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Original article

Bombus-plant interactions defined by bipartite network analysis in an underexplored Mediterranean island (Sicily)

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Abstract – Bumblebees (Apidae: *Bombus*) are abundant pollinators in Mediterranean habitats; however, interaction networks with plants have not yet been investigated in large areas of Italy, including its islands. Here, we analyzed plant-bumblebee networks through seasonal transects in a suburban park and a nature reserve of Eastern Sicily. After molecular and morphological identification of bumblebees, we built bipartite networks extracting complementarity, niche overlap, modularity and nestedness. In total, we sampled 10 of the 15 species of *Bombus* known from Sicily. Richness was close to that predicted by accumulation curves, and no differences in community diversity were found between the two sites. At both sites, the networks were not nested, highly specialized and modular, with high complementarity and low niche overlap, again with no differences between sites. In both sites, species-level specialization varied considerably and was independent from sample size. The network topologies suggest a possible role of local interspecific competition and/or of interspecific morphological variation among generalist bumblebees. Comparison of previously published data revealed that networks in Mediterranean areas are more specialized than those with a continental climate. This suggests the possibility of increased competition and/or phenotypic variation under harsh Mediterranean conditions. The vulnerability of the Mediterranean basin to droughts caused by climate change calls for detailed studies on pollinator-plant networks for conservation plans.

Bombus **/ Bipartite network / Mediterranean island / Italy / Pollination**

1. INTRODUCTION

There are approximately 265 species of bumblebees (genus *Bombus*, Hymenoptera: Apidae) worldwide (Rasmont et al. 2021). The Northern Hemisphere hosts the highest known diversity (Williams 2018), essentially because the biogeographical origin of the genus and its subsequent initial diversification are placed in cold habitats of Central Asia (Hines 2008). The Mediterranean basin is known to host a good diversity of bumblebees, though this is relatively low compared with other wild bee lineages (Balzan et al. 2016a; Nielsen et al. 2011; Petanidou and Ellis 1993; Varnava et al. 2020), which have Southern Europe as the main hotspot (Michener 1979, 2000; Nieto et al. 2014).

Despite this relatively well-known pattern of diversity across Europe, many aspects of bumblebee ecology and behavior are still largely unknown in many parts of the continent,

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especially in the Mediterranean basin, including its major islands. Most of bumblebee species are eusocial (i.e. they live in matrifiliar colonies including a queen and their daughters, the workers), while only few species are social parasites of other bumblebee species (i.e. the parasitic queen usurps a nest of the host species and uses host workers to rear its own brood) (Goulson 2010). Each colony may have a few hundreds of workers actively foraging on plants, making bumblebees numerically dominant and excellent pollinators (Neff and Simpson 1993). Except for a few oligolectic (i.e. specialized) high-mountain species, most European species of *Bombus* are polylectic (i.e. generalist) (Nayak et al. 2020). They forage on many plant species from different families, including crops and orchards. Thus, bumblebees provide a crucial ecosystem service through pollination in both natural and agricultural ecosystems (e.g. Free 1993; Klein et al. 2007). In the context of the documented decline of bumblebees (Williams and Osborne 2009; Carvalheiro et al. 2013; Rasmont and Iserbyt 2010–2014), it is important to analyze different ecological aspects of these insects across their entire geographical range and across different European habitats and climates.

In particular, the detailed relationships between *Bombus* species and plant species — i.e. the ecological bipartite network they form in a given area — are still unexplored in many Mediterranean habitats. These networks take into account the identity of the connected species and the frequency of interactions and are effective in revealing both the structure of the interactions and the role of each species (Bascompte and Jordano 2007; Blüthgen 2010). Such networks are represented by bipartite graphs in which plants and pollinators are the nodes and the links between the nodes represent the interactions between the two trophic levels (Bascompte and Jordano 2007). Hence, the graphs obtained from this network analysis explicitly illustrate the reciprocity of interactions and help to understand the complex patterns that emerge in diverse mutualisms (Bascompte et al. 2003; Bascompte and Jordano 2013). This leads to a better understanding of ecological and evolutionary processes and provides elements for species and habitats conservation plans (Forup and Memmott 2005; Kaiser-Bunbury et al. 2010).

The use of bipartite network analysis is also interesting in the case of bumblebees and the plants they forage on, as bumblebee species can coexist through flexibility in their preferences for specific floral traits, which can support the co-occurrence of high numbers of species and individuals (Ye et al. 2024). However, differences can arise either from body size variation among species (Goulson and Darvill 2004; Goulson 2010) or as a response to interspecific competition for floral resources (Heinrich 1976; Inouye 1978). As far as we know, in the Mediterranean basin, such type of network analyses (focusing only on, or including, bumblebees) were performed to date only on the Mount Olympus (Greece), near Bologna (Italy), in a locality in the Lombardy Apennines (Italy), at one site in Occitanie (France) and at several localities in Spain (Fisogni et al. 2021; Minachilis et al. 2020; Bartomeus et al. 2008; Della Rocca et al. 2023; De Manincor et al. 2020; Lara-Romero et al. 2016; Lázaro et al. 2020). To date, the Mediterranean islands have been totally neglected.

Sicily (Italy), the major of the Mediterranean islands, is one of the most important biodiversity hotspots in the Mediterranean basin (Médail and Quézel 1999) and ranks second (562 species) after Lesvos (at least 600 species) in known bee species richness among the Mediterranean islands (Scheuchl and Willner 2016; Ascher, unpublished data cited in Varnava et al. 2020), with new species occurrence emerging frequently (e.g. Bella et al. 2020; Barletti et al. 2023; Haris and Józan 2018; Nobile and Turrisi 2015; Cornalba et al. 2024; Seminara et al. 2009). Here, bee diversity was proven to be high both in natural and cultivated ecosystems (e.g. Bella et al. 2023; Haris and Józan 2018; Mazzeo et al. 2019; Nobile 1995; Nobile and Turrisi 2015; Quaranta et al. 2004; Turrisi et al. 2021). In the island, 15 species of *Bombus* are currently known (Bella et al. 2023; Haris and Józan 2018; Mazzeo et al. 2016; Reverté et al. 2023), which is almost one-third of the total number of species recorded for

Italy (Reverté et al. 2023). To date, studies on bumblebees in the island were confined to the Mount Etna and its foothills. While some of these studies reported some ecological information (e.g. identity of foraged plants) together with abundance and diversity of species (Bella et al. 2020; Las Casa et al. 2022; Mazzeo 2002; Mazzeo et al. 1999, 2001, Mazzeo et al. 2004, Mazzeo et al. 2016, Mazzeo et al. 2019; Quaranta et al. 2004; Turrisi et al. 2021), none analyzed in detail the *Bombus*-plant relationships by building bipartite networks.

