



Perspective



Opportunities and challenges in Asian bee research and conservation

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ABSTRACT

The challenges of bee research in Asia are unique and severe, reflecting different cultures, landscapes, and faunas. Strategies and frameworks developed in North America or Europe may not prove applicable. Virtually none of these species have been assessed by the IUCN and there is a paucity of public data on even the basics of bee distribution. If we do not know the species present, their distribution and threats, we cannot protect them, but our knowledge base is vanishingly small in Asia compared to the rest of the world. To better understand and meet these challenges, this perspective conveys the ideas accumulated over hundreds of years of cumulative study of Asian bees by the authors, including academic, governmental, and other researchers from 13 Asian countries and beyond. We outline the special circumstances of Asian bee research and the current state of affairs, highlight the importance of highly social species as flagships for the lesser-known solitary bees, the dire need for further research for food security, and identify target research areas in need of further study. Finally, we outline a framework via which we will catalyze future research in the region, especially via governmental and other partnerships necessary to effectively conserve species.

1. Special challenges for pollinator research in Asia

Concerns about potential insect declines and the subsequent loss of essential ecosystem services such as pollination are increasing worldwide (IPBES, 2016; Harvey et al., 2020; Wagner, 2020). Bees are widely acknowledged as the most important terrestrial pollinators, with many plants reliant on their actions (Klein et al., 2007; Ollerton et al., 2011; Requier et al., 2022); their conservation depends on our knowledge of all facets of their life history and distribution (Hortal et al., 2015). Asia holds 15 % of total bee diversity, with many unique lineages (Fig. 1), but these many species comprise only 1 % of public global bee specimen data (Orr et al., 2021). In addition, the most recent complete catalog

treating the region was published in 1896 (Dalla Torre, 1896), over a century ago, demonstrating a severe gap in our knowledge of Asian bee biodiversity.

The knowledge gaps in Asia are alarming, as bee extinctions have been only recently documented in well-studied areas such as Singapore (Ascher et al., 2019). In another worrying example, the largest bee in the world, *Megachile pluto* Smith, has been sold online multiple times despite conservation concerns (Fig. 1K; Vereecken, 2018). The remaining Asian bee fauna remains virtually unexplored from a conservation perspective, because monitoring bees and verifying declines is challenging and requires baseline data that do not yet exist (Orr et al., 2021). Most research and pollination conservation actions or policies rely heavily on, or may

be augmented by, information from specimen databases and, when available, IUCN Red List status assessments, but we are only beginning to build these foundational resources.

No-regret solutions can be enacted now as a first step, including

reduction of pesticide use and pollution of water, light, and air; increase in landscape heterogeneity and semi-natural areas; implementation of pollinator-friendly practices across landscapes; protection and restoration of biodiverse areas and threatened species; and control of alien



Fig. 1. Asian bee biodiversity. Apidae: A. *Xylocopa insularis* Smith; B. *Xylocopa myops* Ritsema; C. *Ceratina collusor* Cockerell; D. *Ctenoplectra chalybea* Smith; E. *Apis dorsata* Fabricius; F. *Geniotrigona thoracica* (Smith); G. *Bombus supremus* Morawitz; H. *Nomada adusta* Smith; and I. *Amegilla andrewsi* (Cockerell). Colletidae: J. *Hylaeus penangensis* (Cockerell). Megachilidae: K. *Megachile pluto* Smith; L. *Megachile atrata* Smith; and M. *Euaspis polynesia* Vachal. Halictidae: N. *Nomia iridescens* Smith and O. *Lasioglossum adonidae* (Cockerell). Photos (©) were taken by ZWW Soh (A,B,C,D,E,F,H,I,J,L,M,N,O), PH Williams (G), and C Bolt (claybolt.com; K).

species (Harvey et al., 2020; Dicks et al., 2021). Where possible, active restoration of more intact or threatened habitat should also be prioritized, given dire threats such as land conversion to palm oil and wide-scale agricultural expansion in the Global South (Grass et al., 2020; Aizen et al., 2022). However, such solutions are generalized and can conflict with economic aims, with both funds and political will limiting their application, making more targeted solutions a priority. To tailor these and other efforts most effectively, we must also quickly increase regional knowledge and tailor conservation planning for the enduring challenges faced in Asia (Sodhi et al., 2010; Dicks et al., 2021).

Local research is needed to generate, consolidate, and verify baseline biodiversity information; identify and fill information gaps; provide appropriate locally-tailored solutions; share information; and establish effective monitoring frameworks (Rabajante et al., 2020; Orr et al., 2022a). The impediments to pollination research and conservation in Asia are unique and severe, and policies or initiatives from North America or Europe are not necessarily effective elsewhere, as regional habitats, fauna, and cultural and political practices differ. Asia is characterized by immense climatic and topographic heterogeneity, from tropics to tundra. Half of the world's human population exists on this continent—increasingly concentrated in fast-growing cities, with many populations now transitioning to more land-intensive and unsustainable diets (e.g., beef) and products (palm oil, rubber, etc.; Grass et al., 2020; Marcacci et al., 2022). Public and governmental knowledge and appreciation of pollinators are rare, making regulations on practices such as landscape alteration, management, and pesticide use difficult to enact or enforce. Trans-boundary research has also been limited by language, political boundary disputes, and cultural practices. Rigid national restrictions on collecting, sequencing, and sample sharing exacerbate these issues (Prathapan et al., 2018).

In this perspective, we enumerate the unique challenges and urgent needs in Asian bee research, with a focus on East, South, and Southeast Asia (Supplemental Note 1). Following a discussion on the current state of research, we review the importance of flagship social bee groups of Asia, and highlight the understudied biodiversity of solitary bees. We then explore the importance of bees in pollination in agricultural and natural ecosystems. We conclude with four sets of recommendations on policies and strategies, field-level implementation, community engagement, and priorities for research and monitoring.

2. The current state of bee research in Asia

In the last decade, many discussions have centered on the need for Asia-wide pollinator research and conservation initiatives. However, due to limited funding, organizational struggles, challenges in data sharing that lead to severe underestimations of true species richness and endemic species numbers (Fig. 2A–D), and travel restrictions, a unified platform has been slow to emerge. The establishment of the Asian section of both the IUCN (International Union for Conservation of Nature) Wild Bee Specialist Group and the Asian Pollinator Initiatives Alliance (APIA) since 2020 will more effectively bring together the expertise, institutions, stakeholders, and data required for a synergistic Asian pollinator initiative and bee conservation assessments.

Challenges faced include limited resources and a lack in many countries of tenure-track university and/or governmental bee researchers well-positioned to participate in equitable international collaborations. This is the case even for many countries with advanced bee research foundations. Both Japan and Russia have species checklists, for example (Tadauchi and Murao, 2014; Lelej et al., 2017), but there is little funding available to digitize the many bee specimens housed in these countries, leading to Eastern Russia being ranked 33rd in *DiscoverLife.org* checklist-based species richness yet only 67th based on public data resources (Fig. 2). Pollinator research in much of the rest of Asia has been relatively recent (Cervancia, 2018; Ren et al., 2018). Thus, region-wide efforts are also still preliminary, and there is much to build on as evidenced by the success of several recently established national

initiatives. We will discuss case studies from China, India, and Thailand in depth in this section.

In the last six years, the Chinese Pollinator Forum has regularly brought together regional and overseas experts to advance research and conservation efforts. Many extensive projects, such as the East China Pollinator Project and the Second Tibetan Expedition Program, have centered on or included strong pollinator components, in an effort to document bee diversity in this world hotspot of bee biodiversity (Fig. 2). The Chinese Entomological Society's Special Committee on Pollinator Insects has been a guiding force in many of these and other initiatives. There is increasing appreciation of the importance of pollinators and the need for their conservation, likely due to international research trends and the central importance of food security and medicinal plants in China. Taxonomic and systematics research is also ongoing in China (Williams et al., 2017; Niu et al., 2020; Williams et al., 2020; Ferrari et al., 2021; Zhang et al., 2022), but given the high expected number of undescribed species in China (Orr et al., 2021), much more support is necessary for these ventures, as presently there exist so few data for the country that its rank in species richness drops from 6th to 40th in public data (Zhu et al., 2022; Fig. 2A–B). This is also the case for many other Asian countries, where metrics such as richness or records per area show them to be outliers with too few data (Fig. 2E–F).

