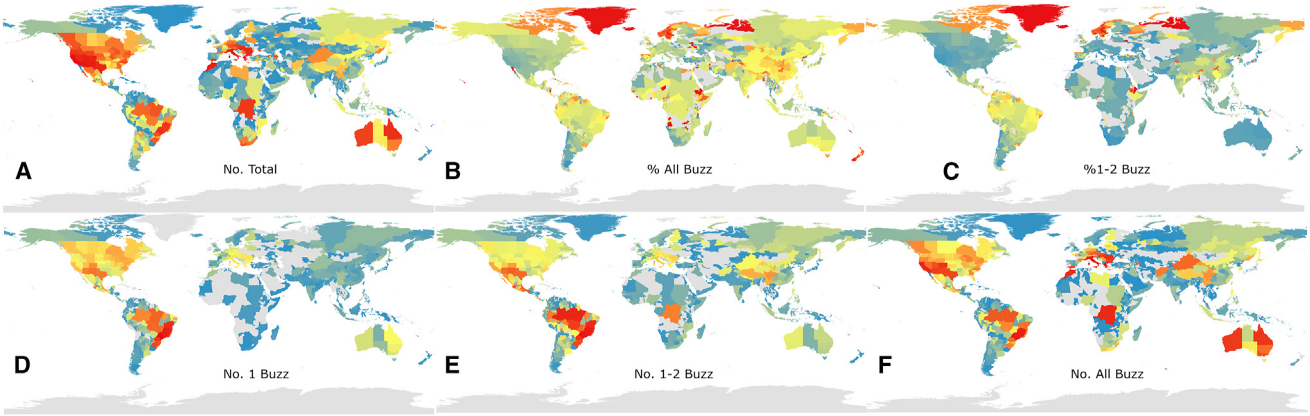

Figure 1. Patterns of richness across regions for all bees and for buzzing bees

Redder colors indicate higher values, blue colors indicate lower values, and gray indicates no species recorded.

(A) Total bee species richness (maximum richness value 1,619).

(B) Percentage of bee species in each region that buzz (categories 1+2+3, the most liberal coding).

(C) Percentage of bee species that buzz (categories 1+2).

(D) Number of buzzing bee species, coded category 1 (maximum 108).

(E) Number of buzzing bee species across categories 1+2 (maximum 238).

(F) Number of buzzing bee species, across categories 1+2+3 (maximum 331). Latitudinal patterns may vary within each family.

Related to Figures S1 and S2 and Data S1 and S5.

"floral sonication," or "buzzing"). Yet where and why this behavior may be selected for, and even just how this trait varies geographically, remain unknown. Although buzzing is a widespread and potentially key driver of bee diversification,[16,17] whether and how global patterns and drivers of bee distribution differ among bee taxa that can buzz versus cannot buzz is unknown.

Buzzing is performed by bee species from across all seven bee families and at least 83 genera (these genera comprise ~58% of all bee species[17]; Data S1). Buzzing typically involves the bee biting the flower (usually the anthers), decoupling its flight muscles from its wings, and contracting these muscles rapidly to shake loose the pollen from the anthers.[18–20] Although bees use buzzing to collect protein-rich pollen more effectively from many kinds of plant species,[20–22] this behavior is most associated with extraction of pollen from so-called poricidal flowers—plant species that conceal pollen within tube-like morphology (typically the anthers). As a result, buzzing often enables access to these key floral resources when they would be otherwise inaccessible. Accordingly, buzzing is typically required for pollination of the more than 28,000 plant species across 87 families with poricidal flowers (an estimated 10% of flowering plant species[18,20,23]). Poricidal plant species are also common in agriculture, and pollination of commercial crops, such as tomatoes, cranberries, blueberries, and kiwis, primarily depend on buzzing bees.[24]

Given the importance of buzzing to bee and plant ecology and evolution, we hypothesize that this behavior should influence patterns of bee distributions and diversity and may even be a significant driver of overall richness patterns in taxa where most species "buzz." In particular, because bee taxa with a greater prevalence of buzzing can effectively access pollen from a broader range of hosts,[17,20,22] we predict that, globally, buzzing bee taxa should be more geographically widespread than taxa that do not buzz. Accordingly, assuming that all other key ecological drivers of buzzing and non-buzzing bee taxa are similar, regions with greater bee diversity should have a proportionally greater diversity of buzzing taxa. For instance, xeric and temperate zones are generally correlated with high bee species richness[2]; thus, we would predict that bee taxa in these zones could have a greater number of buzzing species compared with other zones, depending on the distribution of suitable hosts. Conversely, given that buzzing is often taxonomically restricted to bee clades with particular traits and habitats (e.g., buzzing is widespread among the mostly temperate bumble bees and rare among the sub/tropical stingless bees[17]), the distribution and drivers of bee biodiversity may generally differ for buzzing and non-buzzing taxa.

In this study we map, model, and compare the known distribution of bee taxa reportedly capable of buzzing flowers with total richness patterns. We examine the overall richness patterns of buzzing bees, and proportions of buzzing species within each bee family, and explore what the major drivers of these patterns may be, including the distribution of plant species with poricidal flower morphology, to more clearly understand these patterns and why they may have developed. This work thus contributes to our general understanding of how functional traits mediate plant-animal interactions and distribution.[10]

RESULTS

Patterns of bee and trait richness

Patterns of overall bee species richness were largely consistent with previous analyses,[2] with richness peaking in North America (especially in the Southwestern United States), and also areas of the Middle East, Southern South Africa, and Australia (Figure 1). However, the proportions of bee species from each family varied by region. For example, in northern North American states, over