Studies on plant-bee bipartite networks are especially important in areas like Sicily when considering the differences in pollination systems between Northern and Southern Europe. For example, Southern Europe have greater bee richness than the Northern regions of the continent and a component of this fauna is relevant for pollination of certain fruit crops (e.g. citrus, almond, watermelon) that are not cultivated in the North (e.g. Rodrigo Gómez et al. 2021). This may result in Southern regions being potentially more vulnerable to pollinator losses than Northern regions (Leonhardt et al. 2013). Additionally, studies linking bee-plant interactions and the ameliorations and politics supporting pollinators (Common Agricultural Policy (CAP 23–27), including the SO-6 eco-scheme 5 for Italy) are still rarely carried out in Southern Europe (Moldoveanu et al. 2024), where pollinator biodiversity is higher (Nieto et al. 2014).

Here, we started filling this knowledge gap by quantitatively studying *Bombus*-plant ecological bipartite networks at two localities in Sicily. In particular, we investigated the networks in two contrasting localities (a suburban park and a natural reserve) in an area of North-Eastern Sicily where studies on bee-plant interactions are particularly underexplored. We aimed to address the following specific questions: (1) Which characteristics define the topology of the two networks? (2) Is there any difference in the network topology between the two study sites? and (3) Do the observed topologies differ with those reported for other European *Bombus*-plant networks?

2. MATERIALS AND METHODS

2.1. Study area and sampling protocol

The study was conducted from 2018 to 2019 in two locations in Messina province, Sicily: a suburban park ("La Rocca di Buticari", municipality of Nizza di Sicilia: 38°00′49″ N, 15°38′65″ E, 360 m a.s.l., Buticari-URB in the following text) and a natural reserve (Fiumedinisi and Monte Scuderi, in the Peloritani mountains: 38°03′53.92″N 15°24′06.58″E, 900 m a.s.l., Fiumedinisi-NAT in the following text) (Figure 1A–B). The Peloritano district, which includes both study sites, is characterized by mild and rainy winters, a long hot and arid summer season and average annual temperatures between 12 and 16 °C. However, due to their geographical position, the Peloritani mountains are exposed to humid currents coming from the Ionian Sea and the Tyrrhenian Sea, which, especially in the mountain range, significantly mitigate the summer drought period (Picone and Crisafulli 2006). The area is also particularly interesting from the point of view of its fauna and vegetation, due to its heterogeneous characteristics where mountainous, hilly, plain, river, lagoon and coastal habitats alternate. One portion of the Peloritano district is protected under the NATURA 2000 (ITA030042), and there is a current proposal to upgrade the protection status by constituting a new a regional park (Giaimi 2008; Spadola et al. 2008).

Through seasonal walking transects (April–July 2018–2019) (Figure 1C–D), specimens of *Bombus* (Figure 1E) were captured with an entomological net, and the plant associated with each capture was identified. We collected *Bombus* specimens that were found to visit and touching flower reproductive organs. Bumblebee species display significant variability in phenology, influenced by latitude, altitude, and the intrinsic traits of each species (Iserbyt and Rasmont 2012). Within the same locality, some species emerge early in the season, while others appear later, with cycle durations also differing among species (Goulson 2010; Alford 1975; Heinrich 2004). For example, *Bombus*

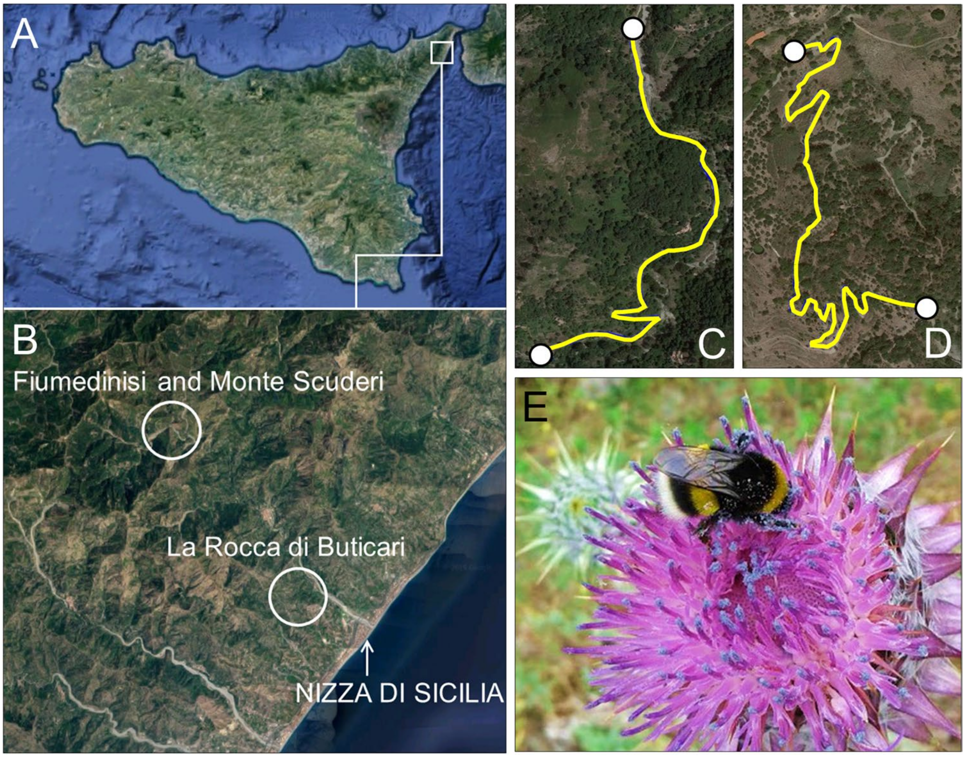

Figure 1. (A, B) Location of the studied sites. (C, D) representation of the two fixed transects used to collect the field data (C: Fiumedinisi-NAT, D: Buticari-URB). E, a worker of *B. terrestris* while foraging on a *Onopordum illyricum* flower.

pascuorum and *B. terrestris* have a long cycle, often extending into late autumn or even winter, while some species enter a summer diapause. Given this variability, sampling was concentrated between April and July — which are months when all species can reliably be found simultaneously.