Great progress is also being made in India, where there are also higher numbers of species and endemics (Fig. 2). Conservation efforts on pollinators saw early support in the All India Coordinated Research Project (AICRP) on honeybees, initiated in 1981 under the Indian Council of Agricultural Research. In 2007, this initiative became the broader AICRP on Honeybees and Pollinators. Presently, the project has 26 centers covering 20 states, most of which are affiliated with state agricultural universities. In addition to providing training to farmers in sustainable beekeeping, some centers also conduct pollination studies involving honeybees, and to a lesser extent, non-honeybees (Krishnan et al., 2017; Belavadi et al., 2021). More recently, the Indian Pollinator Initiative (InPollin, inpollin.com) was founded as a platform to enhance studies on non-social bees, facilitate interactions between researchers, and to standardize methods that will allow regional studies to be combined to generate India-wide datasets. The InPollin has organized several national meetings, student workshops, and two international online seminar series. In-person national meetings have previously received international researchers from both nearby and distant countries, leading to several collaborative downstream efforts (e.g., this paper; Kitnya et al., 2022). One of the initiative's future goals is to launch a country-wide effort to document bee diversity in India.

Bee research in Thailand has been greatly enhanced by two large projects: (1) the USA-Thai project “Thailand Inventory Group for Entomological Research” (TIGER, 2022) and (2) the Global Biodiversity Information Facility-Biodiversity Information Fund for Asia (GBIF-BIFA). They have resulted in an impressive collection of bees. Morphological study of this collection enables reliable identifications, expediting further research (Chatthanabun et al., 2020; Nalinrachatakan et al., 2021). A next step for Thailand is to collate molecular diagnostic resources and to integrate them with morphology using an integrative taxonomy approach across borders (Orr et al., 2020), helping build a foundation for Southeast Asian bee research. Broader testing and application of species concepts would ensure that the use of species names is standardized across countries. An additional promising avenue for bee research in Thailand and throughout Asia is the Asian Pollinator Initiatives Alliance (APIA, 2023), founded in early 2020 by several NGOs and foundations based in Thailand and surrounding countries. It has been instrumental in connecting private, public, and educational sectors (e.g., researchers, political foundations, non-profit organizations, farmers and other interested stakeholders). To date, most of APIA's activities have been based in Thailand, but with increasing network connections in other Asian countries the organization is keen to achieve broader regional impact.

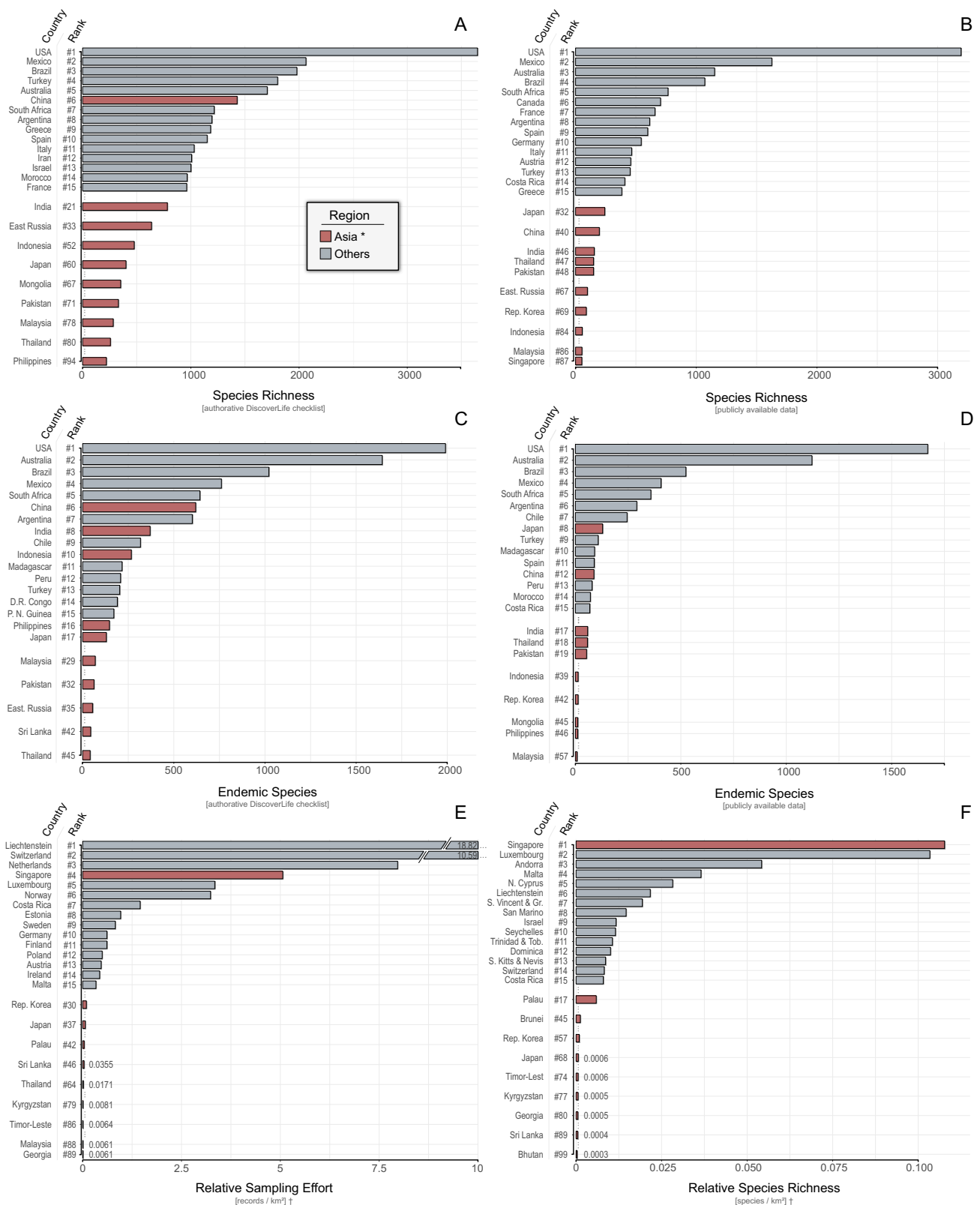


Fig. 2. Ranking of countries in terms of biodiversity and data resources. Based on authoritative checklist data (Ascher and Pickering, 2022) and public data (Dorey et al., in review), focusing on the areas of East and South Asia listed in Supplemental Note 1. The top 15 global areas are given first, with Asian areas listed thereafter with other regions excluded. A. Species richness via checklist. B. Species richness via public data. C. Endemic species via checklist. D. Endemic species via public data. E. Relative sampling effort via public data, using specimens per area. F. Relative species richness via public data, using species per area. Underlying data are in Supplemental Table 1. Overall, the public data vastly underestimate biodiversity compared to the checklist (for instance, China moving from #6 to #40 in species richness, from checklist to public data, and Indonesia going from #10 to #39 for number of endemic species). Based on E and F, only Singapore appears to be relatively well-known within Asia.

3. Eusocial bees as flagship groups in Asia

Eusocial species are abundant in many ecosystems and often managed for agricultural and horticultural crops, making them familiar to all. Such flagship species are often essential for effective conservation messaging and support. Asian ecosystems harbor the richest diversity of honeybee species (*Apis* L.; Apidae), both managed and wild (Smith, 2021). The Western Honeybee, *Apis mellifera* L., is the most prominent managed bee worldwide (Garibaldi et al., 2013), even in many parts of Asia where it has been introduced. Contrastingly, recent analyses suggest there may be 14 or more Asian honeybee species (Smith, 2021; Kitnya et al., 2022; Su et al., in review). Few of these taxa are regularly managed for honey production, and they receive much less research or conservation consideration (Abrol, 2020). The full potential of endemic Asian honeybees to pollinate crops remains unrealized, despite their importance (Klein et al., 2003; Krishnan et al., 2017; Garibaldi et al., 2013; Marcacci et al., 2022). However, there has been substantial progress in certain fields, and the genomes of three species (*A. florea* Fabricius, *A. dorsata* Fabricius (Fig. 1E), and *A. cerana* Fabricius) were recently sequenced and are being actively explored (Karpe et al., 2016; Ji et al., 2020; Fouks et al., 2021). Still, many knowledge gaps persist. Ultimately, the combination of problems facing honeybees and pollination services in Asian ecosystems are specific to the region and require local expertise and research.

Another eusocial group, the stingless bees (Meliponini (Apidae)), has gained more attention in the Asian research and management communities in the last 20 years. More than 57 species from 10 genera are described from Asia (Ascher and Pickering, 2022; Fig. 1F). They are some of the most common bees in subtropical and tropical environments, including in human-modified landscapes such as agricultural (Klein et al., 2003; Sritongchuy et al., 2019, 2022) and urban (Stewart et al., 2018; Stewart and Waitayachart, 2020) habitats, which makes them attractive management candidates. They have long been used for indigenous meliponiculture in Asia, but have been poorly studied when compared to the Neotropical fauna (Engel et al., 2019). Stingless bees are increasingly managed commercially in many parts of Asia, including in Bhutan, China, India, Indonesia, Malaysia, the Philippines, and Thailand (Chuttong et al., 2014; Rattanawanee and Duangphakdee, 2019; Salatnaya et al., 2021; Nidup, 2021; Qu et al., 2022). Although less studied than honeybees, the medicinal properties claimed of stingless bee propolis and honey have increased public perception and funding for research in Asia in recent years (Al-Hatamleh et al., 2020).