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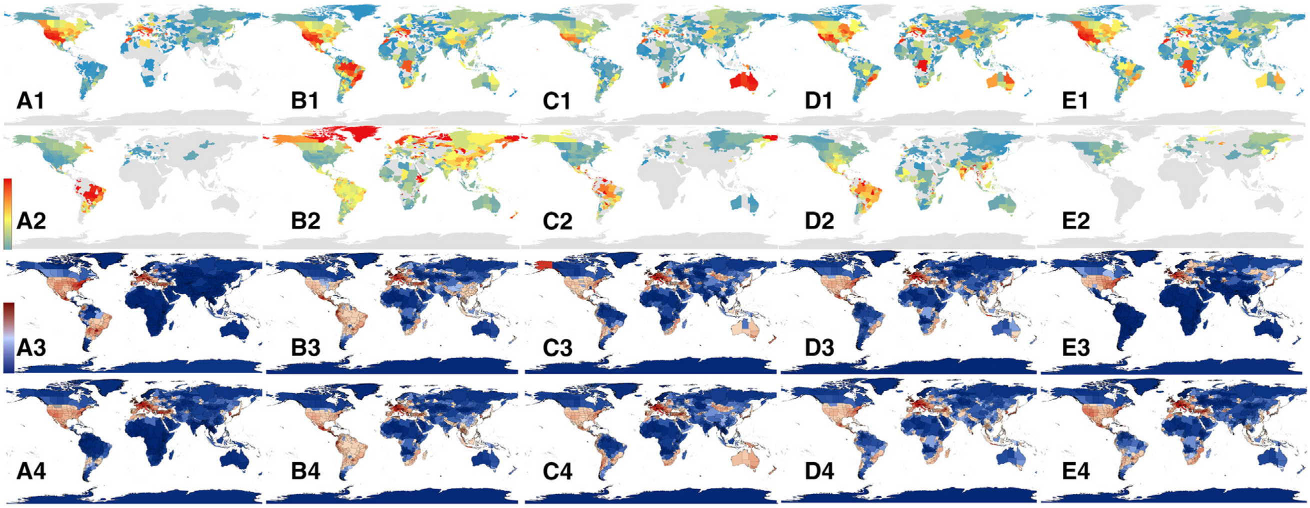

Figure 2. Patterns of richness by family, with redder colors indicating higher values, bluer colors indicating lower values, and gray color indicates no species recorded

(A) Andrenidae (max richness 548), (B) Apidae (max 388), (C) Colletidae (max 334), (D) Halictidae (max 212), and (E) Megachilidae (max 400). Numerical ordering is (1) richness of each family, (2) percentage of buzzing species (categories 1+2), (3) areas with more species than expected per unit area relative to the global average, and (4) areas with more or less species per unit area relative to the global average. Patterns may further differ among genera.

Related to Figures S1–S3 and Data S1, S3, and S5.

50% of bee species were halictids (Figure S1A), but with decreasing latitude, the ratio of Apidae to Halictidae increases so that Apidae eventually becomes the dominant group in terms of species richness. This pattern is similar in South America, with Halictidae dominating in the southeast, followed by Colletidae. In Africa-Europe (Figure S1B), Halictidae overall dominates, followed by Apidae, then Colletidae, but Halictidae dominates in equatorial regions in part given Nomiinae bee dominance, whereas Apidae becomes dominant in southeast Africa. In Asia, Apidae dominates in northern latitudes, but Halictidae becomes more dominant at lower latitudes, in addition to Australia (Colletidae becomes more diverse in Australia-New Zealand) (Figure S1C). Colletidae also generally holds a larger share in the Southern Hemisphere, especially Australia. Thus, global patterns should generally be broken down by region and family because patterns (and likely their drivers) are clearly different between families and regions.

Patterns for buzzing species depart from the overall patterns of richness. In Andrenidae, the patterns in North America (Figures S2A and S2B) and Europe are similar (Figures S2C and S2D); however, a greater percentage of species buzz in South America, where there are many buzzing panurgine bees. By contrast, a much smaller percentage buzz in East Asia or North Africa (where non-buzzing *Andrena* dominates), although these show latitudinal gradients that differ by region. Conversely, in Apidae, patterns are overall similar in most regions, but a greater percentage of species buzz in Northeast Asia (Figure 2), and fewer species buzz in parts of Southern and Southeast Asia (Figures S2E and S2F). For Colletidae, patterns are quite similar between buzzing and non-buzzing species. Halictidae also show similar patterns, although fewer species buzz in western South America. Megachilidae show some distinct differences, with very few species in the Southern Hemisphere buzzing and more temperate species buzzing.

When the percentage of species buzzing per family and region are plotted, different patterns emerge, and these vary depending on how stringent the definition of buzzing is. In the Americas, Apidae and Halictidae buzzing peaks in tropical regions (Figure S2A), where up to around 60% of species buzz in tropical regions using the consensus definition of buzzing (categories 1+2), decreasing at higher latitudes (Figures 2 and S2A). Colletidae also shows this pattern, but not as strongly (and with lower diversity in the tropics), whereas Andrenidae exhibits greater proportions of buzzing at higher latitudes. These patterns shift if a liberal definition of buzzing is used (categories 1+2+3), such that, although Apidae still shows a tropical peak in the proportion of bees that buzz (Figure S2B), Halictidae tends to increase in the Northern Hemisphere, where richness is also higher. However, patterns in other groups change less; thus, a stricter definition was used when trying to understand drivers of the buzzing trait.

In the Europe-Africa region, Halictidae shows a slight peak in the proportion of bees that buzz in equatorial regions (categories 1+2), but Apidae peaks in buzzing in northern latitudes in Europe (Figures 2, S2C, and S1B), and Andrenidae and Colletidae peak slightly in the north, although largely due to low diversity elsewhere. These patterns somewhat disappear if the liberal categorization (1+2+3) is used, although Colletidae shows a much higher percent increase in buzzing in northern latitudes (Figure S2D).