The insects were collected along a fixed route, based on the linear transect method (Banaszak 1980, 1995; Westphal et al. 2008). Each transect, approximately 1-km long and 1-m wide (Figure 1C–D), was walked at a constant speed (transect duration: 2 h). A total of 13–14 sampling rounds *per* site and *per* year were performed, during the hours of greatest bee activity (from 10.00 to 14.00). The sampling was always performed by the same collector. Once captured, the insects were brought to the lab and stored in absolute ethanol at –4°C (King and Porter 2004; Quicke et al. 1999) until subsequent analyses. Each tube was marked with a unique code, identifying the location and date of collection, as well as the species identity of the associated plant. The latter information was added to the tube after identification of the plant directly in the field or after evaluation of the photographs taken (see below). For few plant species was necessary the removal of an individual and the help by a specialist botanist (see Acknowledgements). A total of 411 *Bombus* specimens were sampled during the study.

2.2. Identification of bees and plants

Bombus specimens were identified to the species level using the molecular barcoding technique (Hebert et al. 2003) at Departamento de Zoología y Antropología Física, University of Murcia (Spain). One individual of *Bombus pratorum* returned an uncertain match with available *Bombus* species barcodes (85.7% match with the bee *Anthophora vallorum*) and was morphologically checked, following the keys in Rasmont et al. (2021) and Cappellari et al. (2018) as well as comparisons with collections preserved at the Council for Agricultural Research and Economics (CREA–AA) in Bologna (Italy). Subspecies was not considered as a taxonomic level for identification.

DNA was extracted using the Chelex method (Walsh et al. 1991). The 658 base pair mitochondrial cox1 gene fragment was amplified with MyTaq™ Red Mix (Bioline). Barbee and MtD9 primers were used (Françoso and Arias 2013). The PCR products were sequenced by Secugen (Madrid). Once the species sequences were obtained, they were edited with MEGA-X (Kumar et al. 2018). The BLAST tool was used for identification (https://blast.ncbi.nlm.nih.gov/Blast.cgi), by comparing the sequences with those available in Genbank (https://www.ncbi.nlm.nih.gov/genbank/). Samples which returned low matching values ($< 99\%$) were checked morphologically, as explained above. Molecular identifications through BLAST are available for all individuals in the Supplementary file BARCODE.xlsx.

To identify the botanical species on field (or in the lab, inspecting the pictures taken on field or the sampled specimen), the following relevant volumes were used: Flora d'Italia (Pignatti et al. 2017–2019), the New Analytical Flora of Italy (Fiori 1923–1929), the Flora Europaea (Tutin et al. 1964–1993) and the online site Acta Plantarum (https://www.actaplantarum.org/). Scientific nomenclature for plants followed Pignatti et al. (2017–2019).

All raw data collected during transects are available in the Supplementary file DATAset.xlsx.

2.3. *Bombus* communities

To evaluate whether a complete species inventory was carried out at the study sites, species accumulation curves (sample-based rarefactions) were constructed, using the number of samples and the cumulative average of the number of species (Colwell et al. 2004). We calculated the Chao 1 species richness estimator (Chao 2005), together with the shape of accumulation curves, to assess how complete our species sampling was.

We described the communities of *Bombus* at the two sites by calculating the following parameters and indices: abundance (*N*, the number of collected individuals), species richness (*S*, the number of sampled species), the Shannon-Wiener diversity index (*H'*, which takes into account both *S* and *N*) (Shannon and Weaver 1949), the Berger Parker's Dominance (*BP*), which is a measure for the numerical significance of the first most abundant species (i.e. the proportion of the most abundant species) (Berger and Parker 1970), and the Simpson's dominance index (*D*, the probability that two individuals taken at random from a community belong to the same species, here expressed as its complementary form) (Simpson 1949). We calculated the 95% confidence intervals of these indices with a bootstrap procedure (9999 random samples). Then, bootstrapped comparisons of *S*, *H'*, *BP* and *D* between the two sites were performed.

Accumulation curves, and calculations and comparisons of indices were carried out in PAST 3.04 (Paleontological Statistics Software Package) (Hammer et al. 2001).

2.4. *Bombus*-plant network analysis

The pollinator-plant networks were built and analyzed with the "*bipartite*" package (Dormann et al. 2008) in R software v.4.2.2 (R Core Team 2021). This package represents the networks as bipartite graphs and calculates the most commonly used quantitative descriptors for the networks (Dormann et al. 2008, 2009). The following quantitative indices have been calculated to describe the network properties.

Complementarity (*H_2'*) measures the global specialization of the network. This metric ranges from 0 to 1, where a lower value indicates higher functional redundancy (high exchange of pollinators and then a lower specialization), while a higher value indicates a higher dependence of the species on a few exclusive partners (Blüthgen et al. 2006). Nestedness (*WNODF*) refers to the way in which the elements (nodes) in a first set (the community of bumblebees) are connected to the elements (nodes) of a second set (the community of the visited plants). In particular, the index takes into account the number of times each *Bombus* species has visited each specific plant species and the asymmetry. This is the degree to which specialist species interact with generalists and the degree to which generalists interact with both specialists and generalists. The higher the asymmetry, the more nested a network is (Bascompte et al. 2003; Dicks et al. 2002). Modularity or compartmentalization represents the degree to which the network is divided into subgroups or modules, i.e. aggregates of species that present a much greater frequency of interactions between themselves (intra-module) than with other species of other modules in the network. On a scale from 0 to 1, 0 indicates the absence of modules within the network and 1 indicates a high degree of subdivision of the network into different subgroups (Dormann and Strauss 2014). Niche overlap (among *Bombus* species), calculated by default as Horn's index, represents the average similarity of interactions pattern between species (Dormann et al. 2009) and ranges between 0 and 1. At last, the *d'* index quantifies the level of specialization (range: 0–1) of each *Bombus* species individually within the network (Bluthgen et al. 2006). We tested, with a Student's *t*-test, if *H_2'*, *WNODF*, and niche overlap differ to what one would expect under random networks (i.e. based on numbers given the observed row and column totals). Random matrices are based on the function *null.t.test* of R *bipartite* package.

In text and tables, mean values are expressed with their standard errors.

2.5. Comparative network analysis across studies

To explore how the network topologies and traits observed in the two study sites compare with other studied *Bombus*-plant networks in Europe, we first retrieved available bee-plant matrices or data from a number of sources. In particular, we looked for previously published bipartite bee-plant networks in Google Scholar (last search 30/04/2022). We then cross-checked these papers conducting a similar search in Web of Life (http://www.weboflife.com/) and Zenodo (https://zenodo.org/). Second, we discarded networks with less than 2 bumblebee species and 3 plant species to ensure a better robustness of the calculated indices. A total of 12 papers were selected (Benadi et al. 2014; Bennett et al. 2018; Dicks et al. 2002; Eeraerts et al. 2021; Fisogni et al. 2021; Hülsmann et al. 2015; Lara-Romero et al. 2016; Maia et al. 2019; Minachilis et al. 2020; Orford et al. 2015; Rakosy et al. 2022; Weiner et al. 2014), from which we were able to collect data from 52 networks (Supplementary file DATAset.xlsx). Either from the publications themselves or by re-analyzing the available matrices, we then obtain the *H_2'* for all 54 networks. For a subset of these networks (28), niche overlap, nestedness and modularity were also available or newly calculated (Supplementary file DATAset.xlsx).