Bumblebees (*Bombus* Latreille; Apidae) also reach their highest richness in Asia, with half of described species found in China (Williams, 1998, Fig. 1G). There has been a great deal of study, historical and ongoing, on the systematics of this challenging group (Williams, 1998; Williams et al., 2017; Williams et al., 2020; Williams, 2022), resulting in tens of thousands of verified specimens in China. These should be leveraged for conservation assessments (e.g., IUCN Red Listing). Their highly-variable color patterns, often attributable to mimicry (Williams, 2007), make identification especially challenging despite publication of identification resources for regions such as the Himalaya (Williams, 2022). The group has seen further study across fields, including the genomic and the molecular bases of color patterns (Tian et al., 2019; Sun et al., 2021). However, behavioral and physiological studies are relatively scarce in the region (Ge et al., 2021). Although native bumblebees are promising managed pollinators similar to other eusocial bees and are being reared in some countries (Hannan et al., 1997; Yoon et al., 2002), the use of commercialized, non-native species in parts of Asia poses a potential major threat for native pollinators (Matsumura et al., 2004; Orr et al., 2022b), as seen in parts of South America (Aizen et al., 2022; Orr et al., 2022b).

Among these selected flagship social bee groups, some species such as *A. laboriosa* Smith, the Himalayan Giant Honeybee, are threatened for reasons that may include habitat specialization, limited distribution and nesting opportunities, unsustainable honey harvesting, and climate

change (Thapa et al., 2018). However, even the much more widespread *A. cerana*, adapted to a wide range of climates (Ji et al., 2020), faces threats of competition and pests from the continued use of the introduced and managed *A. mellifera* (Theisen-Jones and Bienefeld, 2016), and in some places they might be largely replaced. Further, highly migratory and forest-dependent species, such as *A. dorsata* (Fig. 1E) have been shown to be impacted by urbanization and air pollution (Thim-megowda et al., 2020) and isolation from natural habitats (Klein et al., 2003). Some of the island-endemic *Apis* species likely face similar threats, but this requires further study (Raffiudin et al., 2022). Stingless bees may also face threats due to unsustainable harvesting practices, or even through species introductions and subsequent competition (Carvalho, 2022; Qu et al., 2022). Competition is again a potential factor threatening native bumblebees, in light of the continued use of the potentially invasive European *Bombus terrestris* (L.) (Orr et al., 2022b). Co-introduced parasites and pathogens could prove even more dangerous when introducing non-native species (Cameron and Sadd, 2020). The spread of such introduced parasites and pathogens can escalate widely through movement of affected native species within the region (Owen, 2017), making disease monitoring imperative. The effects of climate change are poorly understood for bees in general but are expected to be much more severe in the case of montane species such as bumblebees (including *Bombus supremus* Morawitz, Fig. 1G; Williams et al., 2015), and could be compounded by grazing (Xie et al., 2008), warranting urgent investigation and actions.

4. Solid taxonomy of native bees of Asia is imperative

Non-eusocial species comprise most bee species worldwide (85–90 %, Danforth et al., 2019), but they are exceptionally understudied in Asia, as evidenced by limited coverage of regional taxa in the most recent global treatise (Michener, 2007; notably, some social taxa such as *Lasioglossum* (Curtis; Halictidae) are also less known; Fig. 1O). Case in point, the public data rankings include only one Asian country in the top 10 for number of endemics (Japan), yet the [Discoverlife.org](https://www.discoverlife.org) checklist lists three different Asian countries in that top 10 ranking (China, India, Indonesia; Fig. 2C–D). The limited study and knowledge of non-eusocial Asian bee species impairs our ability to protect them, given that most IUCN listings of insects rely on distributional data. In China, for instance, nearly 1300 species have been recorded, but estimates from Yan-Ru Wu and others anticipate the presence of at least 1000 additional species. Orr et al. (2021) also demonstrated that China was one of the three major under-described regions globally (plus Australia and Chile-Argentina). In addition, many described species are unidentifiable as fully verified ranges are typically fragmentary or erroneous. Furthermore, many data remain unshared, at times a consequence of local regulations, or due to the difficulty of generating data and a hesitancy of taxonomists to share it without proper recognition (Zhu et al., 2022). All this greatly complicates bee identification in the region, especially when the undescribed species belong to difficult groups such as the sweat bee genus *Lasioglossum*. These challenges are exacerbated because many species-defining type specimens are held outside of their countries of origin, which reduces the identifiability of Asian species and highlights the moral imperative for such institutions to fully image their type specimens, including extensive imaging of all useful characters (Orr et al., 2020). Further, many institutes focus too much on “high-impact” publications in hiring and promotion (Zhu et al., 2022), reducing the appeal to students. All of this contributes to a dramatic deficit in bee experts in Asia. Knowledge of the life histories of Asian bee species is lagging still further behind, limiting our ability to develop effective and targeted conservation strategies.

A major challenge to taxonomic work is that there are dwindling career incentives to do taxonomy (Orr et al., 2020; Zhu et al., 2022). The delimitation and description of new species and the building up of essential identification resources have historically been slow processes, exemplified by the ongoing centuries of taxonomic research in areas

such as Europe, while Asia has seen far less focus. Coupled with quickly-increasing career advancement expectations, there is a huge risk that hiring committees and funding agencies will fail to recognize the importance of supporting basic, especially taxonomic, research (Zhu et al., 2022).

To counter these challenges, we must better integrate new technologies into taxonomic research programs (Orr et al., 2021; Hartop et al., 2022). Streamlining and expediting training, when coupled with shared data on species (Orr et al., 2022b), would stabilize the taxonomic foundation necessary for regional and trans-boundary research on bees, even enabling monitoring via newer molecular technologies once reliable DNA libraries are available (Tang et al., 2015). Additionally, as a community we should actively seek to recognize and cite taxonomic hypotheses and works wherever possible. Given that many fields (e.g., ecology, conservation biology) are currently hindered by taxonomic uncertainty in many Asian bee taxa, increasing research effort, training, and funding in taxonomy could be an investment beneficial to all.

5. The understudied importance of bees for pollination in agricultural and natural systems in Asia

If practitioners and researchers cannot identify bees beyond a small subset of eusocial species, we cannot measure, monitor, and maintain pollinator services. Although methods may be transferable, knowledge itself is not, and many endemic crops and growing systems in Asia cannot be assumed to function in the same way as elsewhere, even for the same species. Apple, for instance, requires hand pollination in numerous countries in Asia due to pollinator shortages, as do numerous less-studied crops in Southeast Asia (Wurz et al., 2021). Key to any region, however, will be sustainable land management and the preservation of semi-natural and natural areas as pollinator habitat (Krishnan et al., 2012; Krishnan et al., 2017; Chatterjee et al., 2020; Garibaldi et al., 2021), because biodiversity generally begets food security more sustainably than conventional agricultural intensification (Murray-Lasley et al., 2013; Requier et al., 2022). Compared to much of North America and Europe, considerable natural landscape heterogeneity still exists in Asia, and urgent evidence-based actions are needed to preserve habitats and the vital pollination services they enable.

The management of the three aforementioned eusocial groups is a cornerstone of agriculture in Asia. However, their importance differs regionally. *Apis* are used in various systems throughout, stingless bees are restricted to subtropical and tropical regions, and bumblebees are used elsewhere in greenhouses (Orr et al., 2022b). Even for native honeybees, much more effort is needed to maximize their potential as managed pollinators (Gupta, 2012; Schreinemachers et al., 2017). Relatively little research has been directed to quantifying the biology and relative importance of non-honeybees in pollination of the large number of crop species grown in the region (Requier et al., 2022), despite the growing body of evidence of their importance as essential crop pollinators (Klein et al., 2003; Klein et al., 2007), irrespective of managed honeybee abundance (Garibaldi et al., 2013). Such research on the biology of wild bees and their contribution to pollination, as has been conducted enacted in at least China and Japan (Sekita and Yamada, 1993; Men et al., 2018).

