

# Invasive Africanized honeybees change the structure of native pollination networks in Brazil

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**Abstract** The Africanized honeybee *Apis mellifera* (AHB) is an invasive species spread over all Brazilian biomes, which has negative impacts on native bee populations, but whose impacts on native plants are still controversial. In order to understand how its impacts extend to the pollination service at the community level, we studied the AHB and its interactions in a multi-

species context using network theory. We analyzed six pollination networks from the Brazilian Caatinga, a xeric biome where beekeeping is increasing very quickly. The AHB occupied a central position in all networks, as it was responsible for a large share of the interactions observed ( $14 \pm 7\%$ ) and bound together different modules. By simulating the removal of the AHB from each network, we observed no effects on connectance, but a strong decrease in nestedness ( $-23 \pm 19\%$ ) and an increase in modularity ( $8 \pm 5\%$ ). The robustness of networks to cumulative random extinctions was on average not affected. In summary, our evidence points out that the AHB induces significant changes in the structure of native pollination networks, mainly by making them more cohesive and monopolizing many interactions. Although the AHB did not affect network robustness, its net impact on the pollination service may be negative, because this invasive species is very generalistic and may not be an efficient pollinator for some native plants.

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## Introduction

Invasive species are a major concern in conservation biology, as they may compete with native populations and disrupt their ecological interactions (Romanuk

et al. 2009). Ultimately, invasions can affect whole ecosystem services, such as pollination (Aizen et al. 2008). In order to understand the impact of invasions on ecosystem services, it is necessary to study interactions in a multi-species context. Network theory is very helpful for this task, as it provides the best conceptual framework and sophisticated tools to analyze complex systems with many elements, such as communities of pollinators and plants, keeping a focus on the interactions (Bascompte and Jordano 2007) and not the species, as in traditional community ecology. Therefore, network and community ecology are complementary to each other, as the first focuses the interactions, whereas the second focuses the species. Some studies have taken important steps towards applying a network perspective to biological invasions. For instance, it is known that food webs in general are sensitive to the introduction of exotic species (Romanuk et al. 2009), that cheaters (i.e., nectar and pollen robbers), in some cases invasive, alter the structure of pollination networks (Genini et al. 2010), and that some exotic plants monopolize interactions in native pollination networks (Lopezariza-Mikel et al. 2007; Padron et al. 2009).

One highly invasive flower-visiting species in the Neotropics is the Africanized honeybee *Apis mellifera* L. (hereafter AHB), which is widely used for the production of honey, propolis, and other products in Brazil (Michener 1975). This variety of honeybee was developed in the country in the 1940's, and was accidentally released in the wild; in a few decades it spread itself all over the country, and now there is not a single habitat where it does not occur (Michener 1975). Due to its economic importance in Brazil, there is some reluctance to consider its potential negative effects on the native biota (Goulson 2003b). Some researchers consider the AHB as an important pollinator in many parts of the world, even where it is invasive (Aebi and Neumann 2011; Aebi et al. 2012). However, evidence shows that invasive bees can have strong negative effects on native bee populations (Brown and Paxton 2009) and other researchers consider the net effect of the AHB as potentially negative (Ollerton et al. 2012). Unfortunately, there are too few studies on the pollination quality of the AHB in most countries, especially in Brazil, where plant diversity is huge; and most positive and negative evidence is still anecdotic.

Regarding the possible negative impacts of invasive species on native pollination systems, it has

already been reported that the AHB visits wild flowers and reduces interactions between native bees and plants (Butz-Huryn 1997). Furthermore, it is known that exotic bees can deplete resources (food and nesting sites) for native bees (Dupont et al. 2004), and exotic bees can monopolize interactions in pollination networks (Aizen et al. 2008). Therefore, we asked how strong is the impact of the AHB on the structure of pollination networks in Brazil. We investigated six bee-plant networks from northeastern Brazil, because in this region beekeeping has become highly intensive in the past decades and feral AHB populations are now abundant, what raises major conservation concerns.