Networks were then divided into two categories: Mediterranean and Continental. These two groups were built based on the location of the study sites. All those falling South to the Alps and the Pyrenees, thus having an overall Mediterranean climate (mainly Csa, Csb, Cfa and BSk climates, following Köppen 1936) were placed in the first group, while all those falling North to these mountain chains, essentially presenting a continental climate (mainly Cfb, Dfa, following Köppen 1936) were placed in the second group. We tested for differences in the number of *Bombus* species and the number of visited plants by *Bombus* in the networks between these two ecoregional groups with a Student's *t*-test. Finally, we tested if *H_2'* varies either with the number of *Bombus* species in the network, the number of plant species in the network, or with the ecoregion, by performing a Linear Model in R software v.4.2.2 (R Core Team 2021). Statistical comparisons and models were not possible for the other network metrics retrieved from the literature (since *N* for Continental = 24 but for Mediterranean = 4), so that for them, we only present descriptive statistics.

3. RESULTS

3.1. Communities

The *Bombus* communities for the two sites included 8 species each (belonging overall to 6 subgenera, see Figure S1), with 5 species in common between the sites (Supporting file DATAset.xlsx) and a total of 10 species across both sites. *B. terrestris* (Linnaeus, 1758) was the most sampled species at both sites, representing the 31.9% of individuals at Fiumedinisi-NAT and the 42.1% at Buticari-URB (Supplementary file DATAset.xlsx). However, the second most abundant species differed between sites. At Fiumedinisi-NAT, *B. lapidarius* (Linnaeus, 1758) and *B. pascuorum* (Scopoli, 1763) made up > 20% of abundance. At Buticari-URB *B. pascuorum* and *B. ruderatus* (Fabricius, 1775) made up > 20% of abundance (Table I). All the other species ranged between 0.4% and 8% (Supplementary file DATAset.xlsx). Three species of bees were recorded as cuckoo species. Two of them, *B. barbutellus* (Kirby, 1802) and *B. vestalis* (Geoffroy, 1758), were collected at Buticari-URB, while one *B. campestris* (Panzer, 1801), was collected at Fiumedinisi-NAT.

Comparing the values for the considered metrics of the two *Bombus* communities between the two sites, no differences appeared except for the number of individuals (*N*), which was twice in natural reserve (Fiumedinisi-NAT, *N* = 253) than in the suburban park (Buticari-URB, *N* = 121). While the number of species of *Bombus* was the same in the two sites, the number of plant species was 20 in Buticari-URB and 33 in Fiumedinisi-NAT (Supplementary file DATAset.xlsx).

The analysis of the accumulation curves for the *Bombus* communities highlighted some differences between Buticari-URB and Fiumedinisi-NAT. Concerning the *Bombus* community at Fiumedinisi-NAT, the curve reached the asymptote (Figure 2A), indicating that all the species present in the area have been collected. In this case, the accumulation curve indicated an estimated richness of 8–9 species (Figure 2A). For the *Bombus* species sampled at Buticari-URB, the curve approached the asymptote, meaning that most of the species present in the area were sampled (Figure 2B). In fact, the accumulation curves indicated an estimated richness of 9–13 species (Figure 2B).

Table I Values (and 95% confidence intervals) of the metrics obtained from the community-level analysis. *P* values refer to permutation tests for comparison between the two sites. Statistically significant results ($P < 0.05$) are boldfaced

Community metric	Fiumedinisi-NAT	Buticari-URB	*P*
Number of species (*S*)	8 (*B. campestris, B. hortorum, B. lapidarius, B. pascuorum, B. pratorum, B. ruderatus, B. sylvarum, B. terrestris*)	8 (*B. barbutellus, B. lapidarius, B. pascuorum, B. pratorum, B. ruderatus, B. sylvarum, B. terrestris, B. vestalis*)	1
Abundance (*N*)	**289**	**122**	**< 0.001**
Simpson's Dominance (*D*)	0.68 (0.64–0.72)	0.72 (0.67–0.76)	0.35
Shannon-Weaver Diversity (*H'*)	1.39 (0.13–1.49)	1.49 (1.39–1.64)	0.29
Berger-Parker's Dominance (*BP*)	0.47 (0.41–0.52)	0.42 (0.33–0.50)	0.45

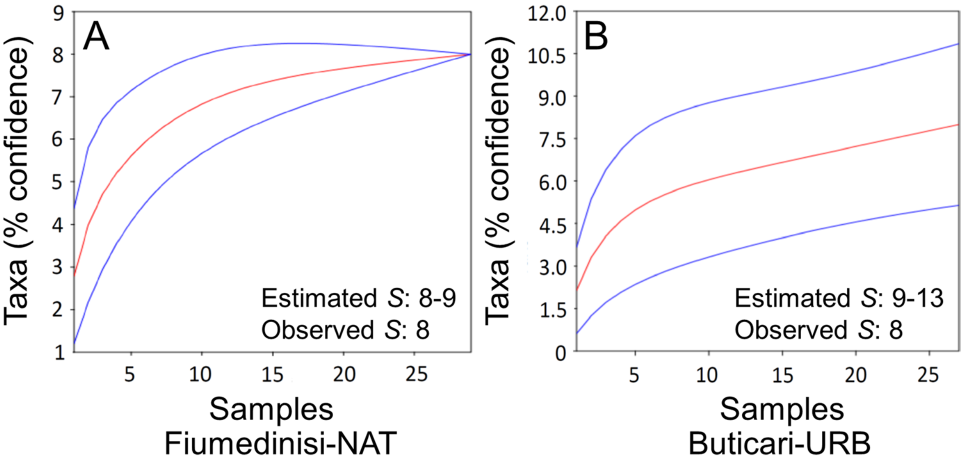

Figure 2. Sample rarefactions (Mao's tau) (accumulation curves, in blue) of the observed *Bombus* species richness and 95% confidence interval (in red), based on the collected samples across the transects ((A) Fiumedinisi-NAT, (B) Buticari-URB). *S* (species richness) is shown for the observed value and for the estimated (Chao 1) value.

