Worldwide occurrence records reflect a global decline in bee species richness

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Abstract

Wild and managed bees are key pollinators, providing ecosystem services to a large fraction of the world's flowering plants, including ~85% of all cultivated crops. Recent reports of wild bee decline and its potential consequences are thus worrisome. However, evidence is mostly based on local or regional studies; global status of bee decline has not been assessed yet. To fill this gap, we analyzed publicly available worldwide occurrence records from the Global Biodiversity Information Facility spanning more than a century of specimen collection. We found that after the 1980's the number of collected bee species declines steeply, and approximately 25% fewer species were reported between 2006 and 2015 relative to the number of species counted before the 1990's. These trends are alarming and encourage swift action to avoid further decline of these key pollinators.

Introduction

Insects are the most specious group of animals and are estimated to encompass a large fraction of the Earth's living biomass[1]. Given their historical abundance and ubiquity, along

with the many familiar examples of extreme resilience to natural or intentional extermination,

some insects have been traditionally viewed as the ultimate survivors of most apocalyptic

scenarios. However, in the last two decades, a series of high-profile reports based mostly on

local or regional evidence have repeatedly warned of a significant decline in insect diversity

and biomass and raised the alarm about the potential consequence of this decline for the

delivery of many ecosystem services [2–5]. Among affected ecosystem services is plant

pollination: insects are the main vectors for pollen transfer of most wild and crop flowering

plant species [6–10]. Bees (Hymenoptera: Apoidea: Anthophila), a lineage that includes about

20,000 described species, are the most important group of insect pollinators [11,12]. Wild bee

species are not only key to sexual reproduction of hundreds of thousands of wild plant

species [7], but also to the yield of about 85% of all cultivated crops [6,13,10]. There is mounting

evidence that a decline in wild bee populations might follow or even be more pronounced

than overall trends of insect decline [12,14–17]. Such differential vulnerability might result from a

high dependence of bees on flowers for food and a diversity of substrates for nesting,

resources that are greatly affected by land conversion to large-scale agriculture, massive

urbanization, and other intensive land uses [18–20]. However, most studies on "bee decline" to

date are based on local-, regional- or country-level datasets, and have a strong bias towards

the Northern Hemisphere, particularly North America and Europe, where most long-term

research projects capable of generating multidecadal datasets have been conducted [4,12,21,22].

To find an alternative approach to assess whether bee decline is a global phenomenon, we

resorted to the data publicly available at the Global Biodiversity Information Facility

(GBIF)[23]. The GBIF collects and provides "data about all types of life on Earth" from

"sources including everything from museum specimens collected in the 18th and 19th century

to geotagged smartphone photos shared by amateur naturalists in recent days and weeks"[23].

GBIF ingests data from a widely diverse range of data sources, localities, recording

strategies, geographic areas, sampling intensities, etc., with each data source potentially

plagued by both systematic and idiosyncratic biases [24–27]. Although usage of GBIF data has

been strongly criticized due to its inherent biases [21,24,28–30], most criticisms are usually aimed

towards using its occurrence data to reconstruct and model species' distribution ranges.

Reconstructing geographic ranges and abundances from such "messy" datasets is indeed

challenging. However, a binning approach in which a simpler question ("has a species been

recorded anywhere during a given period?") yields a yes/no answer can potentially be much

more robust to sampling effort heterogeneity and geographic uncertainty [31]. We reasoned that

if bees are experiencing a global decline in the last few decades, then a generalized decrease

in population size and range would result in increased rarity, diminished chance of

observation and collection and, consequently, a diminished number of total species being

observed and recorded worldwide each year.