Many crops are grown in Asia, and recent efforts have begun examining smallholder landscapes (Motzke et al., 2016; Shi et al., 2021; Sritongchuay et al., 2019, 2022; Li et al., 2023), but most systems require further study (Klein et al., 2007). Each region, if not each crop, in Asia could be the subject of its own review paper. Similarly, the diversity and abundance of crop pollinators change across space, time, and focal crop (Senapathi et al., 2021). Despite such complexities, active research on and optimization of crop systems is paramount, not just for food security, but also because there is potential for wild pollination in many systems, which could be hindered by unbridled agricultural expansion (Aizen et al., 2022). Some economically important insect-pollinated crops are grown in unsustainable monocultures elsewhere,

but diverse small-holdings still dominate many Asian landscapes (Krishnan et al., 2017; Zou et al., 2017; Sritongchuay et al., 2022). Less sustainable systems will require active restoration to facilitate recovery of wild pollinator populations. Land-use pressures in Asia preclude the conversion of large arable areas into flower-rich habitats. Hence, there is a need to identify local wildflower species that efficiently attract and support pollinators to small-agricultural holdings in various agro-ecological regions (Laha et al., 2022). Furthermore, the impacts on pollinators of increased land fragmentation and urbanization remain understudied in rapidly expanding Asian urban and peri-urban spaces (Thimmegowda et al., 2020; Wenzel et al., 2020). There is still potential to better align modern practices with new research on sustainability and with indigenous practices that have been honed over millennia and may prove to be more sustainable (IPBES, 2016). There is an urgent need to identify and understand the impacts of different interacting drivers of pollinator decline across the region.

Natural ecosystems have seen markedly less research and consequently remain less understood, as food security demands have made agricultural landscapes higher priority targets for study (Requier et al., 2022). Yet bee pollinators are critical across settings, as an estimated 87% of flowering plant species depend on animal pollinators (Ollerton et al., 2011), with bees being by far the most common (Willmer, 2011). Bees thus impact natural systems across scales, from individual plants (offspring quantity and quality) to populations and species (plant genetic diversity, gene flow, and evolution), to entire communities and ecosystems (structures and function) (Willmer, 2011). Most bee pollination research to date conducted in natural and semi-natural environments in Asia has focused on either specific plant taxa or specific bee taxa (Corlett, 2004; Ren et al., 2018). Community-wide studies are scarce, in large part due to the difficulty of collecting data. However, recent technological advances such as using environmental DNA (eDNA) or metagenomics to study plant-pollinator interactions may improve prospects (Ruppert et al., 2019), but will remain a challenge for regions with insufficient technological bases. Knowledge of bee-plant interactions in natural habitats is essential for conservation efforts, not only for assessing bee species with specific habitat, foraging, and/or nesting requirements, but also for the conservation of plant species that depend on them. Such research is imperative in the face of rapidly disappearing natural habitats and rising species extinctions (Hughes, 2017).

6. Looking forward – building a foundation and catalyzing bee research in Asia

There is no silver bullet or panacea for the myriad of challenges faced by stakeholders and researchers trying to achieve bee conservation in Asia. Both multisectoral, cross-border regional initiatives and nationally-tailored approaches will be needed to advance bee research in the region. We provide the following suggestions to improve bee research efforts in Asia, with cross-border capacity building and knowledge sharing as paramount goals.

On an international scale, pollinator conservation action is currently framed largely within the Convention on Biological Diversity's (CBD) International Pollinator Initiative and its current, second Plan of Action (for 2018–2030). Below we discuss the opportunities for Asia around the four elements of this action plan: (1) enabling policies and strategies; (2) implementing field-level change; (3) engaging civil society and the private sector; and (4) monitoring, research, and assessment.

6.1. Enabling policies and strategies

Scientists will need to demonstrate to policymakers the importance of pollinators. Thus, engagement is central to enacting policy changes and legislative protections. Current modeling shows that by 2050, five of eight billion people worldwide may be negatively impacted through insufficient nutrition stemming from losses to pollinator-dependent

crops (Chaplin-Kramer et al., 2019). In the same study, the impacts across all scenarios were the largest for Africa and South Asia. The importance of policies, legislation, and regulations associated with pollinators should ideally be reflected within national reports submitted by CBD member countries. In a brief review of the most recent national reports submitted by the 48 countries within broader Asia (including the Middle East), only 22 (46 %) mentioned pollinators. Additionally, Indonesia, South Korea, and Cyprus were the only countries that mentioned pollinators at least four times, highlighting the lack of engagement on the importance of pollinators in Asia. The explicit inclusion of pollinators or pollination services within National Reports or National Biodiversity Strategies and Action Plans signal that these issues are a conservation priority and could promote funding and stimulate research in this direction. Further, most mitigation policies for anthropogenic pressures such as pesticides and pollution are determined by their effects on humans, not plants and animals (Thimmegowda et al., 2020), highlighting a clear knowledge and policy gap. The conservation profiles of pollinators in Asia could be raised through science communication and public engagement using selected bee species as flagship representatives, messaging strongly on the benefits of native bees for crop and home garden yields (Klein et al., 2003; Klein et al., 2007; Garibaldi et al., 2013).

6.2. Field-level implementation

Land use, land management practices, pollution, and pesticide use are important drivers influencing pollinator populations in parts of Asia (Dicks et al., 2021). Agriculture in Asia has had and will continue to have a relatively high pollinator-dependency, based on current and forecasted rates of agricultural expansion and crop diversification (Aizen et al., 2019). Despite some work in agriculture, the prerequisite data for syntheses on wild pollinator population trends are still largely lacking for Asia (IPBES, 2016; Orr et al., 2021). Efforts to fill these gaps must be standardized as best as possible, and balanced with practicality (Rabajante et al., 2020). Farm- and landscape-level research involving pollinator-friendly interventions and sustainable agricultural practices are lacking. Policy incentives for ecologically-friendlier agricultural practices, and enforcement of existing regulations are also major challenges in most countries. Furthermore, few studies exist on pollinator conservation using co-design and participatory approaches in Asia. These approaches can be used to promote pollinator conservation in all human-modified habitats, across developmental gradients. As policy action is lacking in some countries, direct engagement with stakeholders may prove a more immediate solution to the many challenges.

6.3. Private sector and civil society engagement

Development is a constant in much of Asia and the explicit incorporation of pollinating invertebrates into mandated environmental impact assessments for building infrastructure or other activities could generate substantial baseline data while providing pollinator habitat. If such data were mandated as public, the transparency of such processes would be enhanced alongside bolstered research prospects. Special efforts could be made in appealing to the Traditional Chinese Medicine industry and others that directly depend on pollinators (medicinal plants; Ren et al., 2014). Further incentives for sustainable development, coupled with better enforced penalties for regulatory violations, could together pave the way for biodiversity conservation.

Community scientists can also play an important role in biodiversity monitoring, providing potential long-term effort without the need for substantial funding and research infrastructure. iNaturalist, a highly-accessible public database for documenting flora and fauna, has more than 64,000 records of nearly 700 bee species in broader Asia (as of February 2023; Dorey et al., in review). This platform provides the first-ever accessible images for many major regional pollinators and better documented distribution, especially for range extensions and rare

species (Koch and General, 2019; Silva et al., 2020; Wilson et al., 2020), while also informing on behavior and bee associations with flowers. A notable example is Singapore, a rare well-documented tropical country (Fig. 2E–F) where over half of its 120 bee species have been recorded on iNaturalist (Ascher et al., 2022); similar usefulness is documented for Cambodia (Ascher et al., 2016). Through carefully planned, large-scale survey-style events like BioBlitzes, invaluable standardized data might even be generated (Orr et al., 2022a). However, caution must be taken with highly-polymorphic or cryptic groups such as bumblebees (Williams et al., 2020) and some difficult solitary groups such as *Amegilla* (*Zonamegilla*) Popov (Fig. 1I), lest misidentifications be made and spread widely in the literature. Lastly, local, national, and global experts should be mobilized and better credited for validating identifications.

6.4. Monitoring, research, and assessment

Basic capacity building is needed to enable region-wide monitoring, as the requisite expertise varies greatly among Asian countries (Cervancia, 2018). The overwhelming majority of countries in Asia lack comprehensive studies and updated information on their fauna or sufficient point data (Fig. 2), rendering the assembly of national bee species checklists nearly impossible, excepting herculean efforts such as those involved in the DiscoverLife checklist (Ascher and Pickering, 2022). The other checklists that exist are regional and non-standardized (Rabajante et al., 2020), reducing the comparability of studies between countries (Orr et al., 2022a).

The Asia group of the newly formed IUCN Wild Bee Specialist Group will prove important for Red List Assessment of regional bees and for promoting and connecting regional networks. Ideally, efforts at Red-Listing will prioritize taxonomic groups that are best-known both in terms of specimen records and their taxonomic trustworthiness, (e.g., *Apis*, *Bombus*, *Meliponini*, and select better-known solitary bee groups such as *Trachusa* Panzer (Megachilidae)), thereby picking the “lowest-hanging fruit” first before approaching more problematic groups. However, this is just a first step, and monitoring should entail collection of all bees, as they may provide baseline data later once species can be reliably identified. Special focus should be given to known hotspots such as the Hengduan mountains where work has been sparse on most bee groups (excepting bumblebees; Williams, 2022), and for areas where historical baselines already exist and can be compared to. These regional initiatives should be supported by Asian countries through governmental and research institution support, as a means to share information and knowledge and strengthen regional networks.