3.2. Networks at the Sicilian sites

At Fiumedinisi-NAT, the network was characterized by few strong interactions and a large majority of weak interactions (Figure 3A). This makes the network significantly specialized (Table II). In the matrix, the plant species with the highest frequency of interaction were *Rubus ulmifolius*, *Galactites tomentosus*, *Hypericum hircinum*, *Onopordum illyricum*. The most frequently interacting pollinator species were *B. terrestris*, *B. pascuorum* and *B. lapidarius*. The network did not result to be nested, being the WNODF value significantly lower than the simulated value (Table II). Niche overlap was lower than that expected by a random network, i.e. *Bombus* species tend to segregate their diets (Table II). The network is composed by 4 modules that differ in size and shape (Figure S1). The two modules formed exclusively either by *B. terrestris* or *B. lapidarius* contain strong relationships with certain plant species, while in the other modules the interactions between pollinators and plants are less strong. It can also be observed that modules comprise bumblebees of different subgenera. Composition of the modules, however, may at least partially depend on the occurrence of short-, medium- and long-tongue species (Rasmont et al. 2021). In Fiumedinisi, one module was made of two medium-tongue species (*B. pascuorum* and *B. sylvarum*) and another one comprised the only two long-tongue species (*B. ruderatus* and *B. hortorum*) (Figure S1). In Buticari, one module was made of two short-tongue species (*B. terrestris* and *B. vestalis*). All modules in general, included either short- and/or medium-tongue species, or long- and/or medium-tongue species.

The specialization at the *Bombus* species-level (*d'*) was variable, with some species highly specialized (e.g. *B. pratorum*), while other species (e.g. *B. pascuorum* and *B. campestris*) quite generalist in the visited plants (Figure 3B). This variation in species-level specialization was not dependent on variation in the number of recorded visits (Simple linear regression: $R^2 = 0.15$, $N = 8$, $P = 0.33$), or on variation in the number of visited plant species (Simple linear regression: $R^2 = 0.17$, $N = 8$, $P = 0.31$).

At Buticari-URB, as well, the network was characterized by few strong interactions and a large majority of weak interactions (Figure 4A). This makes the network significantly specialized (Table II). In the matrix, the plant species with the highest frequency of interaction were *Carlina hispanica*, *Galactites tomentosus*, *Sixalix atropurpurea* and *Salvia officinalis*. The most frequently interacting species were *B. terrestris*,

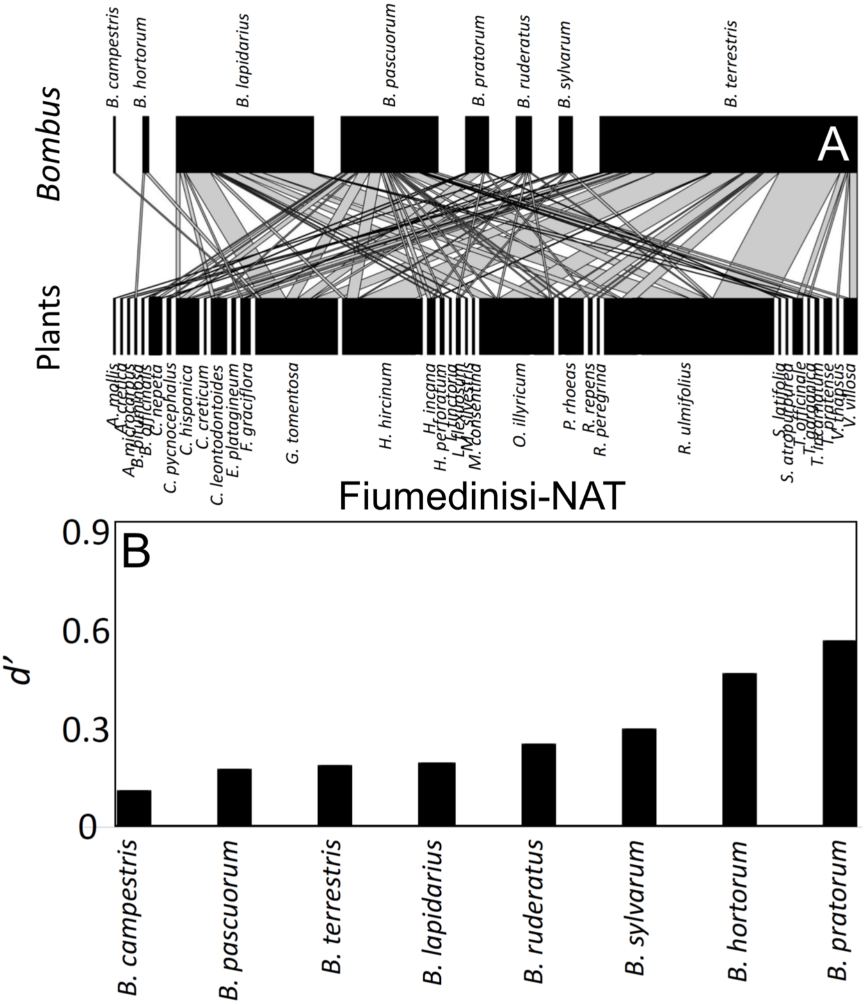

Figure 3. Graphical outputs of the network analysis for Fiumedinisi-NAT. (A) Bipartite network graph; link width indicates the frequency of visits to plants by a given *Bombus* species, while widths of the upper and lower bars indicate the total frequency of observations for bumblebee species and plant species, respectively. (B) values of *Bombus* species-level specialization (*d'*).

B. pascuorum and *B. ruderatus*. The network did not result nested, being the WNODF value significantly lower than the simulated value (Table II). Niche overlap was lower than that expected by a random network, i.e. *Bombus* species tend to segregate their diets (Table II). The network is made up of 5 modules that differ in size and shape (Figure S1). In the module of two pollinators interacting with six plants, only the species of *B. terrestris* has a strong interaction with *Carlina hispanica*. In the other modules the interactions between pollinators and plants are less strong. It can also be observed that modules comprise species of different subgenera.