Results and Discussion

To test our hypothesis of global bee decline, we queried GBIF for all occurrence records

of Hymenoptera prior to 2020 with either "Preserved specimen" or "Human observation"

bases of record [32] (see Methods section below). Records of preserved specimens originate in

vouchered collections such as those from museums and universities, or associated with

biodiversity surveys and molecular barcoding initiatives, among others. Human observations,

on the other hand, are records in which a given species was observed, but no voucher was

collected; this category of records has been growing exponentially since citizen science

initiatives became increasingly popular[33]. Because the preserved specimen records are likely

to represent the most taxonomically traceable source of information within the GBIF

dataset[33,34], we made parallel analyses for both the full dataset and the specimens-only subset.

We filtered the datasets to six families of the superfamily Apoidea that conform the

Anthophila or "true bees": Melittidae, Andrenidae, Halictidae, Colletidae, Megachilidae and

Apidae (we excluded the small family Stenotritidae from our analysis, since it has only about

21 species restricted to Australia) [11].

Plotting the total number of records per year in both datasets show that the number of

worldwide bee occurrence records follows a mostly monotonic increasing trend that becomes

steeper after 1990 (Fig. 1A). Since the four most recent years (2016-2019, marked with * in

Fig. 1A) show a noticeable drop in records, likely due to time lags in data entry [35], we

excluded those years from further analyses to avoid a downward bias in most recent years. In

contrast, while the number of recorded species per year during the same period also increases

initially, it reaches a steady maximum after 1950 but then shows a noticeable decline starting

near the end of the 20th century (Fig. 1B). This negative temporal trend persisted even when

number of records and of contributing collections, institutions and datasets are considered

(generalized least squares estimate $\pm$ s.e. for the period 1986-2016: -31.9±11.0, t value: -2.9,

$p = 0.008$). Thus, fewer species have been reported globally within GBIF records since

approximately the 1990s.

To remove potential biases introduced by year-to-year heterogeneity of data sources, we

binned records every 10 years starting from 1946 (after the end of World War II, which

caused a noticeable dip in collection intensity, see Fig. 1A) and until 2015 inclusive; we call

these bins "idecades" and name them by the multiple-of-ten year in the middle. We then used

rarefaction based interpolation/extrapolation curves (iNEXT) and asymptotic richness

estimators [36,37] to compare idecadal changes in richness of species records. In this analysis,

accumulation curves are very similar from the 1950's to the 1990's but flatten considerably to

reach lower asymptotes for the 2000's and 2010's (Fig. 1C,E), again showing that the number

of species among bee specimens collected worldwide is showing a sharp decline. More

specifically, we found a reduction of about 8% during the 2000s in both datasets, and of 22%

and 26% during the 2010s for the full and specimen-only datasets, respectively (Fig. 1D, F).

Bee families in our dataset are heterogeneous in term of richness and abundance, and the

observed trends might be driven by just a few bee clades. To make a more phylogenetically-

explicit analysis exploring whether bees show a differential temporal trend compared to their

closest relatives, and whether particular bee families are more endangered than others, we re-

analyzed the specimen dataset, this time retaining also records for two families of carnivorous

apoid wasps, Crabronidae and Sphecidae, that are sister to Anthophila, and for another highly

diverse, non-apoid hymenopteran family, the Formicidae (ants) [38]. The results show different

patterns of species richness in records of each family, with noticeable phylogenetic structure

(Fig. 2). Long-tongued bees (Megachilidae and Apidae) show a steepening decline starting at

2000's, while short-tongued bees show declines starting earlier (Andrenidae and Halictidae)

or later (Colletidae). These declines in richness of recorded species relative to the average

number found between 1950 and 1990 ranged from 17% for Halictidae to over 41% for

Melittidae. Comparisons between Antophila families and two families of apoid wasps sister

to bees, and to a more distantly related family, the true ants (Formicidae) revealed contrasting

trends (Fig. 2). While both wasp families also show declining trends, they present different

patterns than bees. Record richness of sphecid and crabronid wasps both show a smoother

decrease initiating earlier than the 2000's. In contrast, ants show very little evidence of global

record richness decline, but rather a trend towards an increase in the number of recorded

species. Although the limited number of bee families precludes a formal analysis of

phylogenetic patterning, closely related families (e.g., Apidae and Megachilidae, or