In the Asia-Australia region, Apidae shows the same pattern as in the Europe-Africa region, with increasing percentages of buzzing in northern latitudes likely due to increasing relative richness of *Bombus* and perhaps *Lasioglossum* species, both when stricter buzzing categories (1+2) (Figures S1B, S1C, and S2E) and the most liberal buzzing categorization (1+2+3) are considered (Figure S2F). Halictidae increases in the percentage of buzzing in equatorial regions when using the stricter categories, and there is no strong pattern when the liberal buzz categorization (1+2+3) is considered. Conversely, the percentage of

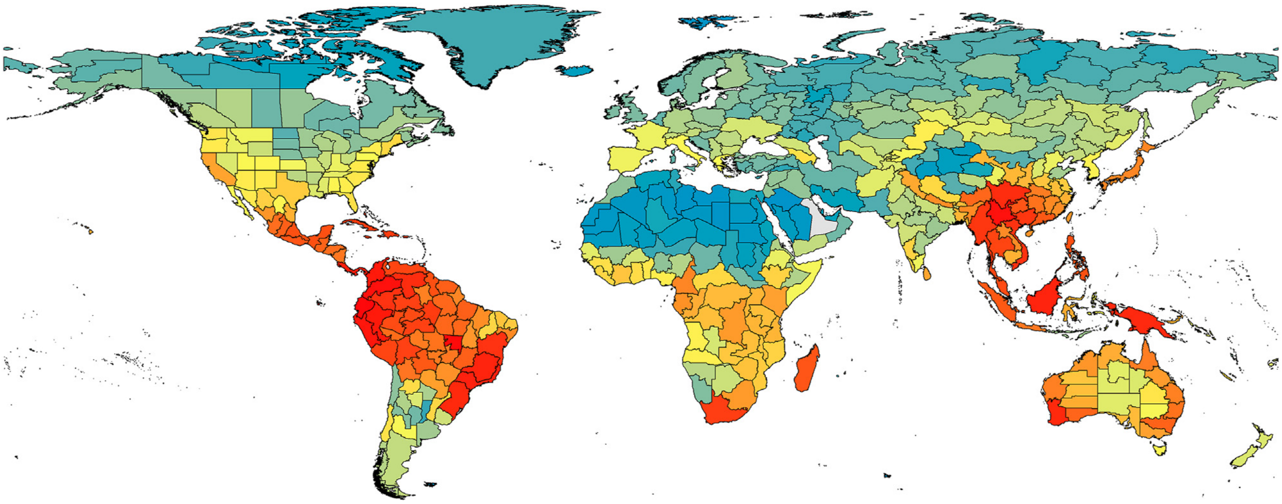

Figure 3. Patterns of richness in poricidal plant species across regions

Maximum richness 2,484.

Related to Data S3, S4, and S5.

buzzing Colletidae species increases in higher latitudes in both the Northern and Southern Hemispheres when the liberal categorization is considered (but only very minor increases in these regions when stricter buzz categories are considered). Megachilidae shows a slight increase in percent buzzing in high latitudes in the Northern Hemisphere (Figure 2).

Some of these regional differences in patterns may reflect the distribution of particular genera with high proportions of buzzing. For example, *Bombus* is a well-studied and widely distributed group of buzzing species, with many of its species in the neotropical regions and few in the paleotropics (Figure S3). This trend and the regional and latitudinal patterns in *Bombus* may be partially responsible for the patterns in percentage of buzzing Apidae species across higher latitudes of Europe, where they are more prevalent and make up a bigger proportion of bee species, and also for Asia (especially the Himalayan region, where *Bombus* are particularly speciose; Figure S3).

Drivers: Broad patterns

There were generally distinct and important differences between models for the percentage of buzzing species and bee overall richness for each family (all regression results are provided in Data S5, see next section for a detailed breakdown of drivers by family). For three of the five families with sufficient diversity and spatial spread for global analysis (Andrenidae, Colletidae, and Halictidae), the richness of poricidal plants was the main variable associated with higher percentages of buzzing species, despite the fact that it was only very weakly correlated with total richness in those families (Data S5), demonstrating a link between buzzing species biodiversity and the plants these bees use. The highly diverse family Apidae also exhibited a positive relationship between poricidal plant richness and buzzing species richness, but there was no relationship of poricidal richness with overall Apidae richness. For Megachilidae, there were no significant relationships with poricidal plant richness; however, we recognize that only a small fraction of species in this family have been observed to buzz flowers (8 of 4,169 total species).

The drivers differed by bee family, and for overall richness versus the percentage of buzzing species (Data S5). These differences may also be amplified in different regions based on species biogeography and prevailing conditions.[25] Given the high importance of poricidal richness for buzzing in many bee taxa, we then explored whether poricidal richness might be driven by elements of arid climates, given its importance to bee richness.[2] Unsurprisingly, total plant species richness was a major correlate of poricidal plant species richness, explaining why poricidal richness rarely appeared in most overall bee species richness models but was in most buzzing species richness models. The next most important correlate for poricidal plant species richness was a negative relationship with continentality and then a strong negative relationship with latitude. Poricidal richness was overall associated with higher plant richness, lower latitudes, low continentality, low wind, high aridity, and high evapotranspiration. The value of poricidal richness in many models of buzz percentage is likely to have reduced model reliance on co-occurring factors of higher aridity and low wind that co-occur with higher poricidal richness. Furthermore, in terms of mean values retrieved from the Lozada-Gobilard et al.[26] dataset, the average altitude and sampling aridity of poricidal versus non-poricidal plants was very similar (1,398.5–1,393.6 m; 4.07–4.3), whereas poricidal plants had a slightly higher mean latitude (18.5° for non-poricidal versus 20.9° for poricidal), and the mean flower size was slightly smaller in poricidal species (3.15 versus 2.98 cm). Additional floral traits of poricidal species are likely also influenced by climatic variables, considering that poricidal richness is associated with particular climate factors (see above).

Drivers: Detailed breakdown by the bee family

In Andrenidae, we see major differences in the drivers between buzzing and overall richness. The top correlated variable, which showed a significant positive relationship in 100% of instances, was the richness of poricidal species (Figure 3), but this was only the case for buzzing species (percentage of species classed as

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1–2). Conversely, the top variable for total richness with buzz variables was latitude, and for total richness with optimized buzz variables, there was a negative relationship with count of months over 10°C. From all analyses, the most important variable for Andrenidae for buzzing species was poricidal richness; this was followed by latitude, which had a significant negative relationship in all models. Conversely, overall andrenid richness had a strong positive relationship with latitude, indicating that in areas with fewer species (at lower latitudes), more species buzz. For buzzing species, the number of months with a mean temperature higher than 10°C also had a positive relationship with buzzing in all cases but a negative relationship with total richness. Continentality and mean evapotranspiration also showed a negative relationship with buzzing percentage (Data S2), but only weak relationships with total richness (and the relationship with continentality was positive). The most important driver for richness overall was latitude (positive) followed by a strong positive relationship with precipitation of driest quarter (which was also positive for percentage buzzing). Overall, although more andrenid species occur in higher (temperate) latitudes with higher moisture during the driest parts of the year, buzzing peaked at lower latitudes.