As the AHB is considered as a generalistic flower visitor (Butz-Huryn 1997), we expected it to have high centrality in bee-plant networks; in other words, it should make a large number of interactions, and so be close to many bee and plant species within the network. The centrality of a species in a mutualistic network is a surrogate for its Eltonian niche (Elton 2001), i.e., the functional role that it plays in the community (see for instance Dupont and Olesen 2009). Furthermore, we expected the AHB to increase connectance, i.e., the level of generalization in the interactions at community level (Jordano 1987). The AHB was also expected to increase the degree of nestedness of the network, i.e., a topology in which species with few interactions are connected to a subset of the mutualistic partners of species with several interactions (Bascompte et al. 2003), as some new plant species are probably added to the network by being visited only by the AHB. Moreover, the AHB was expected to decrease modularity, i.e., how strongly the network is structured in cohesive subgroups (Olesen et al. 2007), as the high generalization of this invasive bee probably leads to a stronger connection among subgroups in the network. Ultimately, as the AHB probably increases the overall network cohesiveness, it should make networks more robust to cumulative extinctions of bees or plants, as lost interactions can be backed-up more easily in cohesive systems.

## Methods

### Study areas and data collection

We built six networks (Table S1) using published (Aguiar 2003; Aguiar et al. 1995) and unpublished data on the interactions between bees and plants

in different sites in the northeastern Brazilian Caatinga.

Our datasets came from six localities in the Brazilian Caatinga. The Caatinga is a xeric biome (Andrade-Lima 1981) and part of the “South American Dry Diagonal” (Prado and Gibbs 1993). This biome comprises xeric vegetations, ranging from shrublands to small forest-like savannas (Prado 2000). Despite this range of vegetations, Caatinga sites are not totally different from each other, both in terms of plant (Takhtajan 1986) and bee species (Zanella and Martins 2003) composition. We used data from the following localities: Itatim (hereafter referred to as Itatim, 12°42'S; 39°46'W) and Casa Nova (hereafter Casa Nova, 9°26'S; 41°50'W) in Bahia state; Cabaceiras (hereafter Cabaceiras, 7°22'S; 36°15'W) and São João do Cariri (hereafter Cariri, 7°25'S; 36°30'W) in Paraíba state; and two sites in Serra Negra do Norte (hereafter Serra 1 and Serra 2, 6°35'S; 37°20'W), Rio Grande do Norte state. The regional climate is semiarid tropical very hot (Bs'h' in Köppen's system), with a long dry season of eight to nine months in some sites, such as Cabaceiras and São João do Cariri, and a short and irregular rainy season, with a low average annual rainfall (300–632 mm). Localities differ in their degree of anthropic disturbance, number and composition of flowering plant species and flower visitors, and in the presence of water reservoirs. Casa Nova's vegetation is an open shrubby arboreal caatinga (trees 6–7 m tall) with a dense herbaceous layer during the rainy season. Itatim's vegetation is dominated by open shrubby caatinga, and trees are sparse. Cabaceiras and Cariri are located in the Cariri Paraibano region. Cabaceiras has an open arboreal shrubby caatinga. Its flat granitic formations (called 'lajedos') have ponds and small lakes during most of the year. Cariri has an open shrubby caatinga. Serra 1 has an open arboreal caatinga. Serra 2 is near a water reservoir and contains non-xerophilous vegetation that differs from the typical Caatinga. In our study, all six networks are comparable in terms of plant and bee composition, although they differ in the length of the dry season and in the type of vegetation. Most importantly, these differences among sites make our selection of data sources good for representing the variability within the Caatinga biome.

In these studies, bees were collected with entomological nets when visiting flowers located on 3-km

trails within each study area. In all areas bees were collected during daytime (from 8 am to 6 pm). Sampling efforts were high for all areas: Casa Nova—one collector, fortnightly sampling for 12 months (October 1987 to September 1988), 26 samples of 8 h each, 208 h in total; Itatim—two collectors, monthly sampling for 15 months (September 1996 to November 1997), 15 samples of 12 h each, 180 h for each collector, 360 h in total; Cabaceiras—one collector, fortnightly sampling for 12 months (February 1992 to January 1993), 24 samples of 9 h each, 216 h in total; São João do Cariri—two collectors, fortnightly sampling for 12 months (June 1993 to June 1994), 24 samples of 8 h each, 192 h for each collector, 384 h in total; two areas in Serra Negra do Norte—one collector, fortnightly sampling for 12 months (September 1994 to August 1995), 24 samples of 4 h each, 96 h in total for each area. Furthermore, several studies have shown that most bee species are easily sampled in the rainy season in Caatinga environments (e.g., Aguiar et al. 1995; Biesmeijer and Slaa 2006; Zanella and Martins 2003), and all sites included in our analysis have been sampled for at least one whole year and during both the dry and the rainy seasons. Therefore, we can assume that each network analyzed is representative of the local pattern of interactions between bees and plants at the community level.