Colletidae and Halictidae) seem to share more similar trends in terms of timing and

magnitude of species richness decline than less related families. This hint of phylogenetic

patterning becomes even more apparent when considering the two apoid wasp families,

Crabronidae and Sphecidae (Fig. 2). Interestingly, a very similar pattern – in which bees

show a strong, recent decline, wasps show a gentler decline starting earlier, while ants remain

steady – was recently reported using a quite different analytical approach on a substantially

different and more geographically limited dataset [39]. Altogether, family-specific trends and

asymptotic richness estimates show that the overall decline in global bee record richness is

not driven by any particular family. Instead, a generalized decline seems to be a pervasive

feature within the bee lineage.

To rule out the possibility that the method we used to estimate richness does not correlate

with actual bee diversity, we compared the asymptotic estimator of total richness for each

family based on GBIF records with the total known number of species and found a linear

correlation between both estimates across families (Fig. S1). Another potential artifact

causing a decline in recorded bee diversity in the last two idecades could be an increasing

loss in taxonomic expertise during that period [40–42]. Under such scenario, we would expect

the fraction of records unidentified to the species level – a reasonable proxy for lack of

expertise [33] – should have stayed approximately constant until the last two decades and then

increased noticeably. While the fraction of records missing species' identification shows an

overall increase in the last 120 years, this trend has actually reversed since the 2000's (Fig.

S2). This result is consistent with previous analyses of the GBIF dataset[33], and shows that

potential loss of taxonomic expertise cannot explain the decline in bee record diversity seen

at the last two decades.

Next, we explored the geographic distribution of the dataset, by sub-setting the data by

continent and repeating the analyses. Overall, GBIF has a strong bias towards North

American and European records [35], and this bias results in a very uneven contribution of each

continent to decadal number of records (Fig. S3). North America (including Central America

and the Caribbean) has the largest and most even representation of records across decades

(between 46 and 75% of global records) and shows its steepest decline in species richness

between the 1990's and the 2010's (Fig. S4). In contrast, Europe shows two separate periods

of decline, one between the 1960's and the 1970's and a more recent drop between the 1980's

and 1990's but stabilizes afterwards (Fig. S4). Africa shows a sustained fall in species

richness since the 1980's, whereas in Asia the decline seems to have started two or three

decades earlier (Fig. S4). The trend in South America is less clear, although estimated

richness also decreases in the last ten years of the dataset (Fig. S4). Overall, analyses of the

dataset at a continental scale show heterogeneity in both the proportional and absolute

contributions to the records, and in the timing and magnitude of the decline in species

richness. However, despite large differences in data availability and, perhaps, except for

Oceania, a decline in species richness of bee records seems to be common to all continents.

A global decline in bee record diversity could relate to a proportional decrease in bee

abundance, so that rare species become rarer or even extinct, and abundant species become

less abundant. Alternatively, the less abundant species could be declining strongly, whereas

abundant species might be declining at a lower rate or even thriving. These different

scenarios are expected to leave a distinctive signature in the temporal pattern of relative

record abundances. Under the first scenario, the sharp decrease in species richness estimates

should not be accompanied by a decrease in evenness, a measure of how equally total record

abundance is partitioned among species, whereas under the second scenario there should be a

parallel decrease in record evenness. As expected from the hypothesis of an abundance-

related differential species decline, plotting Pielou's index (a common measure of

evenness [43]) per year of bee records shows a strong decreasing trend since the 1990's for both

datasets (Fig. 3). Therefore, this decline in species richness of records can relate to either a

global change in how an invariant bee diversity is sampled, leading to more infrequent

reporting of many species and much more frequent reporting of a few other species, or to a

global phenomenon by which thousands of species are becoming too rare to be sampled while

fewer species are becoming dominant and perhaps even increasing in abundance. These two

alternatives are not mutually exclusive, and both increased sampling and reporting bias and

declining bee biodiversity should be a matter of concern.