For Apidae, although buzzing was less correlated with poricidal species richness, there was a strong negative relationship with maximum annual temperature. Conversely, total richness had a weak relationship with maximum temperature. Climate moisture index also had a consistently positive relationship with the percentage of buzzing species, as well as richness overall. Mean temperature of the coldest quarter had a negative relationship with the percentage of buzzing species; therefore, areas with higher temperatures during the coldest parts of the year had smaller proportions of buzzing species, but this was more ambiguous for total richness. Poricidal richness showed the next (4th) most consistent (and positive) relationship with percentage of buzzing species, as well as for richness overall. Areas with high-temperature seasonality also had a higher percentage of buzzing species and richness overall. Buzzing percentage also decreased with higher latitudes but did not have a strong relationship with richness overall. Overall richness had an interesting relationship with aridity, showing a negative relationship with the Thornwaite aridity index but a positive relationship with other metrics of maximum aridity; demonstrating a nuanced but important impact from aridity.

Colletidae also showed poricidal richness as having the most consistent and positive relationships with percentage buzzing but only a weak contribution to overall richness (Data S2). The number of months with a mean temperature higher than 10°C also showed a consistent positive relationship with buzzing but a negative relationship with richness overall. Potential evapotranspiration (PET) seasonality had a negative relationship with percentage of buzzing but a strongly positive relationship with richness overall. Mean monthly PET of the wettest quarter had a consistent positive relationship with the percentage buzzing, as well as with richness overall. Plant richness overall was the next most important variable for percentage buzzing in Colletidae and had a positive relationship, although this is more variable than with richness. For overall colletid richness, PET seasonality had a strong negative relationship, whereas there was no consistent relationship with the percentage buzzing. Maximum solar radiation had a strong positive relationship with richness. Mean temperature of the wettest quarter also had a strong and consistent relationship with richness, which was followed by mean monthly PET of the warmest quarter (also with a positive relationship).

For Halictidae, poricidal richness had a strongly positive relationship with buzzing percentage, but none with overall richness. This was followed by mean temperature of the wettest quarter, which had a positive relationship with buzzing but no relationship with richness overall. Percentage of buzzing species showed a negative relationship with annual temperature range but a slight positive relationship with richness overall. Minimum temperature of the warmest month also had a negative relationship with the percentage of buzzing species and a positive relationship with richness overall. Mean evapotranspiration also showed a negative relationship with percentage of buzzing species, but a positive relationship with richness. For overall richness, minimum isothermality was the most consistent variable but showed a negative relationship with richness. This was followed by maximum aridity index, which showed a positive relationship with richness but no relationship with buzzing. Maximum mean diurnal range had a positive relationship with richness but no relationship with buzzing. Plant richness had the next most consistent positive relationship with halictid richness.

For Megachilidae, mean wind had the most consistent (positive) relationship with the percentage buzzing, as well as a weaker but positive relationship with richness overall. Latitude shows a positive relationship with buzzing but a less consistent relationship with richness overall. Minimum precipitation of driest month also had a positive relationship with the percentage buzzing, but no relationship with richness overall. Growing degree days 5 shows a strong negative relationship with the percentage of buzzing species but no relationship with richness overall. Maximum evapotranspiration also has a negative relationship with buzzing percentage but a positive relationship with richness. For Megachilidae richness overall, the mean diurnal temperature range had a strong positive relationship, as did potential evaporation seasonality. Minimum solar radiation showed a strong negative relationship with richness but a positive relationship with mean temperature of wettest quarter and plant richness.

DISCUSSION

In this study, we explored the environmental conditions that facilitated the biogeography of buzzing bees and poricidal flowers. Patterns of overall bee diversity differ from patterns of richness for buzzing bees, with patterns varying across regions among bee families, and differences particularly pronounced in some bee families. In the Americas, overall richness peaks in North America, but the percentage of species that buzz is disproportionately high in temperate regions (latitudes 40 and −40) for Andrenidae, Colletidae (latitudes 20/−20 to 40/−40), and Megachilidae (latitudes 30–60), whereas Apidae and Halictidae largely show peak buzzing proportion in equatorial regions, although Apidae also shows a peak at higher latitudes in part due to *Bombus* (Figures S1–S3). Patterns in Europe-Africa echo those of the Americas, although the peak in Europe for proportion of species that buzz is even more pronounced (Figures S1

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and S2). Asia-Australia shows a somewhat different pattern, with stronger peaks of proportion buzzing in temperate regions (for all groups except Apidae) but with proportion buzzing peaking even more strongly in temperate northern regions. In most families, the drivers of richness for buzzing species were different from those of overall bee richness, and in many cases, if the model was optimized for buzzing species, there was not a significant relationship with overall plant species richness. This highlights that buzzing has been selected for and persists in certain conditions but that these conditions vary between different regions and taxa. Overall, we find that poricidal richness is one of the main predictors for the global biogeography of buzzing bee richness for most bee families.