The specialization at the *Bombus* species-level (*d'*) was variable (Figure 4B, Table II), with some species (e.g. *B. pratorum* and *B. barbutellus*) highly specialized, while other species (e.g. *B. sylvarum* and *B. lapidarius*) quite generalist in plant use (Figure 4B). Such variation in species-level specialization did not depend either on variation in the number of recorded visits (Simple

Table II Observed and random-produced (null) values, and their 95% confidence intervals, of the metrics obtained from the network analysis. Student's *t* and associated *P* values refer to comparison between observed and random (null) values. Statistically significant results ($P < 0.05$) are boldfaced

Network metric	Observed	Null mean	Lower CI	Upper CI	*t*	*P*
Fiumedinisi-NAT						
Nestedness (*WNODF*)	**29.5**	**38.82**	**37.56**	**40.07**	**15.55**	**< 0.0001**
Complementarity (H_2')	**0.23**	**0.11**	**0.1**	**0.12**	**−31.9**	**< 0.0001**
Niche overlap (*Bombus*)	**0.35**	**0.47**	**0.45**	**0.48**	**16.88**	**< 0.0001**
Modularity	0.58	-	-	-	-	-
Species specialization (*d'*) (*Bombus*)	0.28 ± 0.05	-	-	-	-	-
Buticari-URB						
Nestedness (*WNODF*)	**23.96**	**38.05**	**35.84**	**40.26**	**13.32**	**< 0.0001**
Complementarity (H_2')	**0.33**	**0.13**	**0.12**	**0.15**	**−30.2**	**< 0.0001**
Niche overlap (*Bombus*)	**0.32**	**0.43**	**0.4**	**0.46**	**8.3**	**< 0.0001**
Modularity	0.87	-	-	-	-	-
Species specialization (*d'*) (*Bombus*)	0.46 ± 0.09	-	-	-	-	-

linear regression: $R^2 = 0.17$, $N = 8$, $P = 0.31$), or on variation in the number of visited plant species (Simple linear regression: $R^2 = 0.29$, $N = 8$, $P = 0.16$).

The two networks did not show apparent difference in any of the considered metrics, suggesting an overall similarity of their topography. Complementarity seems just slightly higher at Buticari-URB, while the other variables had very similar values (Table II).

3.3. Comparative network analysis across studies

The bumblebee-plant networks used for comparative analysis ($N = 54$) showed overall a great variation in the number of *Bombus* species (2–24), number of plant species (3–112) and H_2' value (0.3–1) (Supplementary file DATAset.xlsx). Continental networks showed, on average, a greater number of *Bombus* species (7.96 ± 0.88) than the Mediterranean networks (6.07 ± 0.37) (Student's *t*-test: $t = 2.11$, $df = 53$, $P = 0.03$). Similarly, continental networks showed, on average, a greater number of visited plant species by *Bombus* (29.29 ± 5.21) than the Mediterranean networks (13.03 ± 1.39) (Student's *t*-test: $t = 3.31$, $df = 53$, $P < 0.001$). The analysis showed an overall significant effect of the ecoregion on the H_2' values ($F = 3.96$, $df = 49, 3$, $R^2 = 0.19$, $P = 0.013$). In particular, Mediterranean networks have higher complementarity (0.51 ± 0.03) than continental networks (0.35 ± 0.03) ($F = 3.19$, $P = 0.002$) (Figure S2), with no effects on such variation by the number of *Bombus* species ($F = -0.64$, $P = 0.52$) and the number of plant species ($F = 0.59$, $P = 0.55$).

Though statistical comparisons and models were not possible for the other network metrics, nestedness (WNODF) were quite similar between the two ecoregions (31.75 ± 2.87 vs. 29.63 ± 7.22, respectively). On the other hand, niche overlap was apparently slightly higher in Continental than in Mediterranean networks (0.39 ± 0.04 vs. 0.27 ± 0.06, respectively). Modularity seems also slightly lower in Continental than in Mediterranean networks (0.62 ± 0.03 vs. 0.73 ± 0.05).

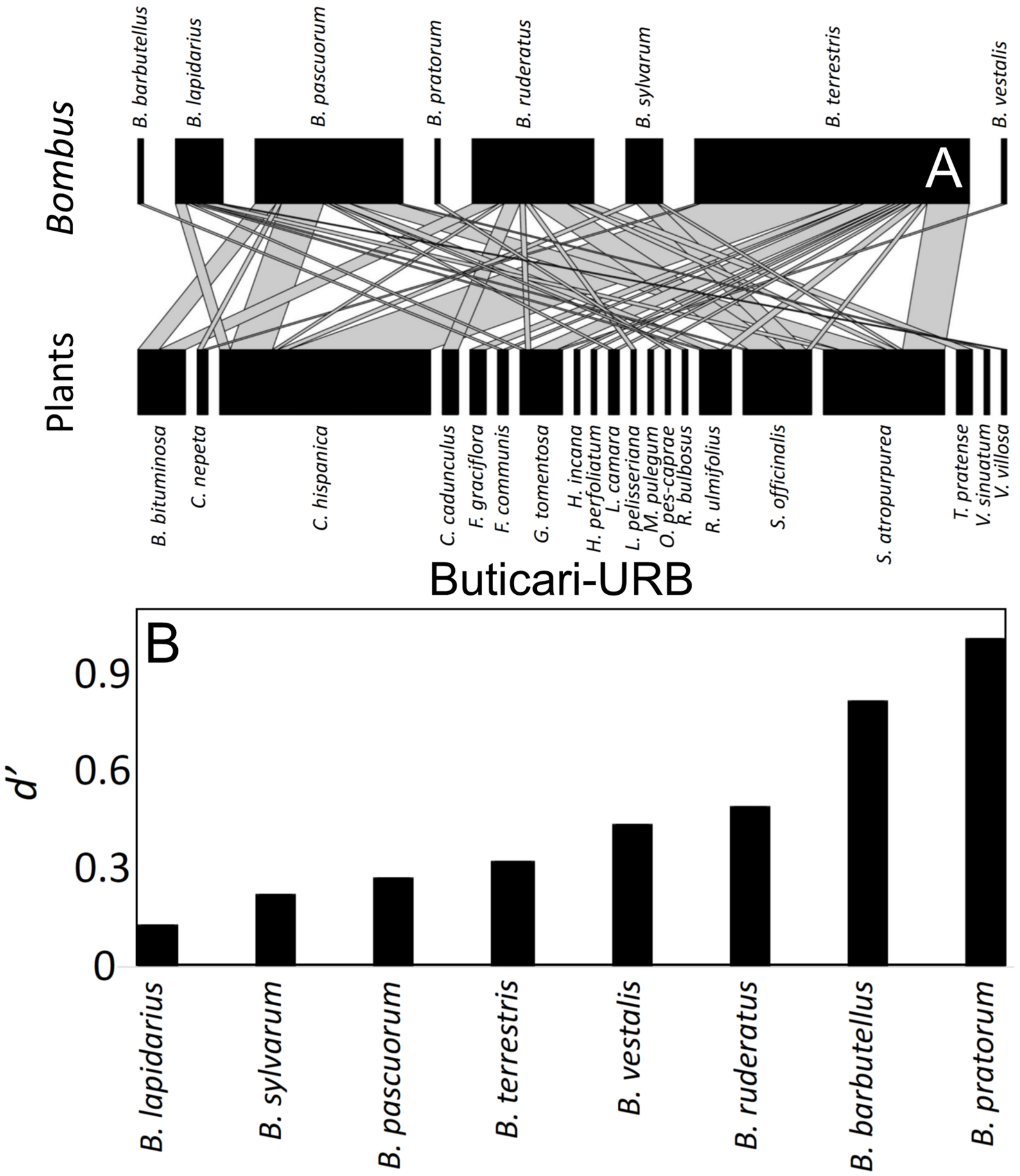

Figure 4. Graphical outputs of the network analysis for Buticari-URB. (A) Bipartite network graph; linkage width indicates the frequency of visits to plants by a given *Bombus* species, while widths of the upper and lower bars indicate the total frequency of observations for bumblebee species and plant species, respectively. (B) Values of *Bombus* species-level specialization (*d'*).