Our results support a hypothesis of overall decline in bee diversity at a global scale. If

trends in species richness of GBIF records are reflecting an actual trend in bee diversity, then

this decline seems to be occurring with distinctive characteristics in every bee family and in

most continents. Interestingly, this trend appears to be a relatively recent phenomenon that

accentuated in the nineties, at the beginning of the globalization era, and continues to the

present. The globalization era has not only been a period of major economic, political and

social change, but also of accelerated land-use transformation [44]. Bees thrive in

heterogeneous habitats, even those driven by man [18,45], where they find a diversity of floral

and nesting resources. However, land devoted to agriculture, particularly to monoculture, has

expanded in several regions of the world since the 1990s [44]. This has led not only to higher

habitat homogeneity, which can relate by itself to more impoverished and spatially

homogeneous bee assemblages [18,46], but also to higher use of pesticides and other agriculture

chemical inputs that have direct and indirect lethal and sub-lethal effects on bee health [47].

Effects of climate change on shrinking bee geographical ranges have been also documented

in Europe and North America [4]. Lastly, a booming international bee trade has involved the

co-introduction of bee pathogens, that may cause bee decline, like the emblematic case of the

giant Patagonian bumble bee, *Bombus dahlbomii* [48]. These drivers can act synergistically,

which can have accelerated a process of bee decline. Phylogenetic patterning in the trend of

recorded species diversity among the different bee families (Fig. 2) suggests that different

lineages can be differentially affected by different drivers, likely based both on their common

geographical distribution and shared clade-specific biological and ecological traits [21,49,50].

Associated with the declining trend of richness of species records is a trend of increasing

dominance of records by a few species. Increasing dominance by one or a few species can be

observed at the regional scale, like the case of invasive *Bombus terrestris* in southern South

America [51] or the western honeybee *Apis mellifera* in the Mediterranean [52]. The western

honeybee has been introduced in every single continent from its original geographical range

in Europe and Africa. Although both domesticated and wild populations of the western

honeybee seem to be declining in several countries, this species is still thriving globally [53].

Correspondingly, an increasing fraction of the total global bee records is composed by *Apis*

mellifera occurrences (Fig. S5). A consequence of increasingly less diverse and uneven bee

assemblages could be an increase in pollination deficits, causing a reduction in the quantity

and quality of the fruits and seeds produced by both wild and cultivated plants. Less diverse

bee assemblages at both local and regional scales have been associated with lower and less

stable yields of most pollinator-dependent crops [13].

GBIF is certainly not a source of systematically collected data, and this should be borne in

mind when interpreting the results of our analyses [21,27,35,54,55]. Spatial and temporal biases in

collection intensity (e.g., targeted programs might enrich the abundance of specific

species/groups at specific spans and regions) can generate spurious trends. In our analysis, we

counted every species only once per year regardless of how many records it had for a given

year; this filters out biases due to sporadic intensive sampling campaigns. Biases introduced

due to targeted collection efforts or local/regional events (e.g., changes in research and

conservation policies, economic downturns, social unrest, etc.) are likely, yet most such

biases tend to be spatially and temporally restricted, and are less likely to systematically

affect trends at the global, multi-decadal scale of this analysis. Indeed, several potential

biases would be expected to deflate, rather than inflate our results. For example, collectors

targeting rare species would be expected to enrich the number of species (unless many

species are becoming so scarce that they just cannot be found).

Nonetheless, our continent-level analysis showed that regions with the best temporal and

spatial coverage (i.e., Europe and North America, Fig. S3) are the ones showing the clearest

signal for decline (Fig. S4); our results agree with several existing reports at local, national

and subcontinental level [14,16,17,39,56–61]. Furthermore, none of those biases can explain the

noticeable phylogenetic contagion seen in the trends (Fig. 2) better than the fact that the

hymenopteran groups we analyzed have a considerable phylogenetic signal in their ecology

and life history traits and would be expected to show phylogenetic clustering in their response

to drivers of decline [50].