### Network analysis

In our study, we followed the network approach currently used to study mutualisms at the community level (Bascompte and Jordano 2007): network metrics were used as surrogates for ecological concepts (as in Mello et al. 2011c). In our graphs, vertices represent bee or plant species, and edges represent interactions of nectar collection, as visits to flowers do not necessarily result in effective pollination. Each bee-plant network was analyzed as a binary adjacency matrix, in which rows are bee species and columns are plant species. In each matrix (see Table S1), 1 s represent records of nectar collection by a *i* bee species from a *j* plant species; 0 s represent the lack of such records.

Our first step was to define the functional role of the AHB in each studied network with two surrogates from network theory, which are centrality concepts (sensu Nooy et al. 2005). First, following Aizen et al. (2008),

we measured the strength of invasion by the AHB with an invasion index ( $I_{ahb}$ ), defined as the average proportion of all interactions that were made by this species in each network. Second, using the simulated annealing analysis proposed by (Guimerà and Amaral 2005), which has already been used in other pollination studies (e.g. Dupont and Olesen 2009; Genini et al. 2010), we assessed the functional role (i.e. Eltonian niche) of each species in the network with the network metric also known as functional role. In order to define network functional roles, first we had to run the mentioned analysis of modularity, in order to identify the structure of modules (i.e., cohesive subgroups, Nooy et al. 2005) within each network. Then we calculated the standardized within-module degree ( $z$ ) and the participation coefficient of each species ( $P$ ), and assigned roles based on a space defined by  $z$  and  $p$  values (for details see Guimerà and Amaral 2005). Each vertex was classified into one of the following roles: (R1) ‘ultra-peripheral vertices’ with all interactions within their module; (R2) ‘peripheral vertices’ with most interactions within their module; (R3) ‘non-hub connector vertices’ with many interactions to other modules; and (R4) non-hub kinless vertices with interactions evenly distributed among all modules. Hubs, i.e. vertices with a disproportionately large number of interactions (high  $z$  value), were divided into three different roles: (R5) ‘provincial hubs’ with most interactions within their module; (R6) ‘connector hubs’ with many interactions to most of the other modules; and (R7) ‘kinless hubs’ with interactions homogeneously distributed among all modules. Roles 5, 6 and 7 are very important because they define hubs, species that are crucial for the maintenance of many other species with fewer interactions. Roles 3 and 6 are also very important, for they represent ‘connectors’, i.e. species that bind together different modules of the network.

The first prediction about the effect of the AHB on network structure was that this species would increase connectance ( $C$ ). Connectance is considered as a surrogate of interaction generalization at the network level (Jordano 1987): the higher the connectance, the more generalized the interactions at community level. Connectance is calculated as the proportion of realized interactions in relation to the number of possible interactions, using the formula  $C = I/(AP)$ , where  $I$  is the total number of interactions observed,  $A$  is the number of bee species, and  $P$  is the number of plant species.

An increase in nestedness was our second prediction. In a nested network the interactions made by species with fewer links represent a subset of the interactions made by species with more links (Bascompte et al. 2003). Nestedness is considered as a topological property that enhances network stability (Bastolla et al. 2009). The degree of nestedness of each network was calculated with the index  $NODF$  (Almeida-Neto et al. 2008), which varies from 0 (non-nested) to 1 (perfectly nested). The significance of  $NODF$  was estimated with a Monte Carlo procedure (1,000 randomizations) with the software Aninhado (Guimarães and Guimarães 2006), using the null model 2 of Bascompte et al. (2003), in which the probability of interaction between two species is proportional to their total number of interactions (null model Ce in Aninhado). Finally, we calculated the  $p$  value as the proportion of random matrices that had a value of  $M$  higher or equal to the value observed in the real matrix.

