1. Introduction

The western honey bee (Apis mellifera L.) provides highly valued pollination services for a wide variety of agricultural crops [1], and ranks as the most frequent single species of pollinator for crops worldwide [2]. A long history of domestication and intentional transport of A. mellifera by humans has resulted in its current cosmopolitan distribution that includes all continents except Antarctica and many oceanic islands. Given the advanced state of knowledge concerning this species and its role in agriculture, it seems surprising that the importance of A. mellifera as a pollinator in natural habitats remains poorly understood [3 5].

Clarifying the role of A. mellifera as a pollinator in natural habitats is important

for several reasons. First, animalmediated pollination represents a vital ecosystem service [6,7]; an estimated 87.5% of flowering plant species are pollinated by animals [8]. Quantification of the pollination services provided by the cosmopolitan, supergeneralist A. mellifera [9] will thus provide insight into the functioning of many terrestrial ecosystems. Second, nonA. mellifera pollinators are declining as a result of habitat loss, habitat degradation and other factors including pesticides, pathogens, parasites and climate change [10 12]. In cases where A. mellifera populations can withstand these perturbations, the degree to which they replace pollination services formerly performed by extirpated pollinators [13 17] deserves scrutiny. Third, recent increases in the mortality of managed

A. mellifera colonies in some regions of the world [11,18] may extend to popu

lations of freeliving A. mellifera [19 21]. Threats to A. mellifera populations could thus affect the reproduction and population dynamics of plants in natural

areas, with potential shifts in the composition of plant assemblages [22,23], and in turn, the ecosystem services (e.g. carbon sequestration, soil retention) that these plants provide. Lastly, where introduced populations of A. mellifera attain high densities [24 26], they may compete with other pollinators [27 29] or compromise plant reproductive success [30]. These phenomena are of broad ecological, evolutionary and conservation importance, but to our knowledge, there currently exists no global quantitative synthesis of the numerical importance of A. mellifera as a pollinator in natural ecosystems in their native or introduced ranges.

Here, we address questions concerning the importance of

A. mellifera by exploiting a recent trend in pollination research the documentation of communitylevel, plantpollinator interaction networks (hereafter pollination networks). Quantitative pollination network studies document the identity and frequency of each type of pollinator visiting each plant species within a locality [31]. Network data are used to address a variety of questions (e.g. [32 34]), but key for our goals here, they provide an underused opportunity to gauge the importance of A. mellifera in natural habitats, particularly

because the role of A. mellifera has rarely been the focus of

these studies [25,26,35]. We compiled a database of 80 quantitative pollination networks from natural habitats worldwide. To further assess the importance of A. mellifera as a pollinator, we also compiled data on pervisit pollination effectiveness of

A. mellifera relative to other floral visitors from studies of 34 plant species.

Our metaanalyses address three interrelated lines of inquiry concerning the ecological importance of A. mellifera in natural habitats: (i) what proportions of floral visits are contributed by A. mellifera foragers to individual networks worldwide, and to individual plant species within networks?

(ii) what environmental factors govern the relative contribution of A. mellifera to communitylevel floral visitation, and do levels of visitation differ between its native and introduced ranges? and (iii) given that pollination network studies often use visitation frequency as a proxy for pollinator importance (e.g. [36]), how does the pervisit pollination effectiveness of A. mellifera compare to the effectiveness of other floral visitors?

2. Material and methods

(a) Database for network synthesis

We used two approaches to compile our dataset of pollination networks. First, we performed a literature search using the ISI Web of Science database with the search terms [ pollinat\* network], [ pollinat\* web] and [ pollinat\* visit\* community], examining all studies available as of August 2016. Second, we downloaded all pollination network data from the Interaction Web Database of the National Center for Ecological Analysis and Synthesis website (http://data.nceas.ucsb.edu/) and the Web of Life Ecological Networks Database (http://www.weboflife.es/) available as of December 2014. We collected all studies and plantpollinator interaction network datasets that documented visitation frequency (i.e. number of individuals observed contacting flowers or number of floral contacts per unit time) between each pair of plant and pollinator taxa. We defined a network as the sum of recorded plantpollinator interactions in all sites from a single study that fell within a 50 km diameter circle, regardless of the number of sites that constitute the network. Sites within the same study that are separated by more than 50 km were treated as separate networks. When we

encountered networks from different studies that were less than 2

50 km apart, we excluded those that sampled a smaller number

of plant or pollinator taxa, or documented fewer interactions. We chose 50 km as a threshold to avoid overrepresenting studies that include many networks within a locality (e.g. [32,37]), while keeping separate those networks originating from distinct localities within the same geographical region, such as networks documented on different islands from the same archipelago (e.g. [38]). When studies included multiple years of data collection at the same sites using the same protocols, we pooled data from all study years into a single network.