Unsurprisingly, when data is disaggregated by country, agreement between country-level

results and existing reports improves as the number of records increases. For example, our

data reflects a clear and continuous decline in bee diversity in the USA [56,57,60] (with over 1

million records), a decline in Brazil[61] during the last two decades (~190k records), but shows

no clear loss of richness in Great Britain (~25k records), or much uncertainty in an apparent

trend in bee species loss in Panama (~9k records), despite reports of bee decline in all those

countries[14,16,17,62] (Fig. S6). Interestingly, reports on decline of British bees are based on

occurrence data that is not publicly available – i.e. ~300k records from the Bees, Wasps and

Ants Recording Society (BWARS: http://www.bwars.com/). This suggests that, besides data

source heterogeneity, a major source of bias and inaccuracy of results derived from GBIF

data result from obstacles to data mobilization, and highlights the need to increase efforts to

remove barriers to data sharing and discourage funding agencies from allowing data

sequestration.

Thus, while the inherent heterogeneity and biases of aggregated datasets as those offered

by GBIF make them unreliable as a direct (i.e., unfiltered, uncorrected) data source of

predictive models, they can still be used within a hypothesis-driven framework to test

whether bees (or any other taxon) as a group are declining worldwide. In this context, our

results largely agree with the hypothesis that current regional reports of declining bee

diversity reflect a global phenomenon.

Conclusions

One of the most important pieces of missing information of the global report on

Pollinators, Pollination and Food Production of IPBES [63] was the lack of data on global bee

decline, despite the many local and few regional reports pointing out that this decline could

add to a global phenomenon. Despite all its shortcomings, GBIF still is probably the best

global data source available on long-term species occurrence and has the potential to

contribute in filling this critical knowledge gap. Its analysis supports the hypothesis that we

are undergoing a global decline in bee diversity that needs the immediate attention of

governments and international institutions. Under the most optimistic interpretation – that

bees are not declining, and the trends we find are an artifact of data collection - our results

would indicate that global efforts to record and monitor bee biodiversity are decreasing over

time. However, and given the current outlook of global biodiversity [4,5,10,12], it is more likely

that these trends reflect existing scenarios of declining bee diversity. In the best scenario, this

can indicate that thousands of bee species have become too rare; under the worst scenario,

they may have already gone locally or globally extinct. In any case, a decline in bee diversity

driven by either increasing rarity or irreversible extinction will affect the pollination of wild

plants and crops, with broader ecological and economic consequences. Slowing down and

even reversing habitat destruction and land-conversion to intensive uses, implementation of

environmentally friendly schemes in agricultural and urban settings, and programs to re-

flower our world are urgently required. Bees cannot wait.

Methods

Datasets

An initial query at the database of occurrence records at the Global Biodiversity
Information Facility (www.gbif.org) using the filters [Scientific Name = "Hymenoptera",
Basis of Record = "PRESERVED_SPECIMEN" | "HUMAN_OBSERVATION", Year
<2020] resulted on 9,176,688 total records involving 2,374 datasets [32]. Data were
downloaded as a text file and filtered for records identified to species levels and belonging to
Anthophila (defined as the families Melittidae, Andrenidae, Halictidae, Colletidae,
Megachilidae and Apidae; 3,459,086 records). We also retrieved records for two closely
related families of apoid wasps (Crabronidae and Sphecidae; 283,331 records), or the true
ants (Formicidae; 1,121,857 records). Phylogenetic relations between all these nine families
follow recent phylogenomic results [38].

Analyses

All datasets were analyzed using a customized script written and executed within the R
computing environment [64]. The complete annotated script is available as Supplementary
Materials, and can be used to fully reproduce all results, or adapted to re-run the analyses on
other datasets. Data was processed using the `tidyr`[65], `dplyr`[66] and `data.table`[67]
packages.