Our results indicate that poricidal plant richness is clearly linked with the percentage of bee species that buzz flowers for the Andrenidae, Halictidae, and Colletidae, and to a lesser but still significant extent, the Apidae. This is surprising, because most buzzing bees are considered to be relatively generalized pollen foragers using a wider variety of plants compared with floral specialists that focus on typically few related species (e.g., Song et al.,[27] Almeida et al.,[28] Houston and Ladd,[29] and Schlindwein[30]) and are often observed collecting pollen from both poricidal and non-poricidal floral resources (e.g., Song et al.[27] and Corbet and Huang[31]). In addition, although buzzing bees dominate access to pollen from poricidal flowers,[20] buzzing behavior is not specialized to poricidal floral morphology and is in fact used by bees to extract pollen from poricidal and non-poricidal plant species.[21,22] One simple explanation for this discrepancy is that buzzing bees may be more closely associated with poricidal flowers than presently understood or that dominance of poricidal plants in some regions may exclude bee species that do not buzz. Much of the research on foraging associations between buzzing bees and flowering plants focuses on temperate regions, but buzzing bees in tropical regions often forage substantially on poricidal hosts (e.g., Schlindwein,[30] Corbet and Huang,[31] González-Vanegas et al.,[32] Mesquita-Neto et al.,[33] and Vit et al.[34]). Given that poricidal species richness is highest in the tropics, and plant species richness is often strongly positively associated with plant abundance (e.g., Delgado et al.,[35] Pemberton,[36] and Bock et al.[37]), poricidal flowers are likely an abundant resource for tropical buzzing bees, such as some sweat bees (Augochlorini) and orchid bees (Euglossini).[31,33,34] Our results also show this, with high poricidal richness and buzzing bee richness in some tropical regions, such as the Amazon (Figures 1 and 2). More generally, poricidal plants can offer particularly protein-rich pollen[38] and produce substantially more pollen per flower compared with non-poricidal species.[18,39,40] Additionally, although pollen is the principal food reward offered by poricidal flowers to bees in exchange for pollination, some non-poricidal species may deter bees from actively collecting pollen via chemical defenses.[41–43] Nonetheless, little is known about the nutritional or metabolic advantages to buzzing bees of foraging on poricidal flowers or the relative importance of poricidal hosts for most buzzing bee species.

Both hotspots and drivers of bee richness varied among families, with different latitudinal patterns among regions likely resulting from both biogeographic factors and niche availability. Furthermore, for highly diverse bee families, drivers likely differ among genera, which should drive distributional differences among regions. Additionally, buzzing behavior is rarely reported in particular groups, such as in the Andrenidae (20 buzzing species documented across 14 genera, out of 3,089 total species across 69 genera) and the Megachilidae (eight buzzing species documented across three genera, out of 4,169 total species across 95 genera) (DiscoverLife[17]). Accordingly, it is possible that underreporting of buzzing species could thus explain the lack of an association between buzzing megachilids and poricidal richness. On the other hand, buzzing species may truly be a rare occurrence in the Megachilidae (and Andrenidae), for instance. By contrast, buzzing behavior is well documented in the largest family Apidae, and the reduced importance of poricidal flowers in buzzing Apidae biogeography is likely legitimate and may be due to the diverse life-histories within the group. For instance, socially parasitic species (kleptoparasites), which do not collect pollen from flowers, comprise nearly a quarter of the Apidae.[44,45] Eusocial species that are extreme generalists and forage from dozens or hundreds of non-poricidal (and poricidal) plant species are prevalent in Apidae and might also dilute any overall association between buzzing and poricidal richness, which warrants further exploration.

The evolution of poricidal flower morphology is frequently attributed to selection to reduce pollen loss by less efficient generalized pollinators, as well as to selection by buzzing bees.[16,18,20,46] Our results suggest that poricidal morphology is an adaptation to certain climates and abiotic conditions. Notably, poricidal richness was positively associated with high aridity and evapotranspiration, suggesting that poricidal flowers, which enclose pollen within tube-like morphology, might be an adaptation associated with keeping pollen viable in desiccating environments.[20,23]

Our results also indicate that how environment and pollinator behavior interact is likely a key factor in the evolution of poricidal plants. During buzz pollination, pollen is ejected from poricidal morphology into the air before landing on the bee.[18,47,48] Windy conditions might therefore reduce the likelihood of pollen transfer to the bee, thus reducing the selective advantage of buzz pollination relative to other pollination systems. Consistent with this hypothesis, we found that poricidal richness was negatively associated with high wind. Similarly, the positive association between increasing aridity and poricidal plant richness may be in part due to associated negative effects of aridity on flower size.[48–51] Pollinator specialization, which tends to enhance pollination success and drives angiosperm evolution,[52–55] also often increases with decreasing poricidal flower size.[33] Although how behavior and environment interact to drive poricidal flower evolution has not been studied to our knowledge, such interactions are known in other pollination mutualisms. For instance, selection for ultraviolet (UV) absorbing patterns of high-altitude flowers is likely often driven by both higher UV irradiance and flower UV color preferences of pollinators (e.g., Koski and Ashman,[56,57] Klomberg et al.,[58] and Koski et al.[59]).

In conclusion, the percentage of bee species that buzz flowers is clearly frequently linked with poricidal plant species patterns (see also Pacheco Filho et al.[60]), which are, in turn, driven by aridity and wind. Accordingly, these traits are interlinked and reflect broad-scale environmental patterns. Although our analysis suggests that poricidal plant richness drives the proportion of buzzing bees, a degree of interdependence between buzzing

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bee and poricidal plant richness is expected and should be explored in future studies. Furthermore, both hotspots and drivers of richness varied for different bee families, but both spatially and taxonomically higher-resolution work is needed to explore the local-level drivers of these patterns, particularly in rapidly changing environments, such as mountain landscapes (e.g., Knight[61]). A major gap in our understanding of these patterns remains the underreporting of buzzing bee species, particularly in less sampled and remote geographic regions.[2,17] This weakness is especially evident when examining hotspots of poricidal plant species richness: many tropical regions with high poricidal richness have a lower richness of recorded buzzing species. Further work will be required to determine whether these patterns are also the result of regional differences in the ecological drivers of buzzing. Additionally, although our focus here lies in patterns of species richness, patterns of species abundance have obvious importance to understanding biogeographical patterns and should therefore be a major focus of future work examining the (co)occurrence of buzzing bees and poricidal plants. Altogether, the results here represent a major step toward understanding the ecological and evolutionary scenarios in which buzz pollination evolves and persists. Finally, looking beyond buzz pollination, our research draws attention to the need to integrate biotic interactions into assessments of biodiversity and biogeography.[10,62]

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2024.05.065.