Finally, we also expected the AHB to decrease network modularity, which is a surrogate of subgroup structure (Mello et al. 2011b) and may be considered as a surrogate of the ecological concepts of guilds and functional groups (Blondel 2003). To measure the modularity of each network we used the index  $M$ , which has already been used in other pollination (Olesen et al. 2007) and seed dispersal (Mello et al. 2011a) studies, and is calculated with the same simulated annealing procedure used for defining functional roles (Guimerà and Amaral 2005).  $M$  which varies from 0 (total absence of modules) to 1 (perfectly modular). We ran calculations in the software Netcarto (Guimerà and Amaral 2005). A module is defined as a cohesive subgroup of vertices in the network, which are more densely connected to each other than to other vertices in the network. The significance of  $M$  was estimated with a Monte Carlo procedure (1,000 randomizations). As the significance analysis in Netcarto was designed for unipartite networks (in which plant–plant and animal–animal links are allowed), but here we analyzed bipartite networks, we used null model 2 of Bascompte et al. (2003) to generate 1,000 randomized matrices for each network with a MatLab script (written by Paulo R. Guimarães Jr.). These randomized matrices were then analyzed in a modified version of Netcarto, which allows calculating the index  $M$  for several networks at a time (Fortran script written by Flavia M. D. Marquitti).

Finally, we calculated the  $p$  value for each matrix with a  $Z$  test.

### Robustness to extinctions

As changes in connectance, nestedness, and modularity are expected to affect network robustness, we also simulated cumulative extinctions of bee and plant species in each network with and without the AHB. We used the method proposed by Burgos et al. (2007), which consists on cumulatively removing species from one side of the network (i.e., plants or bees) at random. When another species on the other side of the network was connected only to the removed species, it was also removed from the network (secondary loss). With this procedure, an extinction curve was generated by plotting the number of remaining species on the one side of the network (e.g., bees) against the cumulative number of species removed on the other side (e.g., plants). Removals were done from each side of the network separately. Finally, we obtained one extinction curve for plants and one for animals for each network. The area below each curve ( $R$ ) was used as a measure of the robustness of the system to random losses, i.e., how quickly the network collapses after cumulative extinctions.  $R = 1$  corresponds to a very slow decrease in the curve, and thus represents a system in which most plants remain after the removal of most animals, or vice versa;  $R = 0$  corresponds to a very fast decrease in the curve, and thus represents a system that already collapses after the first few species have been removed. We ran 100 randomizations for each network. This analysis was carried out in the package bipartite for R (Dormann et al. 2008).

### Statistical analysis

In order to assess how the AHB changes the network structure, we measured the percentage of change in each network parameter with the formula:  $A_p = 100((A_N - A_i)/A_i)$ , where  $A$  is the index of interest (i.e.,  $C$ ,  $NODF$  or  $M$ ),  $A_p$  is the change in the index caused by the AHB,  $A_i$  is the value of the index for the original complete network containing the invasive AHB, and  $A_n$  is the value of the index for the network of native species without the AHB. In order to build native networks without the AHB, we excluded this species and all of its interactions, including plant species that were connected only to it.

To test whether removal of the AHB changed the values of the network parameters (i.e.,  $C$ ,  $NODF$ ,  $M$  and  $R$ ), we used paired  $t$  tests. To test whether the invasion index of the AHB ( $I_{ahb}$ ) explained the changes observed in network parameters (i.e.  $C$ ,  $NODF$ ,  $M$  and  $R$ ) we used linear correlations. All statistical analysis followed Zar (1996).

## Results

On average, the studied bee-plant networks were composed of  $102 \pm 29$  species (mean  $\pm$  SD, bees and plants together) (Table 1), and the proportion of bee and plant species (species richness ratio) was close to 1 in all networks (bees/plants =  $1.2 \pm 0.3$ ).

The AHB interacted with a large proportion of the available partners in each network (from 20 to 75 % of all plants), and was also responsible for a very large proportion of the interactions in all studied networks, as shown by the invasion index ( $I_{ahb} = 14 \pm 7$  %) (Table 1). Furthermore, the AHB played very important network functional roles in all networks, ranging from R3 (non-hub connector) to R7 (kinless hub), and in four cases it reached the highest role observed in the network (Table 1) (Fig. 1).

Connectance was very low in all networks, considering the possible range of variation ( $C = 0.07 \pm 0.01$ ). The same was true for nestedness, which varied from low to intermediate ( $NODF = 0.28 \pm 0.06$ ). Modularity was intermediate on average ( $M = 0.49 \pm 0.05$ ), and there were 7 modules in six networks, while one had 9 modules (Table 1).