After removing records without "year" data, yearly counts of records and species were
plotted using `ggplot2`[68]. Significance of a negative trend was tested by fitting yearly counts
of records, species, collections, institutions and datasets a generalized least squares model
with the formula `sp ~ year + records + collections + institutions +`
`datasets`, with an autoregressive-moving average autocorrelation structure of order (1,0).
Then, each year was assigned to a 10-year period termed "idecade" (for inter-decade),

corresponding to a regular decade shifted four years into the past (e.g, the 1990's idecade

spans 1986 to 1995). Records by species and idecade were counted and stored in a matrix of

m species × *7* idecades (1950's to 2010's). This matrix was used as abundance data input for

the `iNEXT` function of the iNEXT package [37] to estimate rarefaction-based

interpolation/extrapolation (iNEXT) curves and Chao1 asymptotic estimators of species

richness [36]. We also compared the asymptotic estimator for species richness for each family

with the total number of species listed for each family in the taxonomic framework of the

Integrated Taxonomic Information System (www.itis.gov).

To estimate potential biases caused by changes of taxonomic expertise over time, we re-

filtered the initial GBIF query without excluding records without a species ID, then counted

the number of records with or without a species id per year [33]. To analyze trends at

continental level, we added a "Continent" field to the base dataset via table joining to a list of

countries, country codes and continents from https://datahub.io/JohnSnowLabs/country-and-

continent-codes-list. We then repeated the analyses splitting the dataset by continent.

Continent and country-specific shapes were taken from https://github.com/djaiss/mapsicon.

To show trends in equitability of species abundance across records over time, we calculated

Pielou's evenness index [43], $J=\Sigma p_i\ln(p_i)/\log(S)$ for $i=1$ to S, the total number of species, for

each year between 1900 and 2018, using the diversity functions from the package `vegan`[69].

The contribution of a given species (e.g., *Apis mellifera*) was calculated as yearly number of

the species records divided the total number of records for that year and plotted as a function

of year.

Acknowledgments

We thank Lawrence Harder, Lucas Garibaldi, Gherardo Bogo, Reto Schmucki, Ignasi

Bartomeus, Castor Guisande and several other colleagues who provided both encouragement

and constructive criticism to earlier drafts of this manuscript, and to the GBIF Secretariat for

maintaining this great resource. This project was inspired by work done at the Safeguarding

Pollination Services in a Changing World (SURPASS) workshops that took place at Puerto

Blest, Bariloche, Río Negro, Argentina in 2018, and Seaton, Devonshire, UK in 2019,

supported by the Researcher Links Workshop grant, ID 2017-RLWK9- 359543120, under the

UK LATAM partnership funded by the UK Department of Business, Energy and Industrial

Strategy (BEIS) and Argentina's CONICET, and delivered by the British Council.

Footnotes

Author contributions: Conceptualization, E.E.Z. and M.A.A.; Data Curation: E.E.Z.;

Formal analysis: E.E.Z. and M.A.A.; Visualization: E.E.Z.; Writing – original draft, E.E.Z.

and M.A.A., Writing – review & editing, E.E.Z. and M.A.A.

Competing interests: Authors declare no competing interests.

Data and materials availability: Occurrence record data used in this paper can be

downloaded from https://doi.org/10.15468/dl.ysjm4x; original sources traceable via

GBIF.org. The R language script used to analyze the data and generate the plots is available

at https://github.com/ezattara/global-bee-decline.