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AUTHOR CONTRIBUTIONS

A.C.H., A.L.R., S.L.B., and M.C.O. conceived the study. A.C.H., J.S.A., and M.C.O. collected the bee data. A.L.R. and R.K. provided the list of poricidal species. D.D.J. helped put together the initial list of poricidal species. A.L.R., M.C.O., and J.S.A. listed the buzzing traits. A.C.H. mapped the distributions, developed the methods, and analyzed the data. Z.H.W. provided the plant distribution data. A.C.H., A.L.R., and M.C.O. wrote the original draft of the manuscript. All authors revised the paper and approved it for submission.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
AI	Aridity Index	https://www.nature.com/articles/s41597-022-01493-1
ai_max	Maximum monthly aridity index	https://csidotinfo.wordpress.com/data/global-aridity-and-pet-database/
ai_min	Minimum monthly aridity index	https://csidotinfo.wordpress.com/data/global-aridity-and-pet-database/
anPET	Minimum evapotranspiration	https://www.nature.com/articles/s41597-022-01493-1
bio1	Annual Mean Temperature	https://www.worldclim.org/data/bioclim.html
bio10	Mean Temperature of Warmest Quarter	https://www.worldclim.org/data/bioclim.html
bio11	Mean Temperature of Coldest Quarter	https://www.worldclim.org/data/bioclim.html
bio12	Annual Precipitation	https://www.worldclim.org/data/bioclim.html
bio13	Precipitation of Wettest Month	https://www.worldclim.org/data/bioclim.html
bio14	Precipitation of Driest Month	https://www.worldclim.org/data/bioclim.html
bio15	Precipitation Seasonality (Coefficient of Variation)	https://www.worldclim.org/data/bioclim.html
bio16	Precipitation of Wettest Quarter	https://www.worldclim.org/data/bioclim.html
bio17	Precipitation of Driest Quarter	https://www.worldclim.org/data/bioclim.html
bio18	Precipitation of Warmest Quarter	https://www.worldclim.org/data/bioclim.html
bio19	Precipitation of Coldest Quarter	https://www.worldclim.org/data/bioclim.html
bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	https://www.worldclim.org/data/bioclim.html
bio3	Isothermality (BIO2/BIO7) (×100)	https://www.worldclim.org/data/bioclim.html
bio4	Temperature Seasonality (standard deviation ×100)	https://www.worldclim.org/data/bioclim.html
bio5	Max Temperature of Warmest Month	https://www.worldclim.org/data/bioclim.html
bio6	Min Temperature of Coldest Month	https://www.worldclim.org/data/bioclim.html
bio7	Temperature Annual Range (BIO5-BIO6)	https://www.worldclim.org/data/bioclim.html
bio8	Mean Temperature of Wettest Quarter	https://www.worldclim.org/data/bioclim.html
bio9	Mean Temperature of Driest Quarter	https://www.worldclim.org/data/bioclim.html
CMI	Climate Moisture Index	https://envirem.github.io/
contin	average temp. of warmest month - average temp. of coldest month	https://envirem.github.io/

(*Continued on next page*)

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Continued

REAGENT or RESOURCE	SOURCE	IDENTIFIER
emberQ	"Emberger's pluviothermic quotient: a metric that was designed to differentiate among Mediterranean type climates	https://envirem.github.io/
et_max	maximum of monthly evapotranspiration	https://csidotinfo.wordpress.com/data/global-aridity-and-pet-database/
et_mean1	mean annual evapotranspiration	https://csidotinfo.wordpress.com/data/global-aridity-and-pet-database/
et_min	minimum of monthly evapotranspiration	https://csidotinfo.wordpress.com/data/global-aridity-and-pet-database/
gdd0	"sum of mean monthly temperature for months with mean temperature greater than 0°C multiplied by number of days	https://csidotinfo.wordpress.com/data/global-aridity-and-pet-database/
gdd5	sum of mean monthly temperature for months with mean temperature greater than 5°C multiplied by number of days	https://csidotinfo.wordpress.com/data/global-aridity-and-pet-database/
max_srad	Maximum solar radiation	https://www.worldclim.org/data/worldclim21.html
max_tcold	max. temp. of the coldest month	https://envirem.github.io/
mean_srad	Mean solar radiation	https://www.worldclim.org/data/worldclim21.html
min_srad	Minimum solar radiation	https://www.worldclim.org/data/worldclim21.html
min_twarm	min. temp. of the warmest month	https://envirem.github.io/
mon_temp10	count of the number of months with mean temp greater than 10°C	https://envirem.github.io/
PET_coq	mean monthly PET of coldest quarter	https://envirem.github.io/
PET_drQ	mean monthly PET of driest quarter	https://envirem.github.io/
PET_WaQ	mean monthly PET of warmest quarter	https://envirem.github.io/
pet_wetq	mean monthly PET of wettest quarter	https://envirem.github.io/
PETseas	monthly variability in potential evapotranspiration	https://envirem.github.io/
Plant richness-max	GIFT plant data	https://gift.uni-goettingen.de/home
Plant richness-mean	GIFT plant data	https://gift.uni-goettingen.de/home
Poricidal richness	Plant distributions	https://en.geodata.pku.edu.cn/index.php?c=content&a=list&catid=199
thermI	compensated thermicity index: sum of mean annual temp., min. temp. of coldest month, max. temp. of the coldest month, x 10, with compensations for better comparability across the globe	https://envirem.github.io/
thorn_AI	Thornthwaite aridity index: Index of the degree of water deficit below water need	https://envirem.github.io/
vapr_max	Maximum water vapour pressure	https://www.worldclim.org/data/worldclim21.html
vapr_mean	Mean water vapour pressure	https://www.worldclim.org/data/worldclim21.html
vapr_min	Minimum water vapour pressure	https://www.worldclim.org/data/worldclim21.html
wind_max	Maximum annual wind	https://www.worldclim.org/data/worldclim21.html
wind_mean	Mean annual wind	https://www.worldclim.org/data/worldclim21.html

(*Continued on next page*)