Although various government programs, outlined earlier, have been initiated by some countries, there are no national assessments of insect pollinators in Asia as seen in Brazil, with its first Brazilian Special Report on Pollination, Pollinators and Food Production (Wolowski et al., 2019). Brazil’s ability to complete a national assessment of pollinators was due in part to financial support from many sources, alongside the monumental efforts of contributors. In Asia, to undertake regional or national assessments of pollinators and pollination, faunal baselines and monitoring, and research, infrastructural and grant support is needed, with clear expectations of results within reasonable timelines, designed to strengthen enduring partnerships between researchers, stakeholders, and policymakers.

7. Summary

We know that almost all regions lack information and data regarding pollinators, and the situation is critical in Asia (Fig. 2). How do we close these knowledge gaps? This paper highlights the importance of improving basic bee knowledge in Asia, as recording and assessing biodiversity is fundamental to measuring progress toward and ultimately achieving conservation goals, including those of the CBD’s Kunming-Montreal Global Biodiversity Framework. Efforts at generating and sharing data must be cross-border and transdisciplinary to

surmount the manifold challenges faced in Asian bee research. This is not just a biodiversity issue, but given the irreplaceable role of bees as pollinators, it is also critical to maintain the economic services provided by bees to enable further sustainable development across the region.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Code used to generate area rankings are public at https://github.com/jbdorey/Asian_Bee_Perspective, based on totals from the DiscoverLife checklist (Ascher and Pickering, 2022; Dorey et al. (in review)).

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References

- Abrol, D.P., 2020. The Future Role of Dwarf Honeybees in Natural and Agricultural Systems. CRC Press, Taylor & Francis Group, Boca Raton, London, New York.
- Aizen, M.A., Aguiar, S., Biesmeijer, J.C., Garibaldi, L.A., Inouye, D.W., Jung, C., Martins, D.J., Medel, R., Morales, C.L., Ngo, H., Pauw, A., Paxton, R., Sáez, A., Seymour, C.L., 2019. Global agricultural productivity is threatened by increasing pollinator dependence without a parallel increase in crop diversification. *Glob. Chang. Biol.* 10, 3516–3527.
- Aizen, M.A., Garibaldi, L.A., Harder, L.D., 2022. Myth and reality of a global crisis for agricultural pollination. *Ecol. Austral.* 32, 698–715.
- Al-Hatamleh, M.A., Boer, J.C., Wilson, K.L., Plebanski, M., Mohamud, R., Mustafa, M.Z., 2020. Antioxidant-based medicinal products of stingless bee products: recent progress and future directions. *Biomolecules* 10, 923.
- APIA, 2023. The Asian pollinator initiatives alliance. <https://www.wwf.or.th/en/scp/ca-mpaign/apia/>. (Accessed December 2022).
- Ascher, J.S., Pickering, J., 2022. Discover Life bee species guide and world checklist Hymenoptera: Apoidea: Anthophila. Draft 56. <http://www.discoverlife.org/mp/20q>. (Accessed December 2022).
- Ascher, J.S., Heang, P., Kheam, S., Ly, K., Lorn, S., Chui, S., de Greef, S., Chartier, G., Phauk, S., 2016. A report on the bees (Hymenoptera: Apoidea: Anthophila) of Cambodia. *Cambodian J. Nat. Hist.* 2016, 23–39.
- Ascher, J.S., Soh, Z.W.W., Ho, B.M., Lee, R.Y.Y., Leong, A.Q.E., Chui, S.X., Lai, J.J.L., Lee, J.X.Q., Foo, M.S., Soh, E.J.Y., 2019. Bees of the Bukit Timah Nature Reserve and vicinity. *Gard. Bull. Singapore* 71 (Suppl. 1), 245–271.
- Ascher, J.S., Soh, Z.W.W., Chui, S.X., Soh, E.J.Y., Ho, B.M., Lee, J.X.Q., Gajjanur, A.R., Ong, X.R., 2022. The bees of Singapore (Hymenoptera: Apoidea: Anthophila): first comprehensive country checklist and conservation assessment for a Southeast Asian bee fauna. *Raffles Bull. Zool.* 70, 39–64.
- Belavadi, V.V., Pannure, A., Tharini, K.B., 2021. Bees of economic importance in India. *ENVIS Newslett.* 27, 2–15.
- Cameron, S.A., Sadd, B.M., 2020. Global trends in bumble bee health. *Annu. Rev. Entomol.* 65, 209–232.
- Carvalho, A.F., 2022. Illegalities in the online trade of stingless bees in Brazil. *Insect Conserv. Divers.* 15, 673–681.
- Cervancia, C.R., 2018. A review of pollination biology research in selected Asian countries. *Philippine Entomol.* 32, 3–36.
- Chaplin-Kramer, R., Sharp, R.P., Weil, C., Bennett, E.M., Pascual, U., Arkema, K.K., Brauman, K.A., Bryant, B.P., Guerry, A.D., Haddad, N.M., Hamann, M., Hamel, P., Johnson, J.A., Mandel, L., Pereira, H.M., Polasky, S., Ruckelshaus, M., Shaw, M.R., Silver, J.M., Vogl, A.L., Daily, G.C., 2019. Global modeling of nature's contributions to people. *Science* 366 (6462), 255–258.
- Chatterjee, A., Chatterjee, S., Smith, B., Cresswell, J.E., Basu, P., 2020. Predicted thresholds for natural vegetation cover to safeguard pollinator services in agricultural landscapes. *Agric. Ecosyst. Environ.* 290, 106785.
- Chatthanabun, N., Ascher, J.S., Pinkaew, N., Thanosing, C., Traiyasut, P., Warrit, N., 2020. Resin bees of genus *Megachile*, subgenera *Callomegachile* and *Carinula* (Hymenoptera, Megachilidae) from Thailand with description of a new species. *ZooKeys* 997, 95–144.