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Figures and figure legends

Fig. 1. Despite increasing number of specimen records, the number of worldwide recorded

bee species is sharply decreasing. (A) Number of worldwide GBIF records of Anthophila

(bees) occurrences per year in the full (blue) and specimens-only (red) datasets. The curves

represent loess fits with a smoothing parameter α = 0.75 up to 2015. The four most recent

years (2016-2019, labeled with *) were excluded from further analysis. (B) Number of bee

species found each year in the full (blue) and specimens-only (red) datasets. (C) Chao's

interpolation/extrapolation (iNEXT) curves based on the full dataset. Data were binned into

ten-year periods (*idecades*) from 1946 to 2015. The symbols show actual number of

specimen records and separate interpolated (left, full line) from extrapolated (right, dashed

line) regions of each curve. (D) Values of the asymptotic richness estimator by idecade (see

main text) for the full dataset (error bars mark upper and lower 95% confidence intervals).

(E) Chao's interpolation/extrapolation (iNEXT) curves based on the specimens-only dataset.

(F) Values of the asymptotic richness estimator by idecade for the specimens-only dataset.

Fig. 2. Decline patterns in worldwide records of bees are generalized but phylogenetically

structured. Phylogenetic relationships among each of the six families of bees (Anthophila,

lower six rows), two related families of non-flower associated apoid wasps (2nd and 3rd

rows), and the less related, highly specious ant family (top row). The left row shows number

of species per year in GBIF records from 1946 to 2015 based on the preserved specimen

dataset – the curves represent loess fits with a smoothing parameter α = 0.75; the middle row

shows Chao's interpolation/extrapolation curves based on GBIF records, grouped by idecade

for the period 1946-2015; the right row show the asymptotic estimates of richness by idecade

for the same period (error bars mark upper and lower 95% confidence intervals).

Fig. 3. Overall representation of worldwide bee species based on global records is becoming

increasingly uneven over time. Estimate of Pielou's index of sample evenness per year in the

full (blue) and specimens-only (red) datasets from 1900 to 2016. The lines show respective

loess fit curves with a smoothing parameter $\alpha = 0.75$.

Supplementary Figures

Figure S1: While often underestimating the known richness of each family, Chao's

asymptotic estimators of species richness based on all-times GBIF global records of

preserved specimens show a linear correlation with actual species diversity. The dotted line

shows the identity diagonal. ITIS stands for Integrated Taxonomic Information System

(www.itis.gov).

Figure S2: Fraction of the dataset records that lack a species ID. Points show the proportion

of records unidentified at the species level in a given year, relative to the total number of

records for that year, and the curve shows a loess-smoothed trend line with a smoothing

parameter α = 0.75.

Figure S3: Contribution by idecade of each continent (Antarctica excluded) to the full bee

record dataset. (A) Absolute number of GBIF records with a species ID for each continent,

grouped by idecade since the 1950's. (B) Relative contribution of each continent to

worldwide idecadal GBIF records with a species ID.

Figure S4: Trends shown in GBIF records for each continent. The left two rows of plots show number of yearly bee records and species in GBIF (blue: full dataset; red: specimens-only dataset); the right two rows show Chao's interpolation/extrapolation curves based on the specimens-only dataset grouped every ten years (idecades) for the period 1946-2015 and bar plots of the asymptotic estimates of richness by idecade for the same period (error bars mark upper and lower 95% confidence intervals).

Figure S5: Increase in the fraction of global records of preserved specimens at GBIF

represented by the honeybee *Apis mellifera* since the year 1900 (blue: full dataset; red:

specimens-only dataset). Points represent yearly proportion of total records belonging to *A.*

mellifera; lines show respective loess fit curves with a smoothing parameter α = 0.75.

Figure S6: Reliability of trends shown in records of GBIF preserved specimens for specific

countries increases with the number of records. The left two rows of plots show number of

yearly bee records and species in GBIF for each country – fitted trends are loess curves with

a smoothing parameter α = 0.75; the right two rows show Chao's interpolation/extrapolation

curves based on records grouped every ten years (idecades) for the period 1946-2015 and bar

plots of the asymptotic estimates of richness by idecade for the same period (error bars mark

upper and lower 95% confidence intervals).

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