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Continued

REAGENT or RESOURCE	SOURCE	IDENTIFIER
wind_min	Minimum annual wind	https://www.worldclim.org/data/worldclim21.html
Flower size	Flower size	https://datadryad.org/stash/dataset/doi:10.5061/dryad.44j0zpcgv
Bee distributions	Bee distributions	Orr et al.[2] https://doi.org/10.1016/j.cub.2020.10.053
Shapefiles of richness, climate variables, and number/proportion buzzing bees	Zenodo	https://zenodo.org/uploads/11115033
Software and algorithms		
ArcMap	ArcMap 10.8	ArcMap Resources for ArcGIS Desktop | Documentation, Tutorials & More (https://www.esri.com/)
SAM	Spatial Analysis for Macroecology	SAM - Spatial Analysis in Macroecology (https://ufg.br/)

RESOURCE AVAILABILITY

Lead contact

Further information and requests on resources should be directed to and will be fulfilled by Alice C. Hughes (achughes@hku.hk).

Materials availability

This study did not generate new unique materials.

Data and code availability

- The lists of poricidal plant genera and buzzing bee species, categories of buzzing bees, and regression analysis are available in the supplemental information. Shapefiles of richness of poricidal groups, maximum plant richness, climate variables, and the number and percentage of buzzing bees overall and in each family examined have been deposited at Zenodo. DOIs are listed in the key resources table.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

This study involved the production of a global State-based inventory of bees, collation of key-traits of both bees (i.e., buzzing) and plants (i.e., if poricidal), the mapping of these traits, and finally an analysis of the drivers of both richness overall for each bee family, and the spatial drivers of buzzing. All analysis was conducted globally, though in addition to models we plotted latitude trends for three regions; Americas, Europe-Africa, Asia-Australia, to explore latitudinal patterns of richness and buzzing across a full latitudinal gradient. Additionally, these divisions follow prior bee biogeographic precedent (Michener[63]; Orr et al.[2]), which acknowledges that bee richness and abundance goes from higher to lower from the Neotropics to Afrotropics to Southeast Asia, and that higher faunal similarity occurs across the Mediterranean as compared to Eurasia.

Bee species data preparation and mapping

Based on Orr et al.,[2] we used an updated version of the DiscoverLife Bee World Checklist of species in various administrative areas (Ascher and Pickering[12]). In most cases State was used as the unit of area, though country, or merged adjacent states were used in the cases of data being unavailable. In total 20,941 species were mapped, generating 136,323 polygons.

Compared to prior efforts to map bees, we increased resolution and used State/province or major island level for most areas. We used the Global Administrative Areas database as a reference (GADM). However, in this study we directly linked species to administrative areas, creating a much larger file, so every species could be separately mapped. We iteratively converted all state-based notations into HASC codes to ensure the country codes were all coded as ISO2 and not FIPS numbers. First, we used the entire checklist and summarized it to provide a list of state and country names, so we had a much easier reference for conversion. All codes and names from the original checklist file were converted to HASC codes, by first downloading all HASC codes with state-names (from Statoids) and then using join and relate in ArcMap 10.8 to connect the inventory of areas noted for species. We also noted if the region referred to was in multiple different regions, and manually corrected such HASC codes when needed (e.g., there are multiple San Jose's). If multiple names fell within one HASC region, they were given the same code, and then duplicates of the same species to the same state were removed. Statoids was used as a reference for converting HASCs. An exception to this was in areas with big states/provinces and good data, such as France, where species were often listed at finer scales, and countries like the United Kingdom where the listing system is slightly different within HASC and counties are exceedingly small. Conversely, some areas had very under-collected regions. Thus, for biogeographically complex regions that include a combination of islands and provinces, as well as for regions that were listed in a range of ways (Indonesia and the Philippines), new island-based divisions were created and species lists corrected as appropriate. Furthermore, for some regions (such as various African countries) inventories are known to be incomplete, thus such countries were left at the country level and a separate list created for state vs country-based listings. Two separate shapefiles were also created to separate countries with enough data for state-level analysis and those that needed to be examined on a country-level.

Once all codes, names and notations were converted to HASC codes, they were cross-linked to the species checklist and then connected to the GADM layer. This gave a total of 136,323 links between the state-based administrative areas and species distributions.

The all-bee analyses included all bee species from all families. In addition, we separated analyses by bee family so we could differentiate patterns that may reflect the different evolutionary and biogeographic histories of different groups, as the percentage of buzzing species does vary by group. However, for family-level analyses Stenotritidae and Melittidae were excluded, because these families are too small (21 and 213 species, respectively), and Stenotritidae is restricted to Australia (which only includes 6 States).

METHOD DETAILS

Coding buzzing

We grouped bees into four behavioral categories. Those in category 0 are assumed to never buzz flowers (no available published studies or expert observer evidence of buzzing) and 1-3 denote different scoring systems for buzzing bees (Data S1). In category 1, the strict approach, we considered only bee species known and published that buzz flowers to extract pollen. In category 2, or the consensus approach, we coded genera (and all species therein) as entirely buzzing only if they contained more than the median percent of buzzing species (9% across genera with bee species recorded as buzzing). In category 3, the liberal approach, we coded genera as entirely buzzing if they contained species documented to buzz flowers to extract pollen (this category was only used for a subset of analyses). This included 14,672 non-buzzing species, 410 species included as "1" for buzzing (the strictest buzzing category), 2, 1674 species included in category 2, and 4185 species included in category 3. Having several definitions better accounts for gaps in our knowledge for some groups and also facilitates future analysis, as each definition reflects a prediction for how these gaps in our knowledge may be filled. Data S1 lists all bee species documented in the literature or observed by us or other bee researchers as buzzing flowers to extract pollen from flowers.

Understanding patterns

To understand broad patterns we used two approaches. First, we calculated the percentage of buzzing bees there were per family and for three regional latitudinal gradients (Americas, Europe-Africa, Asia-Australia). These values were averaged for each latitude with more than 10 species for each family and the three regions, then plotted.

Second, we ran area-cartograms for both overall richness and number of buzzing species within ArcMap 10.8 for each group to assess if regions had more or less species buzzing than the global average for each bee family. Cartograms basically calculate a global average richness per unit area, and then either grow or shrink each administrative area based on whether the chosen metric exceeds or falls below its global average (Figures S1–S10). To quantify this in a standard way, we then calculated for each region what percentage increase or decrease the area showed and then both mapped the increases and decreases, and calculated the trends per group as averages.

For plots of species richness, where percentage of species that buzz is calculated, areas with under 10 species were excluded, as percentages in values below this are likely to be highly stochastic. For example, 100% of 1 is 1, so if only a single species is present and did or did not buzz, comparing that 100% or 0% to more species-rich areas would not be meaningful or representative. Averages were taken for all regions at each latitude for each of the three global areas to examine overall patterns.

Drivers of buzzing

Various drivers were considered to understand the overarching patterns of richness (Data S2), the proportion of buzzing bee species, and how patterns varied geographically. We considered 52 different variables as potential drivers of taxonomic diversity and buzzing (most of these are climatic, or relate to productivity see Data S2), and for each of these variables we included maximum, minimum, mean, and standard deviation within each administrative area, with the exception of plant richness (just maximum and mean) and poricidal plant richness (total per administrative area). These variables included different elements of climate, as climate and its facets are likely primary drivers of buzzing, including possibly via their impacts on plants. Environmental variables were selected based on their potential to drive richness patterns, and our previous analysis (Orr et al.[2]). With respect to biotic variables (e.g., plant richness and poricidal plant richness), causality can likely be inferred given that we used the percentage of buzzing bee species rather than the absolute number of species; however, there will be a degree of interdependence, as having high numbers of buzzing bee species may also drive further increases in poricidal plant richness.

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Mapping plant and poricidal plant richness

Maps of maximum and mean plant richness, as well as total number of poricidal species per administrative area were calculated as variables.

Plant richness was calculated by taking the mean and maximum richness of the Ensemble_Prediction_7774_Eckert-IV from the GIFT shiny app (https://gift.uni-goettingen.de/shiny/predictions/) based on Denelle et al.[64] This was then integrated with a stencil of our administrative regions using the Intersect tool in ArcMap to map both the maximum and mean richness per administrative area.

For poricidal plant richness, we first created a list of poricidal genera (Data S3) from Russell et al.[23] and then extracted the species ranges for all species referenced in the Peking University database (https://en.geodata.pku.edu.cn/index.php?c=content&a=list&catid=199).[65] The list was generated at the genus level, because numerous well characterized genera are monomorphic for the presence/absence of poricidal morphology (e.g., *Solanum*, *Senna*, *Miconia*) and information for all species in rarer and/or tropical genera is frequently sparse. However, we recognize that monomorphism within genera should not be taken for granted and potential exceptions are hypothesized (e.g., Renner[66] and Gavrutenko et al.[67]). We also confirmed non-poricidal morphology for monomorphic genera when morphological information was available. See Russell et al.[23] for a complete description of the methods used to find and characterize poricidal plants. Five additional genera were later appended to the list, with their species extracted from the Kew Plants of the World Online (https://powo.science.kew.org/). We used the PKU database, as not only is it carefully checked, but the completeness and certainty of data has been mapped (which is not the case for other global checklists) and efforts have been made to increase completeness in regions like the African continent, where there are major data-gaps in the GIFT checklist. As the regions did not exactly align between the Kew Database and those used by the PKU team, administrative units were intersected in ArcMap with the stencil used by the PKU team and the Kew maps to ensure all species were mapped accurately.

The number and dimensions of administrative units varied between our administrative map and that used by the PKU group. Thus, having mapped the richness of poricidal plants for the PKU stencil (using the summary statistics tool in ArcMap), we then used a spatial join where the PKU stencil units were larger than our existing stencil. For areas where several units within the PKU units fitted within our administrative units (i.e., parts of the Amazon, much of Australia), we extracted the species maps for these regions, intersected them with our administrative stencil, then used the summary statistics to first list and then count the species within each of our administrative units.

It is important to note that these biotic variables are likely interdependent to a degree on pollinator richness, and thus only a correlative rather than a causative relationship with bee richness can be inferred. These factors were evaluated for their role in driving all bee – and buzzing bee – distributional patterns, as detailed below.

QUANTIFICATION AND STATISTICAL ANALYSIS

General linear models were run in Spatial Analysis for Macroecology (SAM;[68]), all based on the same administrative areas as above. First, we ran single regressions for overall richness (as well as percent buzzing) with each variable, then we used this to make the best model by using initially the variables with the strongest relationships with richness for the group, and sequentially removing variables which were not significant in the model until all variables were significant. A maximum of 22 variables were included in final models, selected on the basis of having the lowest AIC. We did not analyze the drivers for buzzing overall for all bees, given that drivers may vary by family; thus including them all within a single analysis would be weighted by the most species-rich families. We then ran the regression analysis within ArcMap (ArcGIS, Esri) using the spatial statistic tools, and regression analysis and an exploratory regression of the preselected variables, as well as exploring the drivers/correlates of poricidal plant richness.

Three versions of models were run for each family. The first used the variables selected for overall species richness within each group, the second was for buzzing species (using the percentage of species coded as 1 or 2 for buzzing), and the third was for total richness patterns, but using the variables for buzzing richness, to understand if the drivers for buzzing differ from that of overall richness. We assessed both the main, and most explanatory variables for each of the three scenarios for each family, then mapped the drivers/correlates of poricidal angiosperm richness. In addition, we explored the drivers of the distribution of poricidal plant richness using the same approach.

Given that climate often affects plant physiology (e.g., Scaven and Rafferty[69]; Xie et al.[25]; Lozada-Gobilard et al.[70]), we also explored if a frequently recorded flower trait – flower size – differed for poricidal and non-poricidal plant species. To accomplish this, we cross listed our list of poricidal genera (Data S3) and the dataset on plant traits from Song et al.[27] (Data S4), and calculated mean trait values as well as information on sampling locality (altitude, latitude provided by Song et al.[27])