4. DISCUSSION

Here we presented the first quantitative analysis of bee-plant interactions for the genus *Bombus* in Sicily, and the first overview of bumblebee species occurring in an area of the island where wild bees are still weakly investigated (Bella et al. 2020; Catania et al. 2022; Turrisi et al. 2021). A strong geographical bias still exists within Europe, despite the successful and extended use of network analyses to study ecological interactions in bees. For example, out of less than 100 studied networks in the continent, around one-third concerns UK and Spain. Even more importantly, while excluding Spain, in Southern Europe only few studies were carried out (in Greece, France and Italian Peninsula), before the present study (Bartomeus et al. 2008; Fisogni et al. 2021; Minachilis et al. 2020; Della Rocca et al. 2023).

The barcoding approach used here proved to be very effective in distinguishing the *Bombus* species, though morphological checks were required to reach a confident identification of one specimen. Similar effectiveness was observed while studying bee species in both local biodiversity surveys (Sheffield, et al. 2009) and in larger regional studies, as exemplified for German (Schmidt et al. 2015) and Irish (Magnacca and Brown 2012) bee faunas. The use of DNA barcoding to assess bee diversity represents the first insight into the molecular biodiversity of bumblebees in Sicily, which is the largest Mediterranean island. This merits future deeper investigations covering more parts of Sicily, an area presenting large biases in bee studies, essentially confined to date to Mt. Etna and its foothills (Bella et al. 2023; Haris and Józan 2018; Mazzeo et al. 2019; Nobile 1995; Nobile and Turrisi 2015; Quaranta et al. 2004; Turrisi et al. 2021).

The communities of *Bombus* at the study sites include overall 10 species. Known Sicilian *Bombus* species that were not sampled in our study were *B. lucorum* (Linnaeus, 1761), *B. bohemicus* (Seidl, 1838), *B. ruderarius* (Müller, 1776), *B. rupestris* (Fabricius, 1739) and *B. sylvestris* (Le Peletier, 1832). *B. maxillosus*, previously reported as present in Sicily by several authors, is currently considered conspecific with *B. barbutellus* (Lecocq et al. 2011).

The studied communities did not differ in their main characteristics (richness, diversity, dominance), but, interestingly, Fiumedinisi-NAT hosted almost twice the individuals than Buticari-URB. This may be because natural habitats host a greater number of wild bee individuals than urban areas (Ahrné et al. 2009). In addition, our results may have been influenced by the lower plant species richness recorded at Buticari-URB compared to Fiumedinisi-NAT. A non-mutually exclusive hypothesis is that a strong disturbance event at Buticari-URB lowered down the overall abundance of bees. This possibility may be supported by the fact that several areas of the park were affected by wildfires in 2018 and 2019, which damaged the soil and stripped out the vegetation. As the study by Petanidou et al. (2013) shows, short-term fires are devastating to pollinator communities.

However, in terms of diversity, our study contrasts with the general trend for natural habitats to host higher bee diversity and for high-altitude sites to host higher bumblebee species richness (Eremeeva and Sushchev 2005; Hostetler and McIntyre 2001; Matteson et al. 2008; Ahrné et al. 2009; Minachilis et al. 2020). On the other hand, a number of studies showed that urban areas can offer valuable habitats for a considerable number of bee species (Banaszak-Cibicka and Żmihorski 2012; Baldock et al. 2015; Cariveau and Winfree 2015; Sirohi et al. 2015; Frankie et al. 2005, 2013), and that urbanization has a smaller effect on bees than on other insects (Deguines et al. 2012).

Interestingly, we also sampled three cuckoo species of *Bombus* (*B. barbutellus*, *B. vestalis* and *B. camestris*). The first two species were observed only in Buticari-URB, while the other only in Fiumedinisi-NAT. The records of two cuckoo species at Buticari-URB are interesting, as in general cuckoo species are less common in anthropized habitats compared to natural areas (Ferrari and Polidori 2022). The presence of socially parasitic bees may indicate good persistence of the host species populations and a high environmental quality (Sheffield et al. 2013). Hence, one may suggest that this urban park is not suffering a strong negative effect from human activities. In any case, the abundance of all cuckoo bumblebees was extremely low at both sites and thus more solid considerations cannot be drawn.

Network analysis revealed that the topologies of bumblebee-plant interactions follow a similar pattern at both sites: specialized, non-nested, with a little overlap between species, with a similar number of recognizable modules, and with a variable degree of species-level specialization. This suggests that the natural site and the peri-urban site here studied have not enough environmental differences to drive network topology diversification. This result is in general agreement with previous studies on bee-plant networks across urbanization gradients which also revealed a generally low variation in network metrics (Ayers and Rehan 2023), and with a study showing that solitary bees-plant interactions were significantly more impacted by urbanization compared with bumblebees-plant interactions (Geslin et al. 2013). Perhaps bumblebees somehow compensate the reduced amount of green areas (and naturally occurring plants) in cities with a more abundant availability of urban ornamental plants.

The previously studied bumblebee-plant networks showed overall a great variation in the number of *Bombus* species and number of plant species. The complementarity of the networks (H_2') we obtained (0.23–0.32) are in the range of those previously recorded for *Bombus*-plants networks (0.13–1, $N = 52$), but lower than the mean value across networks (0.44 ± 0.02) (Supplementary file DATAset.xlsx). However, overall complementarity was statistically greater in Mediterranean areas than in Continental areas. We may suggest that generalist bumblebee species may segregate more their trophic niches under the harsher Mediterranean conditions to limit local inter-specific competition, and/or because of higher inter-specific morphological variation in these habitats (Hanski 1982; Heinrich 1976).