- Chuttong, B., Chanbang, Y., Burgett, M., 2014. Meliponiculture: stingless bee beekeeping in Thailand. *Bee World* 91, 41–45.
- Corlett, R.T., 2004. Flower visitors and pollination in the Oriental (Indomalayan) Region. *Biol. Rev. Camb. Philos. Soc.* 79, 497–532.
- Dalla Torre, C.G., 1896. *Catalogus Hymenopterorum: Apidae (Anthophila)*. 1896, vol. 10. G. Engelmann, Leipzig.
- Danforth, B.N., Minckley, R.L., Neff, J.L., 2019. *The Solitary Bees: Biology, Evolution, Conservation*. Princeton University Press.
- Dicks, L.V., Breeze, T.D., Ngo, H.T., Senapathi, D., An, J., Aizen, M.A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L.A., Gemmil-Herren, B., Howlett, B.G., Imperatriz-Fonseca, V.L., Johnson, S.D., Kovács-Hostyánszki, A., Kwon, Y.J., Lattorff, H.M.G., Lungharwo, T., Seymour, C.L., Vanbergen, A.J., Potts, S.G., 2021. A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nat. Ecol. Evol.* 5, 1453–1461.
- Dorey, J.B., Cheshire, P.R., Bolanos, A.N., O'Reilly, R.L., Bossert, S., Collins, S.M., Lichtenberg, E.M., Tucker, E.M., Smith-Pardo, A., Falcon-Brindis, A., Guevara, D.A., Ribeiro, B., de Pedro, D., Fischer, E.E., Hung, K.L.J., Parys, K.A., McCabe, L.M., Rogan, M.S., Minckley, R.L., Velzco, S.J.E., Griswold, T., Zarrillo, T.A., Jetz, W., Sica, Y.V., Orr, M.C., Guzman, L.M., Ascher, J.A., Hughes, A.C., Cobb, N.S., 2023. A globally synthesised and flagged bee occurrence dataset and cleaning workflow. *Sci. Data*. <https://www.biorxiv.org/content/10.1101/2023.06.30.547152v1> (in review).
- Engel, M.S., Kahono, S., Pegg, D., 2019. A key to the genera and subgenera of stingless bees in Indonesia (Hymenoptera: Apidae). *Treubia* 45, 65–84.
- Ferrari, R.R., Niu, Z.Q., Kuhlmann, M., Zhang, D., Zhu, C.D., 2021. The cellophane bees of *Colletes* Latreille (Hymenoptera: Colletidae) from Xizang (Tibet), China. *Zootaxa* 5022, 1–72.
- Fouks, B., Brand, P., Nguyen, H.N., Herman, J., Camara, F., Ence, D., Hagen, D.E., Hoff, K.J., Nachweide, S., Romoth, L., Walden, K.K.O., Guigo, R., Stanke, M., Narzisi, G., Yandell, M., Robertson, H.M., Koeniger, N., Chantawannakul, P., Schatz, M.C., Worley, K.C., Robinson, G.E., Elsik, C.G., Rueppell, O., 2021. The genomic basis of evolutionary differentiation among honey bees. *Genome Res.* 31, 1203–1215.
- Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhöffer, J. H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tshartke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M., 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339 (6127), 1608–1611.
- Garibaldi, L.A., Oddi, F.J., Miguez, F.E., Bartomeus, I., Orr, M.C., Jobbágy, E.G., Kremen, C., Schulte, L.A., Hughes, A.C., Bagnato, C., Abramson, G., Bridgewater, P., Carella, D.G., Diaz, S., Dicks, L.V., Ellis, E.C., Goldenberg, M., Hually, C.A., Kuperman, M., Locke, H., Mehrabi, Z., Santibañez, F., Zhu, C.-D., 2021. Working landscapes need at least 20% native habitat. *Conserv. Lett.* 14, e12773.
- Ge, J., Zhou, X., Ge, Z., Zhu, D., Nie, X., Wang, X., 2021. Phased contests allow rapid hierarchy formation in paired bumble bee workers. *Anim. Behav.* 179, 125–138.
- Grass, I., Kubitzka, C., Krishna, V.V., Corre, M.D., Mußhoff, O., Pütz, P., Drescher, J., Rembold, K., Ariyanti, E.S., Barnes, A.D., Brinkmann, N., Brose, U., Brümmer, B., Buchori, D., Daniel, R., Darras, K.F.A., Faust, H., Fehrmann, L., Hein, J., Hennings, N., Hidayat, P., Hölscher, D., Jochum, M., Knohl, A., Kotowska, M.M., Krashevka, V., Krefth, H., Leuschner, C., Lobite, N.J.S., Panjaitan, R., Polle, A., Potapov, A.M., Purnama, E., Qaim, M., Röhl, A., Scheu, S., Schneider, D., Tjoa, A., Tshartke, T., Veldkamp, E., Wollni, M., 2020. Trade-offs between multifunctionality and profit in tropical smallholder landscapes. *Nat. Commun.* 11, 1186.
- Gupta, A., 2012. Pesticide use in South and South-East Asia: environmental public health and legal concerns. *Am. J. Environ. Sci.* 8, 152.
- Hannan, M.A., Maeta, Y., Hoshikawa, K., 1997. Colony development of two species of Japanese bumblebees *Bombus (Bombus) ignitus* and *Bombus (Bombus) hypocrita* reared under artificial condition (Hymenoptera, Apoidea). *Jpn. J. Entomol.* 65, 343–354.
- Hartop, E., Srivathsan, A., Ronquist, F., Meier, R., 2022. Towards large-scale integrative taxonomy (LIT): resolving the data conundrum for dark taxa. *Syst. Biol.* 71, 1404–1422.
- Harvey, J.A., Heinen, R., Armbrrecht, I., Basset, Y., Baxter-Gilbert, J.H., Bezemer, T.M., Böhm, M., Bommarco, R., Borges, P.A.V., Cardoso, P., Clausnitzer, V., Cornelisse, T., Crone, E.E., Dicke, M., Dijkstra, K.-D.B., Dyer, L., Ellers, J., Fartmann, T., Forister, M. L., Furlong, M.J., Garcia-Aguayo, A., Gerlach, J., Gols, R., Goulson, D., Habel, J.-C., Haddad, N.M., Hallmann, C.A., Henriques, S., Herberstein, M.E., Hochkirch, A., Hughes, A.C., Jepsen, S., Jones, T.H., Kaydan, B.M., Kleijn, D., Klein, A.-M., Latty, T., Leather, S.R., Lewis, S.M., Lister, B.C., Losey, J.E., Lowe, E.C., Macadam, C.R., Montoya-Lerma, J., Nagano, C.D., Ogan, S., Orr, M.C., Painting, C.J., Pham, T.-H., Potts, S.G., Rauf, A., Roslin, T.L., Samways, M.J., Sanchez-Bayo, F., Sar, S.A., Schultz, C.B., Soares, A.O., Thancharoen, A., Tshartke, T., Tylianakis, J.M., Umbers, K.D.L., Vet, L.E.M., Visser, M.E., Vujic, A., Wagner, D.L., WallisDeVries, M. F., Westphal, C., White, T.E., Wilkins, V.L., Williams, P.H., Wyckhuys, K.A.G., Zhu, Z.-R., de Kroon, H., 2020. International scientists formulate a roadmap for insect conservation and recovery. *Nat. Ecol. Evol.* 4, 174–176.
- Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M., Ladle, R.J., 2015. Seven shortfalls that beset large-scale knowledge of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 46, 523–549.