All networks retained for analyses met the following criteria. The data were collected in natural habitats, here defined as largely unmanaged assemblages of plant species where the identities and relative abundances of plant species are not purposefully manipulated (thus excluding, for example, agricultural, urban and experimental habitats; see the electronic supplementary material, table S11). Each network consisted of observations on five or more plant species when pooled across the sites making up an individual study. All networks documented a broad range of pollinators; studies with a narrow taxonomic scope (e.g. social bees, bird pollinators with incidental observations of A. mellifera) or those that a priori excluded

A. mellifera were not included. We also excluded networks from

sites that were known to be heavily influenced by A. mellifera colonies stocked for adjacent agricultural pollination. Thus, our estimates of the numerical importance of A. mellifera may be conservative with respect to mosaic landscapes where natural habitats are intermixed with agricultural fields with managed

A. mellifera colonies [39]. We did not a priori exclude networks from localities outside of the presumed climatic niche of

A. mellifera [40], or where A. mellifera was never introduced. In all, we obtained 80 networks (see the electronic supplementary material, table S11) from 60 peerreviewed studies and three graduate theses [37,41,42]. While lacking coverage in some regions (figure 1), our dataset attains geographical coverage comparable to other recent studies that examine the importance and conservation of pollinators at a global scale [2,12,43].

For each network, we obtained the following data from their associated publications or from study authors when data were not available from publications: latitude, longitude and final year of data collection. When these data were not available and authors could not be reached, we used the approximate geographical centre of the study locality listed in the publication, and the year of publication as the last year of data collection. We defined the native status of A. mellifera based on [40] and

[44]; although we caution that the native status of A. mellifera

in the British Isles and northern Europe remains unresolved. We also extracted the following information from each study, when available: the proportion of all floral visits contributed by A. mellifera (in two networks this metric was estimated by calculating the proportion of the total visitation rate, summed across plant species, contributed by A. mellifera; see the electronic supplementary material, table S11), the proportion of plant species receiving at least one visit by A. mellifera, and the rank of A. mellifera with respect to both the proportion of all floral visits contributed and the proportion of plant species visited. Additionally, we used geographical information system (GIS) analysis to obtain elevation data and bioclimatic variables ([45], http://www.worldclim.org) for each network based on its global positioning system (GPS) coordinates. We also categorized

each network as being on an island or a mainland; the latter category includes all continents as well as islands greater than 200 000 km2, namely Great Britain (United Kingdom), Honshu (Japan) and Greenland. For studies for which raw data were not available, we contacted the corresponding authors to request data, or, in cases where data could not be shared, requested summary statistics on plantpollinator interactions. When raw

Figure 1. Proportion of all floral visits contributed by the western honey bee (Apis mellifera) in 80 plantpollinator interaction networks in natural habitats worldwide. Apis mellifera is generally considered a native species in Europe, the Middle East, and Africa; and introduced elsewhere. (Online version in colour.)

numeric data were unavailable from the publication or from authors, we used IMAGEJ to extract data from figures, where possible (see the electronic supplementary material, table S11). Owing to the different methodologies and data reported by each study, not all of the abovementioned variables were extracted from all networks.

(b) Frequency and patterns of Apis mellifera visitation

We calculated the global mean and median proportion of all floral visits contributed by A. mellifera, using each network as a data point (n 80 networks). Calculations were repeated after excluding networks that documented no A. mellifera visits, in order to examine the role of A. mellifera specifically in localities where it occurs. Additionally, we examined plant species in 41 networks in which (i) A. mellifera was present, and (ii) data on the number of visits contributed by A. mellifera and nonA. mellifera visitors were available for each plant species. Across these networks, we calculated the mean and median proportion of plant species that were (i) not visited by A. mellifera, (ii) numerically dominated by

A. mellifera (i.e. A. mellifera contributing 50% of all floral visits), and (iii) visited exclusively by A. mellifera. Because plant species

receiving few visits overall may tend to have extreme values of proportion of visits by A. mellifera, we restricted the analysis to 834 plant taxa with 10 visits recorded. Additionally, to aid in visualizing the distribution of the numerical importance of

A. mellifera across plant species, we also calculated for each network the proportion of plant species that fell into each of 10 bins with respect to the proportion of visits contributed by A. mellifera (range 0 1; bin width 0.1). We then constructed a histogram by calculating the mean and 95% confidence intervals of each bin across all 41 networks.

(c) Environmental correlates of Apis mellifera visitation frequency

We constructed multiple regression models to identify environ

mental factors that best explain variation in the visitation frequency of A. mellifera among networks. The response variable in these regression models was the proportion of all floral visits in each network contributed by A. mellifera. Owing to the strongly nonnormal distribution of the data as well as the presence of numerous zeroes, we performed zeroinflated, multiple b

regression using package gamlss [46] in R (v. 3.3.1 [47]). One network located above the Arctic Circle [48] was excluded from this analysis because bioclimatic data were unavailable (hence, n 79). We note that the exclusion of networks with no A. mellifera visits did not qualitatively alter our results (see the electronic supplementary material, table S21).

To incorporate bioclimatic variables [45], we first performed principal components analysis (PCA) to avoid constructing models with highly collinear terms. We performed one PCA for the 11 variables measuring temperature, and a separate PCA for the eight bioclimatic variables measuring precipitation (see the electronic supplementary material, table S3). We then reduced bioclimatic variables to the first two principal components of the temperature and precipitation variables, which accounted for 86% and 89% of the variance, respectively. We constructed a full model containing the following explanatory variables, without interactions: