



Information retrieved from specimens at Natural History Collections can improve the quality of field-based ecological networks

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Abstract: Numerous studies analyze the interactions between plants and their pollinators in ecological communities using a network approach. However, field studies rarely record all the interactions occurring in the field. In this sense Natural History Collections (NHCs) can provide information on interactions that may have been missed by field sampling. In this study we compare a network based on field sampling with a network based on data retrieved from specimens at NHCs, and we assess the degree to which these two sources of data are complementary. For this we used data available from a bee biodiversity study conducted in Southern Argentina for the South American bee genus *Corynura* (Halictidae: Augochlorini). Data on the floral associations of the specimens at NHCs were retrieved from the specimens' labels, as the name of the plant species on which a given bee was captured is often recorded for many specimens at NHCs. Although field sampling recorded an unusually high number of insect-plant interactions, it misses some unique interactions present in the NHCs networks. Some structural properties of these networks are briefly analyzed, and usefulness and limitations of using NHCs data are discussed. We conclude that the information about insect-plant interactions extracted from NHCs could complement field-based data, especially in poorly sampled communities.

Abbreviations: AIG–Anne-Isabelle Gravel, CONICET–Consejo Nacional de Investigaciones Científicas y Técnicas, FAUBA–Facultad de Agronomía of the Universidad de Buenos Aires, INTA–Instituto Nacional de Tecnología Agropecuaria, MACN–Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', NHCs–Natural History Collections, RAGV–Rocio Ana González-Vaquero

Introduction

Natural History Collections play a significant role in different fields of Biology, even in those not directly linked to taxonomy. In general, specimens housed at NHCs have a significant amount of data associated with the sample, such as date, location, collecting method and collector. These data are extremely valuable as they can be used in theoretical and applied studies such as ecological niche modeling (Sánchez-Cordero and Martínez-Meyer 2000, Burns et al. 2003, Townsend Peterson and Navarro-Singüenza 2009, Labay et al. 2011), detecting areas of endemism (Domínguez et al. 2006, Szumik et al. 2012) and recording the decline of plant and insect diversity (Biesmeijer et al. 2006, Farnsworth and Ogurcak 2006, Colla and Packer 2008, Cameron et al. 2011).

Many wild and cultivated plants are pollinated by insects, usually by bees (Michener 2007, Ollerton et al. 2012). Bees (Hymenoptera: Apoidea) are a biologically diverse group of insects whose origin in the Cretaceous is directly related to the first flowering plants (Michener 2007). Considering the degree of pollen specialization and constancy for gathering floral resources, bee species can range from narrowly oli-

golectic to broadly polylectic (Cane and Sipes 2006). Early bee collectors did not fully acknowledge the importance of registering the plant associations on the labels of every captured specimen and only occasionally mentioned them in published work (Alfken 1913, Friese 1916, Herbst 1922). Nowadays it is common to record on the label the name of the plant species on which the bee specimen was captured (what most mellitologists call its 'host plant'). This can be done using e.g., a net sweeping method, as opposed to other more passive capturing techniques (pan traps, malaise traps).

Interactions between pollinators and plants are the result of ecological and evolutionary processes that can be analyzed as complex networks (Memmott 1999, Bascompte and Jordano 2007, Vázquez et al. 2009). Several indices have been proposed to analyze these networks (Blüthgen et al. 2008, Dormann et al. 2009) and numerous recent studies have evaluated the processes that determine the patterns observed (see Vázquez et al. 2009 for a review). These networks share common structural patterns such as nestedness (Bascompte et al. 2003) and modularity (Olesen et al. 2007). Networks are nested when the species interacting with specialists are a proper subset of the species interacting with generalists

(Bascompte et al. 2003). In addition, networks may be partitioned into modules (also called compartments), which are groups of species that are linked more tightly together than they are to species in other modules (Olesen et al. 2007). Nestedness and modularity may reflect evolutionary and ecological processes that shaped species interactions (Bascompte and Jordano 2007, Olesen et al. 2007, Dalsgaard et al. 2013).

The quality of field data used to build networks has been rising steadily in the last decade. However, despite increasing sampling efforts, the number of interactions recorded in the field rarely reaches the number of interactions theoretically expected to occur (Chacoff et al. 2012). In addition, the seasonal and interannual species turnover (Petanidou et al. 2008) and the insects' flexible foraging preferences (Waser et al. 1996) further hinder recording all the biologically possible interactions in the field.

Sampling effort may be increased by investing more time in visual surveys, which increases the cost of any field study. The analysis of the pollen taken from the body (Bosch et al. 2009) or the nest (Dorado et al. 2011) of pollinators was recently proposed as a complementary method to visual surveys. These studies revealed a very significant number of interactions undetected in the field made by abundant as well as by rare pollinator species. As a result, when the pollen data were added to the respective visual survey-based data, many network properties were modified. In this context, the aim of this paper is to analyze how interaction data recovered from specimens at NHCs may complement the data that arise from a field study.

Materials and methods

Field-based interaction data

We compiled data available from a bee biodiversity study conducted in an experimental station of the INTA (43°7'23.8"S 71°33'42.9"W) near Trevelin, in the province of Chubut, Argentina. This study was led by AIG in the spring-summer of 2005–2006 and 2006–2007 (Gravel 2010). Inside the station, the native forest consisted mainly of maitén (*Maytenus boaria*), radial (*Lomatia hirsuta*), various species of southern beech (*Nothofagus*) and many bee-attracting shrubs and plants. A result of the experiments held at the station was the formation of large areas of land at early successional stages (i.e., old field-like areas) after clear cuts. Four sites were selected for the study according to their physical characteristics and gradient of human disturbances. The area sampled covered 31.5 km² in total, at an elevation from 270 m to 680 m. All sites were sampled by two collectors using the opportunistic method (Droege 2008) in which collectors walk through the entire site, sweeping an entomological net over flowering plants and potential nesting sites where bees were observed. Bee sampling occurred at a single site on dry and sunny days only, between 11:00–16:00 h. Total sampling effort in the field amounted to 307 hours (184 hours in 37 days for 2005–2006 and 123 hours in 35 days for 2006–2007). The bees in this study were identified to species (or otherwise

morphotyped) by AIG. A total of 24,238 bees (representing 50 species from 21 genera) were captured on 55 flowering plant species. Most of the specimens are housed at the MACN. Plants were identified by AIG and confirmed by experts (see Acknowledgements).

In this study, we only considered the female and male specimens of *Corynura* (Halictidae: Augochlorini), a bee genus endemic to the Argentinean Patagonia and Chile which currently includes 18 species (Moure et al. 2007). The choice of this genus in particular was due to the fact that *Corynura* is under revision by RAGV, and data from specimens at NHCs were available. The frequency of interactions was counted as the number of specimens collected on the flowers of a given plant species. From these data we built a matrix representing the interactions between plant species (each represented by a row) and their visitor species (in columns). An interaction between a given plant and a given visitor species was represented by the number of times that interaction was recorded, and the absence of a recorded interaction by a '0'. This matrix, which was named 'Field', had a total of 3436 interactions from all the specimens of *Corynura* captured, resulting in 115 unique interactions among seven bee species and 31 plant species.

NHCs interaction data

Some species of *Corynura* are typical of semi-arid environments in central Chile, while others inhabit humid *Nothofagus*-dominated forests. We limited our analysis to the bees that had been collected in the Subantarctic and Patagonian subregions along the Southern Andes (Morrone 2006), as they inhabit the same environments as where the field study was carried out. The identifications of all *Corynura* specimens housed at the entomological NHC of the MACN and the FAUBA were verified by RAGV. Some of the specimens were given a morphospecies status as the revision of the genus is still in progress. All the specimens had been collected by researchers from these institutions. Data on the floral associations of each species were retrieved from the specimens' labels. The identification of the 'host plants' was not verified for it had been done by experts at MACN and FAUBA. We did not include data involving plants not identified to species level.

Specimens that had no plant associated to it (51.1% of all specimens housed at MACN and FAUBA) or had one only identified to the genus level (3.8%) were not included in the analysis. In total, data from 181 specimens housed at MACN and 135 specimens housed at FAUBA were included in a presence-absence matrix. We considered only the unique interactions out of the 316 interactions detected. Therefore, we followed the same method as for the Field matrix, but here an interaction between a given plant and a given visitor species was represented by a '1', and the absence of a recorded interaction by a '0'. An interaction matrix named 'Collections' which contained 53 unique interactions among nine bee species and 20 plant species was used in all subsequent analysis.

Comparison and complementarity between NHCs and field-based networks

The Field matrix was compared to the interaction matrix obtained from NHCs. In order to assess the degree to which NHCs enrich the information obtained from a field survey, the Field matrix was compared to a third matrix ('Field+Collections', a "presence-absence" matrix as 'Collections') which combined both data sets, including only the bee and plant species observed in the field study. The properties compared were nestedness, connectance, number of compartments, mean number of links per species, mean number of shared 'host plants', number of plants visited by each bee species (also referred to as the degree) and number of unique links. Connectance represents the proportion of possible links actually observed in a network (Blüthgen et al. 2008). The number of compartments was defined as the number of sub-sets of the web which were not connected at all to another sub-set. The degree of bee species was calculated as the number of unique links that each bee species presented for a given network. The number of unique links was calculated as the sum of the degree of bee species of each network, as it represents the number of insect-plant interactions unique from that network. The properties were calculated with package 'bipartite' (Dormann et al. 2009) of R statistical software (R Development Core Team 2008) (see Appendix).

To estimate sampling completeness of plant-visitor interactions for the Field network we computed the individual-based rarefaction curve of unique interactions. For this we treated the number of recorded visits to flowers by insects as 'individuals'. Based on this curve we estimated the maximum number of interactions expected (I_E) using the Chao 1 estimator of asymptotic species richness. This index is defined as

$$I_E = I_O + (f_1^2/2f_2)$$

where f_1 is the number of interactions observed once, f_2 is the number of interactions observed exactly twice and I_O is the number of observed interactions. Rarefaction curves and the

number of expected interactions were calculated using functions *rarefy* and *estimateR* in the R package 'vegan' (Oksanen et al. 2010) of R program. We used this approach instead of the sample-based rarefaction curves originally proposed by Chacoff et al. (2012) because the information on individual samples could not be retrieved from museum specimens.

Results

The Field network (Fig. 1) had a high connectance: nearly 50% of all potential links were actually realized. The number of links per species, the number of shared 'host plants', and the number of unique links showed higher values in this network when compared to the Collections network (Table 1). The nestedness values were quite similar between the three matrices, but only the Collections network was significantly nested ($p < 0.05$). The three networks obtained had only one compartment (i.e., there were no isolated groups of interacting species).

The number of plant species visited by each *Corynura* species (Table 2) showed higher numbers for the Field network than for the Collections network, although when ranked, the relative position of each bee species was quite similar in both networks. *Corynura aureoviridis* and *C. rubella* were the species with the highest degree in both networks, despite the difference in the data source. Neither *C. corinogaster* nor *Corynura* sp.1 were detected in the Field network, probably because of their low abundance.

When we added interaction data from the Collections matrix to the Field matrix, connectance and the number of unique links increased (Table 1). Both data sets had 22 interactions in common, but the Collections network contained nine not previously recorded interactions increasing the number of unique links of the Field network from 115 to 124 (Fig. 2a). An estimation of sampling completeness showed that the field study was able to detect 88.5% of the expected interac-

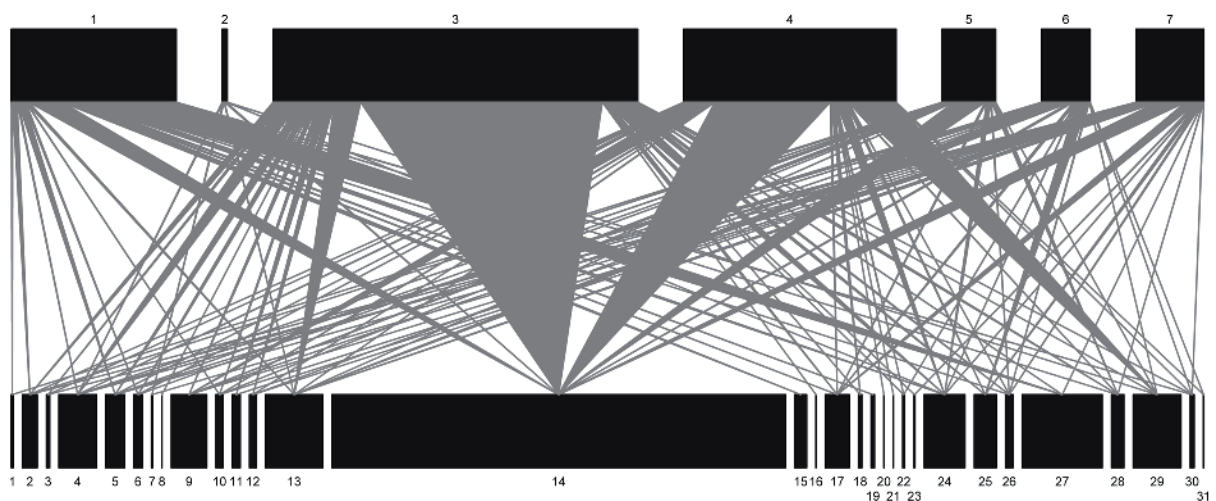


Figure 1. Ecological network obtained from the Field data set showing the interactions among the species. Species codes are given in the Supplementary Table S1.

Table 1. Properties of the networks obtained from the Field matrix, from the Collections matrix and from the sum of both data sets considering only the species of the field study (Field+Collections). *Figures considering the total number of bee (9) and plant (42) species (see Table S1).

	Field	Collections	Field + Collections
# spp. <i>Corynura</i>	7	9	7
# spp. Plants	31	20	31
# Bee species missing*	2	0	2
# Plant species missing*	11	24	11
Nestedness	38.94 (p=0.22)	39.10 (p=0.01)	31.38 (p=0.06)
Connectance (%)	53.0	29.4	57.1
Mean number of links per species	3.03	1.83	3.26
Mean number of shared 'host plants'	2.14	0.97	2.45
# Unique links	115	53	124

tions (Fig. 2b), which increased to 95.4% when the interactions from the Collections network were added.

The field study detected an average of ca. 0.37 unique interactions per hour of sampling (115 interactions/307 hours of field sampling). Thus, the additional 9 unique links obtained from NHCs data roughly represent 24 'saved' sampling hours.

Discussion

Our study is the first one to use information from specimens at NHCs in the context of a network analysis. We compared an interaction network based on field sampling against a network based on data obtained from specimens at NHCs, for a particular South American bee genus. In this section we will first discuss some limitations of using data from NHCs in ecological studies, then we will discuss our results in the context of the present study. Finally, we will discuss the applicability of our approach to the study of networks of ecological interactions.

Limitations

One of the problems with using data from specimens collected in different places and seasons is the potential lack of geographical/phenological overlap between the plant and pollinator species considered. For example, if an attempt was made to create a network based solely on NHCs data, *Corynura* species from central Chile (not considered for the present analysis) may only interact with a subset of plants from that region. This may lead to an incorrect interpretation of results, since a pollinator species cannot interact with plant species that are not present within their distributional range. Lack of phenological overlap is practically unavoidable because field trips to collect specimens are rarely conducted throughout the season, and NHCs also receive scattered spec-

Table 2. Number of plant species visited by each *Corynura* species in the Field and the Collections networks.

	Field	Collections
<i>Corynura ampliata</i>	14	6
<i>C. analis</i>	6	4
<i>C. aureoviridis</i>	24	14
<i>C. chilensis</i>	16	3
<i>C. corinogaster</i>	–	1
<i>C. rubella</i>	22	8
<i>Corynura</i> sp. 1	–	4
<i>Corynura</i> sp. 3	14	6
<i>Corynura</i> sp. 5	19	7

imens from different sources (donations, exchanged specimens, etc.). However, a recent study suggests that these limitations might actually not be so relevant since heterogeneous sampling effort was found to have a small impact on network metric biases (Rivera-Hutinel et al. 2012).

In networks from data of NHCs specimens it is difficult to consider all the factors mentioned above since we have a set of interactions from specimens collected on different dates, in different places and using different methodologies. This makes any attempt to estimate abundances unreliable. Even if we restrict the analysis to a month or a locality in particular, we would usually have too few interactions for an accurate representation of the network. Furthermore, it is known that the number of interactions influences several attributes of the network and a generalist species may be considered as a specialist just because of a lack of data (Blüthgen et al. 2008). Rivera-Hutinel et al. (2012) estimated the sensitivity of six network metrics to sample effort, keeping constant network size and sampling evenness. Their results suggested that connectance may give underestimated values when sampling completeness is below 70% of the expected pollinator assemblage, while nestedness and modularity may be less sensitive to sampling completeness. Accordingly, we believe that it is more cautious to only consider the new interactions that may emerge from NHCs data instead of analyzing the data as in a regular ecological network study. It is here that NHCs may provide particularly useful additional data. Due to the fact that such collections are usually from numerous places, collected at various times and by many individuals, their addition to a thorough field study may express a broader range of interactions than a single field study alone.

The Field network and its complementarity with NHCs data

Some network properties, such as linkage density, generality and connectance, depend strongly on the number of species considered (Banasek-Richter et al. 2004, Tylianakis et al. 2007). Particularly for connectance, there are at least four possible causes for the remarkably high value obtained. Given there is a negative correlation between the number of species in a network and its connectance, the first cause could be the low number of species in our field network. Second,

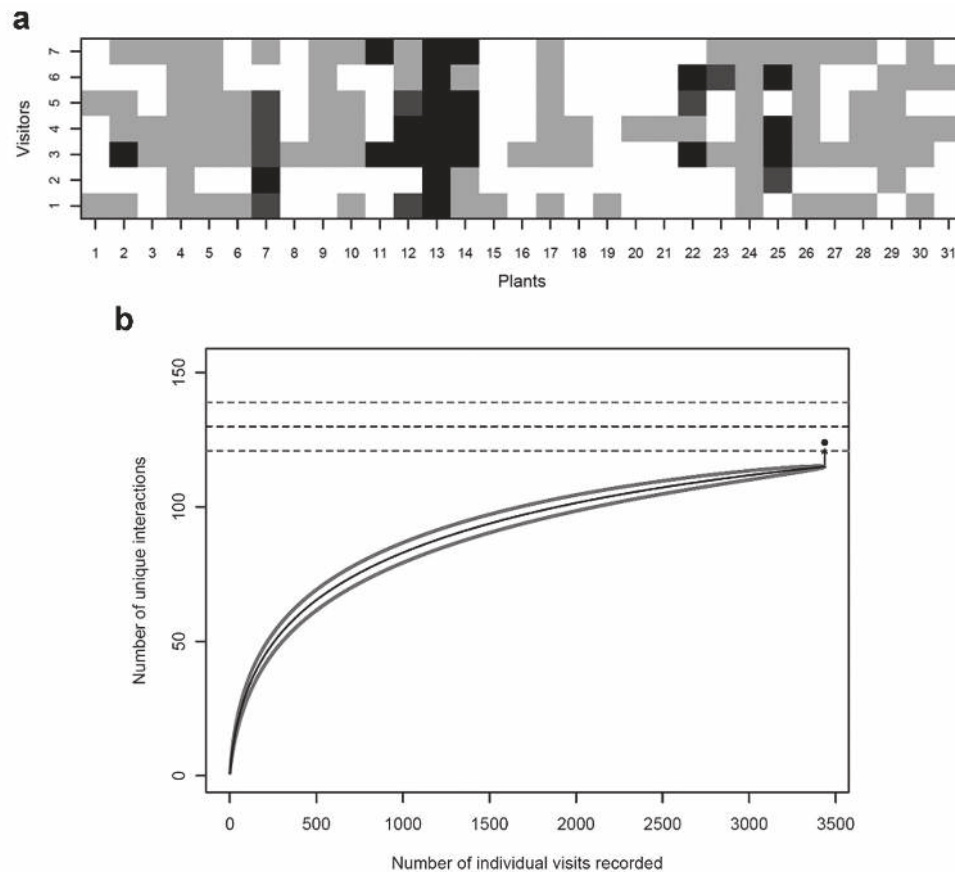


Figure 2. a: Overlapped display of the matrices that represent the interaction between visitors (in rows) and plants (in columns) in the Field and Collections networks. Interactions shared by both networks (in black), interactions unique to Field (in light grey) and interactions unique to Collections (in dark grey) are displayed. Species codes are given in the Supplementary Table S1. **b:** Rarefaction curve (black solid line; 95% confidence interval in grey) of unique interactions for the Field network. The black dot and arrow indicate the increase in the total number of interactions detected when the Collections data are combined to the Field data. The number of theoretically expected interactions (black dashed line) with its SE (grey dashed line) are also shown. Only the species in the Field network were considered for both analyses.

the fact that most halictid bees are known to be generalists (Michener 2007) may contribute to the high number of links in the network. Third, there is a well-known relationship between the abundance of flower visitors and the degree of generalization recorded in the field (Vázquez and Aizen 2003). In our own study, the species that visited the highest number of plant species in all networks, *C. aureoviridis*, is by far the most abundant *Corynura* species in Argentina (RAGV, unpublished). Thus, a sampling method whereby only abundant species were captured may bias the measurement of connectance. A fourth cause could be the fact that the Field network was intensively sampled, as connectance rely directly on the number of interactions recorded. Field network included 3436 interaction events for a total of 38 species, which is why the additional information from NHCs increased the number of unique interactions recorded only by 7.83%. Nevertheless, we believe that NHCs interaction data may be a more important complement to ecological studies in poorly sampled communities.

As the two datasets have different sizes and resulted from deployment of different collecting methodologies, they can-

not be compared in terms of connectance. However, they can be compared when considering the mean number of links per species and the number of unique links, which is higher in the network from the field sampling. Considering this and the difference in the degrees of many of the bee species present in the systems studied (Table 2), we can note that the field study shows far more insect-plant interactions than the data from just NHCs. For example, *C. chilensis* was associated with 16 plant species in the field sampling, but the data from NHCs associated this bee species with only three plants, missing several interactions. The previous statement is logical since NHCs usually have specimens collected in isolated events as said before, and most of them with no plant association.

On the other hand, if we consider the number of species of *Corynura*, we see that not all the species of the genus were found at the field study's collecting sites. This may be due to the low abundance of some species (*C. corinogaster* and *Corynura* sp.1 in our study), although the absence of some species in a single community cannot be rejected either, even though the sampled area was within its distributional range. This shows that while field sampling at a local community

is essential for a particular ecological study (e.g., ecological network study), in order to cover as many species of a genus or family as possible along with their floral ‘host plants’ species, it is necessary to fall back on NHCs specimens or to sample the entire distributional range of the study group. This is particularly important when evaluating floral preferences of some pollinator species, as a species may be a good pollinator of a certain crop in a particular area, but it prefers to visit another plant when in another location.

Recently, some studies have attempted to increase the number of interactions detected by using a pollen analysis approach (Bosch et al. 2009, Dorado et al. 2011). This is a time consuming analysis, and a pollen reference collection of the area is needed. Moreover, pollen may be difficult to identify, and pollen from species belonging to the same genus may be undistinguishable (Dorado et al. 2011). Even though pollen loads tend to prevail on the legs of hairy pollinators, even after some manipulation of the specimens, we do not consider pollen analysis from specimens at NHCs as a reliable source of data. In the field all pollinators from a certain plant species are usually sacrificed in a single killing jar, where pollen loads can be contaminated with pollen grains that previously belonged to another specimen. As we do not know the methods used to collect the bees in the NHCs used in our study, analyzing their pollen load would have rendered misleading results.

Perspectives

The analysis of ecological networks, such as insect-plant networks, could provide additional information to taxonomic studies. For example, the presence of compartments in a network of a particular pollinator genus may reflect the co-evolution of some species with their associated plants (Lewinsohn et al. 2006). Phenotypic complementarity, and phylogenetic and climatic history can significantly contribute to the interaction patterns among species (Rezende et al. 2007, Dalsgaard et al. 2013). Given the amount of data available for *Corynura* in particular, the next step should be to analyze if there is evidence of co-evolution between closely related species of this genus and the plant species they pollinate. This supports the new approach that is being given to taxonomy known as ‘integrated taxonomy’, which proposes the delimitation of species taking into consideration morphological, molecular and behavioral data (Dayrat 2005, DeSalle et al. 2005).

Nowadays numerous initiatives facilitate this new approach by the management and availability of biological data, such as Global Biodiversity Information Facility (www.gbif.org), Inter-American Biodiversity Information Network (www.iabin.databasin.org/) and Morphbank (www.morphbank.net). The Pollinator Information Network of the Americas (www.pollinator.org/PINA.htm) has the purpose of developing a network of linked and integrated databases among major pollinator data sources, through a common set of data standards and exchange protocols. This online catalogue of pollinators of the western hemisphere includes data on insect-plant associations, which could be very useful in many ecological studies.

Our study shows that data from specimens at NHCs may add some information, such as species or interactions missed, to a standard field sampling of interactions. This can be done as long as there is a substantial amount of reliable data available, which highlights the need to get accurate data in the field (in this case, the plant species visited by bees) as well as the importance of NHCs as additional sources of information for different fields in biology.

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Appendix

Supplementary methods and Table S1. The file may be downloaded from www.akademai.com.