- Hughes, A.C., 2017. Understanding the drivers of Southeast Asian biodiversity loss. *Ecosphere* 8, e01624.
- IPBES, 2016. The Assessment Report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on Pollinators, Pollination and Food Production. IPBES, Bonn, Germany.
- Ji, Y., Li, X., Ji, T., Tang, J., Qiu, L., Hu, J., Dong, J., Luo, S., Liu, S., Frandsen, P.B., Zhou, X., Parey, S.H., Li, L., Niu, Q., Zhou, X., 2020. Gene reuse facilitates rapid radiation and independent adaptation to diverse habitats in the Asian honeybee. *Sci. Adv.* 6, eabd3590.
- Karpe, S.D., Jain, R., Brockmann, A., Sowdhamini, R., 2016. Identification of complete repertoire of *Apis florea* odorant receptors reveals complex orthologous relationships with *Apis mellifera*. *Genome Biol. Evol.* 8, 2879–2895.
- Kitnya, N., Otis, G.W., Chakravorty, J., Smith, D.R., Brockmann, A., 2022. *Apis laboriosa* confirmed by morphometric and genetic analyses of giant honey bees (Hymenoptera, Apidae) from sites of sympatry in Arunachal Pradesh, North East India. *Apidologie* 53, 1–17.
- Klein, A.M., Steffan-Dewenter, I., Tschamtké, T., 2003. Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. R. Soc. B Biol. Sci.* 270, 955–961.
- Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tschamtké, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.* 274 (1608), 303–313.
- Koch, J.B., General, D.E.M., 2019. A preliminary assessment of bumble bee (Hymenoptera: Apidae) habitat suitability across protected and unprotected areas in the Philippines. *Ann. Entomol. Soc. Am.* 112, 44–49.
- Krishnan, S., Kushalappa, C.G., Shaanker, R.U., Ghazoul, J., 2012. Status of pollinators and their efficiency in coffee fruit set in a fragmented landscape mosaic in South India. *Basic Appl. Ecol.* 13, 277–285.
- Krishnan, S., Cheppudira, K.G., Ghazoul, J., 2017. Pollinator services in coffee agroforests of the Western Ghats. In: Dagar, J.C., Tewari, V.P. (Eds.), *Agroforestry: Anecdotal to Modern Science*. Springer, Singapore, pp. 771–795.
- Laha, S., Chatterjee, S., Das, A., Smith, B., Basu, P., 2022. Selection of non-crop plant mixes informed by arthropod-plant network analyses for multiple ecosystem services delivery towards ecological intensification of agriculture. *Sustainability* 14, 1903.
- Lelej, A.S., Proshchalykin, Yu, M., Loktionov, V.M. (Eds.), 2017. Annotated catalogue of the Hymenoptera of Russia. Volume I. Symphyta and Apocrita: Aculeata. *Proc. Zool. Inst. RAS (Suppl.)* 6 (475 pp.).
- Li, K., Grass, I., Zemp, D.C., Lorenz, H., Sachsenmaier, L., Nurdiansyah, F., Tschamtké, T., 2023. Tree identity and canopy openness mediate oil palm biodiversity enrichment effects on insect herbivory and pollination. *Ecol. Appl.* 33, e2862.
- Marcacci, G., Grass, I., Rao, V.S., Kumar, S.S., Tharini, K.B., Belavadi, V.V., Nölke, N., Tschamtké, T., Westphal, C., 2022. Functional diversity of farmland bees across rural-urban landscapes in a tropical megacity. *Ecol. Appl.* 32, e2699.
- Matsumura, C., Yokoyama, J., Washitani, I., 2004. Invasion status and potential ecological impacts of an invasive alien bumblebee, *Bombus terrestris* L. (Hymenoptera: Apidae) naturalized in Southern Hokkaido, Japan. *Glob. Environ. Res.* 8, 51–66.
- Men, X., Li, L., Lu, Z., Ouyang, F., Liu, L., Xu, H., Yu, Y., 2018. Biological characteristics and pollination service of Mason bee. *Chin. J. Appl. Entomol.* 55, 973–983.
- Michener, C.D., 2007. *The Bees of the World*. Johns Hopkins University Press.
- Motzke, I., Klein, A.M., Saleh, S., Wanger, T.C., Tschamtké, T., 2016. Habitat management on multiple spatial scales can enhance bee pollination and crop yield in tropical homegardens. *Agric. Ecosyst. Environ.* 223, 144–151.
- Murray Lasley, R., Jain, A., Kunte, K., 2013. Alleviating poverty in India: biodiversity's role. *Science* 341 (6148), 840–841.
- Nalinrachatakan, P., Triayusut, P., Khongnak, A., Muangkam, M., Ascher, J.S., Warrit, N., 2021. The resin bee subgenus *Rhognathidium* in Thailand (Megachilidae, Anthidiini): nesting biology, cleptoparasitism by *Stelis*, and new species. *ZooKeys* 1031, 161–182.
- Nidup, T., 2021. Report on the stingless bees of Bhutan (Hymenoptera: Apidae: Meliponini). *J. Threat. Taxa* 13, 18344–18348.
- Niu, Z.Q., Yuan, F., Ascher, J.S., Kasperek, M., Orr, M.C., Griswold, T., Zhu, C.D., 2020. Bees of the genus *Anthidium* Fabricius, 1804 (Hymenoptera: Apoidea: Megachilidae: Anthidiini) from China. *Zootaxa* 4867 (1).
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321–326.
- Orr, M.C., Ascher, J.S., Bai, M., Chesters, D., Zhu, C.D., 2020. Three questions: how can taxonomists survive and thrive worldwide? *Megataxa* 1, 19–27.
- Orr, M.C., Hughes, A.C., Chesters, D., Pickering, J., Zhu, C.D., Ascher, J.S., 2021. Global patterns and drivers of bee distribution. *Curr. Biol.* 31, 451–458.
- Orr, M.C., Hughes, A.C., Costello, M.J., Qiao, H., 2022a. Biodiversity data synthesis is critical for realizing a functional post-2020 framework. *Biol. Conserv.* 274, 109735.
- Orr, M.C., Ren, Z.X., Ge, J., Tian, L., An, J., Huang, J., Zhu, C.D., Williams, P.H., 2022b. The rising threat of the invasive bumblebee *Bombus terrestris* highlights the need for sales restrictions and domestication of unique local biodiversity in Asia. *Entomol. Gen.* 42, 655–658.
- Owen, R., 2017. Role of human action in the spread of honey bee (Hymenoptera: Apidae) pathogens. *J. Econ. Entomol.* 110, 797–801.
- Prathapan, K.D., Pethiyagoda, R., Bawa, K.S., Raven, P.H., Rajan, P.D., 2018. When the cure kills—CBD limits biodiversity research. *Science* 360 (6396), 1405–1406.
- Qu, Y., Wang, S., Wang, K., Wang, Z., 2022. The newly rising meliponiculture and research on stingless bees in China—a mini review. *J. Apic. Res.* 61, 730–737.
- Rabajante, J.F., Tubay, J.M., Jose, E.C., Cervancia, C.R., 2020. Pollinator diversity and density measures: survey and indexing standard to model, detect, and assess pollinator deficits. *Model. Earth Syst. Environ.* 6, 363–371.
- Raffiudin, R., Ariyanti, S.A., Aprilianingrum, I., Anwar, H., Shullia, N.I., Bening, S., Wiyati, S.Y., Priawandiputra, W., Saleh, S., Suardi, Fahri, F., Putra, R.E., Soesilohadi, R.C.H., Purnobasuki, H., 2022. Flight activity and pollen resources of *Apis nigrocincta* and *Apis cerana* in Central Sulawesi, Indonesia. *Agric. Nat. Resour.* 56, 463–472.
- Rattanawanee, A., Duangphakdee, O., 2019. Southeast Asian meliponiculture for sustainable livelihood. In: Ranz, R.E.M. (Ed.), *Modern Beekeeping-bases for Sustainable Production*. IntechOpen. Chapter 10.
- Ren, Z.X., Wang, H., Bernhardt, P., Li, D.Z., 2014. Insect pollination and self-incompatibility in edible and/or medicinal crops in southwestern China, a global hotspot of biodiversity. *Am. J. Bot.* 101, 1700–1710.
- Ren, Z., Zhao, Y., Liang, H., Tao, Z., Tang, H., Zhang, H., Wang, H., 2018. Pollination ecology in China from 1977 to 2017. *Plant Divers.* 40, 172–180.
- Requier, F., Pérez-Méndez, N., Andersson, G.K., Blareau, E., Merle, I., Garibaldi, L.A., 2022. Bee and non-bee pollinator importance for local food security. *Trends Ecol. Evol.* 38, 196–205.
- Ruppert, K.M., Kline, R.J., Rahman, M.S., 2019. Past, present, and future perspectives of environmental DNA (eDNA) metabarcoding: a systematic review in methods, monitoring, and applications of global eDNA. *Glob. Ecol. Conserv.* 17, e00547.
- Salatnaya, H., Fuah, A.M., Engel, M.S., Sumantri, C., Widiatmaka, Kahono, S., 2021. Diversity, nest preferences, and forage plants of stingless bees (Hymenoptera: Apidae: Meliponini) from West Halmahera, Indonesia. *Indonesian J. Anim. Vet. Sci.* 26, 167–178.
- Schreinemachers, P., Chen, H.P., Nguyen, T.T.L., Buntong, B., Bouapao, L., Gautam, S., Le, N.T., Pinn, T., Vilaysone, P., Srinivasan, R., 2017. Too much to handle? Pesticide dependence of smallholder vegetable farmers in Southeast Asia. *Sci. Total Environ.* 593–594, 470–477.
- Sekita, N., Yamada, M., 1993. Use of *Osmia cornifrons* for pollination of apples in Aomori Prefecture, Japan. *Jpn. Agri. Res. Q.* 26, 264–270.
- Senapati, D., Fründ, J., Albrecht, M., Garratt, M.P., Kleijn, D., Pickles, B.J., Potts, S.G., An, J., Andersson, G.K.S., Bänisch, S., Basu, P., Benjamin, F., Bezerra, A.D.M., Bhattacharya, R., Biesmeijer, J.C., Blaauw, B., Blitzer, E.J., Brittain, C.A., Carvalho, L.G., Cariveau, D.P., Chakraborty, P., Chatterjee, A., Chatterjee, S., Cusser, S., Danforth, B.N., Degani, E., Freitas, B.M., Garibaldi, L.A., Geslin, B., de Groot, G.A., Harrison, T., Howlett, B., Isaacs, R., Jha, S., Klatt, B.K., Krewenka, K., Leigh, S., Lindström, S.A.M., Mandelik, Y., Mc Kerchar, M., Park, M., Pisanty, G., Rader, R., Reemer, M., Rundlöf, M., Smith, B., Smith, H.G., Silva, P.N., Steffan-Dewenter, I., Tschamtké, T., Webber, S., Westbury, D.B., Westphal, C., Wickens, J.B., Wickens, V.J., Winfree, R., Zhang, H., Klein, A.-M., 2021. Wild insect diversity increases inter-annual stability in global crop pollinator communities. *Proc. R. Soc. B Biol. Sci.* 288 (1947), 20210212.
- Shi, X., Xiao, H., Luo, S., Hodgson, J.A., Bianchi, F.J.J.A., He, H., van der Werf, W., Zou, Y., 2021. Can landscape level semi-natural habitat compensate for pollinator biodiversity loss due to farmland consolidation? *Agric. Ecosyst. Environ.* 319, 107519.
- Silva, D.P., Castro, A.C.F., Vilela, B., Ong, X.R., Thomas, J.C., Alqarni, A.S., Engel, M.S., Ascher, J.S., 2020. Colonizing the east and the west: distribution and niche properties of a dwarf Asian honey bee invading Africa, the Middle East, the Malay Peninsula, and Taiwan. *Apidologie* 51, 75–87.
- Smith, D.R., 2021. Biogeography of honey bees. In: Starr, C.K. (Ed.), *Encyclopedia of Social Insects*. Springer, Cham, Switzerland.
- Sodhi, N.S., Koh, L.P., Clements, R., Wanger, T.C., Hill, J.K., Hamer, K.C., Clough, Y., Tshamtké, T., Posa, M.R.C., Lee, T.M., 2010. Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biol. Conserv.* 143, 2375–2384.
- Sritongchuay, T., Hughes, A.C., Memmott, J., Bumrungsri, S., 2019. Forest proximity and lowland mosaic increase robustness of tropical pollination networks in mixed fruit orchards. *Landsc. Urban Plan.* 192, 103646.
- Sritongchuay, T., Dalsgaard, B., Wayo, K., Zou, Y., Simla, P., Tanalgo, K.C., Orr, M.C., Hughes, A.C., 2022. Landscape-level effects on pollination networks and fruit-set of crops in tropical small-holder agroecosystems. *Agric. Ecosyst. Environ.* 339, 108112.
- Stewart, A.B., Waitayachart, P., 2020. Year-round temporal stability of a tropical, urban plant-pollinator network. *PLoS ONE* 15, e0230490.
- Stewart, A.B., Sritongchuay, T., Teartitup, P., Kaewsoomboon, S., Bumrungsri, S., 2018. Habitat and landscape factors influence pollinators in a tropical megacity, Bangkok, Thailand. *PeerJ* 6, e5335.
- Su, Y.-C., Chiu, Y.-F., Warrit, N., Otis, G.W., Smith, D.R. In review. Phylogeography and species delimitation of the Asian cavity-nesting honey bees. *Insect Systematics and Diversity*.
- Sun, C., Huang, J., Wang, Y., Zhao, X., Su, L., Thomas, G.W.C., Zhao, M., Zhang, X., Jungreis, I., Kellis, M., Vicario, S., Sharakhov, I.V., Bondarenko, S.M., Hasselmann, M., Kim, C.N., Paten, B., Penso-Dolfin, L., Wang, L., Chang, Y., Gao, Q., Ma, L., Ma, L., Zhang, Z., Zhang, H., Zhang, H., Ruzzante, L., Robertson, H.M., Zhu, Y., Liu, Y., Yang, H., Ding, L., Wang, Q., Ma, D., Xu, W., Liang, C., Itgen, M.W., Mee, L., Cao, G., Zhang, Z., Sadd, B.M., Hanh, M.W., Schaack, S., Barribeau, S.M., Williams, P.H., Waterhouse, R.M., Mueller, R.L., 2021. Genus-wide characterization of bumblebee genomes provides insights into their evolution and variation in ecological and behavioral traits. *Mol. Biol. Evol.* 38, 486–501.
- Tadauchi, O., Murao, R., 2014. *An Illustrated Guide to Japanese Bees*. Bun-ichi Sogo Shuppan Co, Tokyo.
- Tang, M., Hardman, C.J., Ji, Y., Meng, G., Liu, S., Tan, M., Yang, S., Moss, E.D., Wang, J., Yang, C., Bruce, C., Nevard, T., Potts, S.G., Zhou, X., Yu, D.W., 2015. High-throughput monitoring of wild bee diversity and abundance via mitogenomics. *Methods Ecol. Evol.* 6, 1034–1043.
- Thapa, R., Aryal, S., Jung, C., 2018. Beekeeping and honey hunting in Nepal: Current status and future perspectives. In: Chantawannakul, P., Williams, G., Neumann, P. (Eds.), *Asian Beekeeping in the 21st Century*. Springer, Singapore, pp. 111–127.