Nestedness (*WNODF*) values found here (23.9–29.5) also seem lower than the mean value across previous networks (31.67 ± 1.95, $N = 28$) at a point that our studied networks resulted statistically non-nested (Supplementary file DATAset.xlsx). This means that at our study sites, specialists do not interact with a subset of generalists. Nested plant-pollinator networks are thought to have greater diversity and community stability (Bastolla et al. 2009) and are generally more robust against extinction (Aizen et al. 2012). In our case, if a bumblebee species is lost, it is unlikely that another functionally equivalent species will be able to take over its role. (Memmott et al. 2004). It was shown that larger networks tend to have smaller values of nestedness (Kantsa et al. 2018; Trøjelsgaard and Olesen 2013), but this is not our case. On the other hand, niche overlap observed here (0.32–0.35) was similar to the mean value across previous networks (0.39 ± 0.02, $N = 28$) (Supplementary file DATAset.xlsx). The low levels of niche overlap could somehow contrast with the non-nested nature of the networks, as low overlap leads to a significant contribution of rare species to the maintenance of plant-pollinator interactions (Winfree et al. 2018).

Modularity values observed here (0.58–0.87) seem also similar to the mean value across previous networks (0.63 ± 0.02, $N = 28$) (Supplementary file DATAset.xlsx). The existence of modules is in accordance with the overall specialization of the networks, since modules only exist because some species do not interact with some others, i.e. because they are specialised (Dormann 2020). The quite strong modularity detected here, especially at Buticari-URB, contrasts with the hypothesis that such pattern emerges when the number of observed bee species is sufficiently large (we had only 8 species of *Bombus* and 20–33 plant species, depending on the network). Indeed, Olesen et al. (2007) analyzed 51 pollination networks including nearly 10,000 species and 20,000 connections and tested their modularity and found that modularity appears in all networks with >150 plant and pollinator species, whereas networks with <50 species were never modular.

Hence, overall, our studied networks point towards a specialized pattern. The mechanisms that lead to such topologies at the study sites remain to be tested with further studies, but we can at least propose for our case two — not mutually exclusive — hypotheses that have been widely used to explain niche segregation in bumblebees. First, co-occurring generalist bumblebee species, often very similar in their plant choices, may potentially share most of the pollen resources, giving rise to inter-specific competition that can be limited by niche segregation (Heinrich 1976; Inouye 1978). Great competition among *Bombus* species is also driven by a similar life-history and close phylogenetic relationship (Burns and Strauss 2011). Second, morphological trait variation among bumblebee species (e.g. body size and tongue length) may influence niche partitioning (Harder 1985; Sponsler et al. 2022). At last, disturbance and/or resource availability can also affect niche overlap among bumblebee species. For example, Miller-Struttmann and Galen's (2014) showed that, along a North-American elevation gradient, *Bombus* species overlap more their diet at the top (unproductive) and at the bottom (disturbed) of the altitudinal gradient. On the other hand, Minachilis et al. (2020), along an elevation gradient at Mt. Olympus, found that bumblebee–plant networks were more generalized at intermediate altitudes (where the highest diversity of both bumblebee and plants occurs), while nestedness peaked at low and high altitudes.

The bumblebee species currently documented for Sicily sum to 14 (Mazzeo et al. 2016; Reverté et al. 2023; Ghisbain et al. 2023). Most of these species are primarily adapted to climates with harsh winter temperatures and mountainous habitats, forming specialized networks with plants even at very high altitudes (Tu et al. 2024; Conti et al. 2024). For example, *B. barbutellus*, *B. campestris*, *B. pascuorum*, *B. pratorum*, *B. ruderatus*, *B. rupestris*, *B. sylvestris*, *B. terrestris* can be found below 500 m in Sicily, with some reaching the island's highest altitudes (Mt. Etna, 3403 m). Others, such as *B. hortorum*, *B. humilis*, *B. lucorum*, *B. sylvarum*, *B. ruderarius* and *B. lapidarius*, are more often found above 500 m. Hence, under the current climate change scenario, which is predicted to increase both temperature and aridity especially in Southern Europe (Giorgi 2006), Sicily's *Bombus* fauna may suffer important range shifts towards higher elevations, if not locally disappearing if shits are not possible above already occupied high altitudes (see Williams et al. 2009 for climate-specialized bumblebees' vulnerability). These worrying predictions already arose in a recent whole-Europe study, in which climate change was shown to likely cause severe future range contractions of four cold-adapted bumblebee species, especially in the Apennines (i.e. in a more Mediterranean context) (Biella et al. 2024).

Furthermore, the greater network specialization found in Mediterranean areas than in Continental areas suggests that a potential modification of interactions with plants may arise under the ongoing climate change. For example, if climate change lead to disappearing of the more cold-adapted *Bombus* species, there will be less competition for the remaining species, possibly decreasing network specialization, with an effect likely mediated by the extent of the climate-change–driven plant community shift itself (Pareja-Bonilla et al. 2023). Large effects of climate on pollinator-plant network were globally shown (e.g. bees are more generalist in the tropics relative to other climate zones (Saunders et al. 2023)). On the other hand, a study using historical data and found that, on islands, quaternary climate-change had weak effects on modularity and no effects on nestedness (Dalsgaard et al. 2013), suggesting that perhaps the major variation in future Sicily's networks will concern specialization rather than the other two variables.

A greater effort is needed to understand *Bombus*-plant networks, especially in the Mediterranean basin, which is reported to be one of the most vulnerable European areas due to the increasing arid conditions caused by climate change (Noto et al. 2023a, 2023b). Increasing aridity and temperature through climate change, together with adverse agricultural practices (Brittain et al. 2010) and urbanization expansion (Ferrari and Polidori 2022) are leading to habitat loss for bees and other pollinators (Steffan-Dewenter and Tscharntke 1999, 2002; Steffan-Dewenter et al. 2006; Winfree et al. 2009). Given the currently known decline of bumblebee populations due to anthropogenic pressure (Goulson et al. 2015), it is important to study in detail how these pollinators and plants interact across a wide range of geographical areas and habitats (Balzan et al. 2016b).

SUPPLEMENTARY INFORMATION

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AUTHOR CONTRIBUTION

CP and PDlR conceived and designed the study. BRB sampled the insects and collected the data and barcoded the insects. MQ morphologically identified the insects. CP, PDlR and AF analyzed the data. CP wrote the first draft of the manuscript. All authors read, improved, and approved the manuscript.

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DATA AVAILABILITY

All the data are reported in the Supplementary file DATAset.xlsx and in the Supplementary file BARCODE.xlsx.

DECLARATIONS

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

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