- Theisen-Jones, H., Bienefeld, K., 2016. The Asian honey bee (*Apis cerana*) is significantly in decline. *Bee World* 93, 90–97.
- Thimmegowda, G.T., Sharma, A., Mullen, S., Sottolare, K., Mohantam, S., Brockmann, A., Perunduraj, D., Olsson, S.B., 2020. A field-based quantitative analysis of sublethal effects of air pollution on wild pollinators. *Proc. Natl. Acad. Sci. U. S. A.* 117, 20653–20661.
- Tian, L., Rahman, S.R., Ezray, B.D., Franzini, L., Strange, J.P., Lhomme, P., Hines, H.M., 2019. A homeotic shift late in development drives mimetic color variation in a bumble bee. *Proc. Natl. Acad. Sci. U. S. A.* 116 (24), 11857–11865.
- TIGER, 2022. Seeing TIGER for the bees: digitizing apian specimens from Thailand's national parks. https://www.gbif.org/project/BIFA6_009/seeing-tiger-for-the-bees-digitizing-apan-specimens-from-thailands-national-parks. (Accessed December 2022).
- Vereecken, N.J., 2018. Wallace's Giant Bee for sale: implications for trade regulation and conservation. *J. Insect Conserv.* 22, 807–811.
- Wagner, D., 2020. Insect declines in the Anthropocene. *Annu. Rev. Entomol.* 65, 457–480.
- Wenzel, A., Grass, I., Belavadi, V.V., Tschamtker, T., 2020. How urbanization is driving pollinator diversity and pollination—a systematic review. *Biol. Conserv.* 241, 108321.
- Williams, P.H., 1998. An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini). *Bull. Nat. Hist. Mus. (Entomol.)* 67, 79–152 (updated at www.nhm.ac.uk/bombus/ accessed December 2022).
- Williams, P., 2007. The distribution of bumblebee colour patterns worldwide: possible significance for thermoregulation, crypsis, and warning mimicry. *Biol. J. Linn. Soc.* 92, 97–118.
- Williams, P.H., 2022. The bumblebees of the Himalaya, an identification guide. *Abc Taxa* 21.
- Williams, P.H., Bystrakova, N., Huang, J., Miao, Z., An, J., 2015. Bumblebees, climate and glaciers across the Tibetan plateau (Apidae: *Bombus* Latreille). *Syst. Biodivers.* 13, 164–181.
- Williams, P.H., Huang, J.X., An, J.D., 2017. Bear wasps of the Middle Kingdom: a decade of discovering China's bumblebees. *Antenna* 41, 21–24.
- Williams, P.H., Altanchimeg, D., Byvaltsev, A., De Jonghe, R., Jaffar, S., Japoshvili, G., Kahono, S., Liang, H., Mei, M., Monfared, A., Nidup, T., Raina, R., Ren, Z., Thanooosing, C., Zhao, Y., Orr, M.C., 2020. Widespread polytypic species or complexes of local species? Revising bumblebees of the subgenus *Melanobombus* world-wide (Hymenoptera, Apidae, *Bombus*). *Eur. J. Taxon.* 719, 1–120.
- Willmer, P., 2011. *Pollination and Floral Ecology*. Princeton University Press.
- Wilson, J.S., Pan, A.D., General, D.E.M., Koch, J.B., 2020. More eyes on the prize: an observation of a very rare, threatened species of Philippine bumble bee, *Bombus irisanensis*, on iNaturalist and the importance of citizen science in conservation biology. *J. Insect Conserv.* 24, 727–729.
- Wolowski, M., Agostini, K., Rech, A.R., Varasin, I.G., Maués, M., Freitas, L., Carneiro, L. T., Bueno, R.d.O., Consolaro, H., Carvalheiro, L.G., Saraiva, A.M., da Silva, C.L., 2019. Relatório Temático sobre Polinização. Polinizadores e Produção de Alimentos no Brasil. BPBES/REBIPP, Editora Cubo, São Carlos, São Paulo.
- Wurz, A., Grass, I., Tschamtker, T., 2021. Hand pollination of global crops—a systematic review. *Basic Appl. Ecol.* 56, 299–321.
- Xie, Z.H., Williams, P.H., Tang, Y., 2008. The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan Plateau of Sichuan. *J. Insect Conserv.* 12, 695–703.
- Yoon, H.J., Kim, S.E., Kim, Y.S., 2002. Temperature and humidity favorable for colony development of the indoor-reared bumblebee, *Bombus ignitus*. *Appl. Entomol. Zool.* 37, 419–423.
- Zhang, D., Niu, Z.-Q., Luo, A.-R., Orr, M.C., Ferrari, R.R., Jin, J.-F., Wu, Q.-T., Zhang, F., Zhu, C.-D., 2022. Testing the systematic status of *Homalictus* and *Rostrohaliectus* with weakened cross-vein groups within Halictini (Hymenoptera: Halictidae) using low-coverage whole-genome sequencing. *Insect Sci.* 29, 1819–1833.
- Zhu, C., Luo, A., Bai, M., Orr, M.C., Hou, Z., Ge, S., Chen, J., Hu, Y., Zhou, X., Qiao, G., Kong, H., Lu, L., Jin, X., Cai, L., Wei, X., Zhao, R., Miao, W., Wang, Q., Sha, Z., Lin, Q., Qu, M., Jiang, J., Li, J., Che, J., Jiang, X., Chen, X., Gao, L., Ren, Z., Xiang, C., Luo, S., Wu, D., Liu, D., Peng, Y., Su, T., Cai, C., Zhu, T., Cai, W., Liu, X., Li, H., Xue, H., Ye, Z., Chen, X., Tang, P., Wei, S., Pang, H., Xie, Q., Zhang, F., Zhang, F., Peng, X., Zhang, A., Gao, T., Zhou, C., Shao, C., Ma, L., Wei, Z., Luan, Y., Yin, Z., Dai, W., Wei, C., Huang, X., Liu, J., Chen, X., Yi, T., Zhang, Z., Aishan, Z., Li, Q., Hu, H., 2022. A joint call for actions to advance taxonomy in China. *Zool. System.* 47, 188–197.
- Zou, Y., Bianchi, F.J.J.A., Jauker, F., Xiao, H., Chen, J., Cresswell, J., Luo, S., Huang, J., Deng, X., Hou, L., van der Werf, W., 2017. Landscape effects on pollinator communities and pollination services in small-holder agroecosystems. *Agric. Ecosyst. Environ.* 246, 109–116.