Removal of the AHB from the networks resulted in  $5 \pm 4$  secondary losses, i.e. co-removal of species that were connected only to the AHB (Table 1). The effects of AHB removal on network structure depended on the parameter analyzed (Fig. 2). First, removal of the AHB resulted in no significant change in connectance ( $C_p = -1 \pm 5$  %,  $N = 6$ ,  $t_{\text{paired}} = 0.44$ ,  $p = 0.68$ ). The decrease in nestedness caused by the removal of the AHB was very strong ( $NODF_p = -23 \pm 19$  %,  $N = 6$ ,  $t_{\text{paired}} = 2.8$ ,  $p = 0.04$ ), and there was also an increase in modularity ( $M_p = 8 \pm 5$  %,  $N = 6$ ,  $t_{\text{paired}} = -4.1$ ,  $p = 0.009$ ) (Table 1). There were no effects on AHB removal on robustness to extinctions (bees:  $R_p = -5 \pm 18$  %,  $N = 6$ ,  $t_{\text{paired}} = -0.61$ ,  $p = 0.57$ ; plants:  $R_p = -0.7 \pm 1.6$  %,  $N = 6$ ,  $t_{\text{paired}} = 1.0$ ,  $p = 0.36$ ;



**Table 1** Network parameters measured for the six local bee-plant networks from the Brazilian Caatinga

Network	Cabaceiras	Cariri	Casa Nova	Itatim	Serra 1	Serra 2
Number of bee species	65	41	36	60	44	80
Number of plant species	50	51	40	50	27	69
Total species richness	115	92	76	110	71	149
Number of interactions	231	147	115	229	98	321
Connectance ( <i>C</i> )	0.071	0.070	0.080	0.076	0.082	0.058
Nestedness ( <i>NODF</i> )	0.38	0.27	0.31	0.29	0.21	0.24
Modularity ( <i>M</i> )	0.43	0.52	0.48	0.44	0.57	0.48
Number of modules	7	9	7	7	7	7
Functional role of the AHB	6	3	6	7	6	6
Maximum role in the network	7	6	6	7	6	6
Relative degree of the AHB	0.28	0.20	0.75	0.66	0.63	0.62
Invasion index for the AHB ( <i>I<sub>ahb</sub></i> )	0.06	0.07	0.26	0.14	0.17	0.13
Secondary losses	1	0	8	5	6	9
Change in <i>C</i> (%)	-2.6	-4.5	-5.0	-3.3	8.7	0.9
Change in <i>NODF</i> (%)	-1.5	-2.8	-50.6	-26.0	-29.1	-29.0
Change in <i>M</i> (%)	5.0	3.9	18.0	9.1	8.1	6.8

All *p* values for the *NODF* and *M* indices were lower than 0.001. The last three parameters were calculated by simulating the removal of the AHB and its interactions from each network

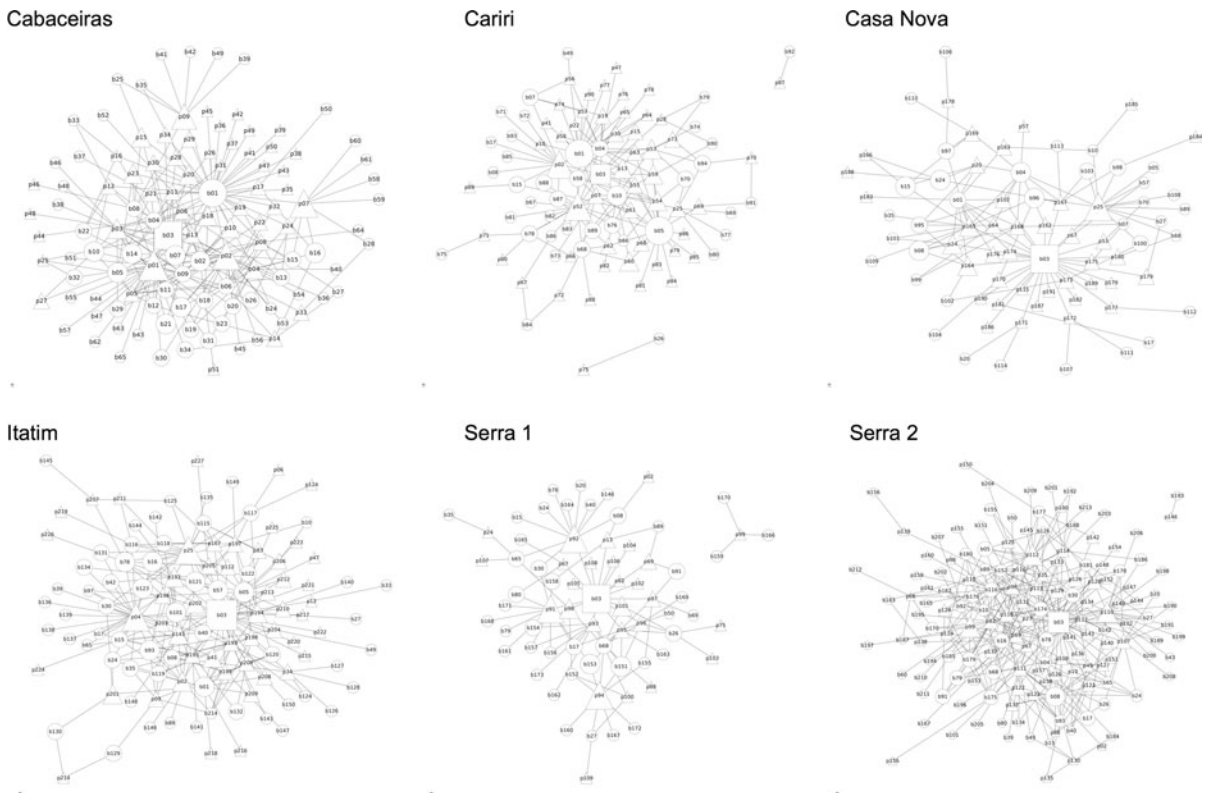
Fig. 2). Changes in connectance ( $N = 6$ ,  $r = 0.12$ ,  $p = 0.83$ ), nestedness ( $N = 6$ ,  $r = 0.41$ ,  $p = 0.43$ ), modularity ( $N = 6$ ,  $r = -0.37$ ,  $p = 0.47$ ), and robustness (bees:  $N = 6$ ,  $r = 0.13$ ,  $p = 0.81$ ; plants:  $N = 6$ ,  $r = 0.39$ ,  $p = 0.45$ ) were not correlated with the invasion index of the AHB (*I<sub>ahb</sub>*).

## Discussion

Our findings suggest that the AHB causes strong changes in the structure of native bee-plant networks. This invasive species occupied the highest functional roles in all networks studied, as it interacted with a large proportion of the plants available and bound together different species subgroups within each network. Although connectance and robustness were not affected by AHB invasion, nestedness and modularity suffered significant changes. The network-level impact of the AHB has important implications for the maintenance of pollination services, which we discuss considering also data on the natural history of native bees and plants, and the previously reported impacts of the AHB at the population level.

It is impressive how a single species, in this case the AHB, can be so influential in a pollination network.

The AHB was responsible for a large proportion of the interactions and played the role of a hub (a “super-generalist”, sensu Jordano et al. 2003) in five of the six networks studied. Hubs are important as they have a much higher number of interactions than other vertices in the network, so they are crucial for maintaining the whole structure of different kinds of complex network (Guimerà and Amaral 2005), and also in pollination networks (Dupont and Olesen 2009). Hubs are also important for maintaining some specialists in the system, i.e., species that have few interactions or are connected only to the hub (Bezerra et al. 2009). Furthermore, the AHB decreased the modularity of the invaded networks, therefore helping to bind together parts of the system that were previously more separated. Such a central position led to a monopolization of many interactions, similarly to observations by Aizen et al. (2008), which can potentially result in a disruption of native coevolutionary systems, as native plant species will tend to interact less with their native pollinators, as nectar is probably depleted by the AHB (Butz-Huryn 1997). However, the true effect of this disruption on native plants remains controversial (Dupont et al. 2004), as other evidence points out that the AHB can be also an effective pollinator (Goulson 2003b). The controversy regarding the effectiveness



**Fig. 1** The Africanized honeybee always occupied a very central position in the six bee-plant pollination networks from the Brazilian Caatinga, making several interactions with other species, increasing nestedness, and binding together different parts of each network. *Polygons* (vertices) represent species,

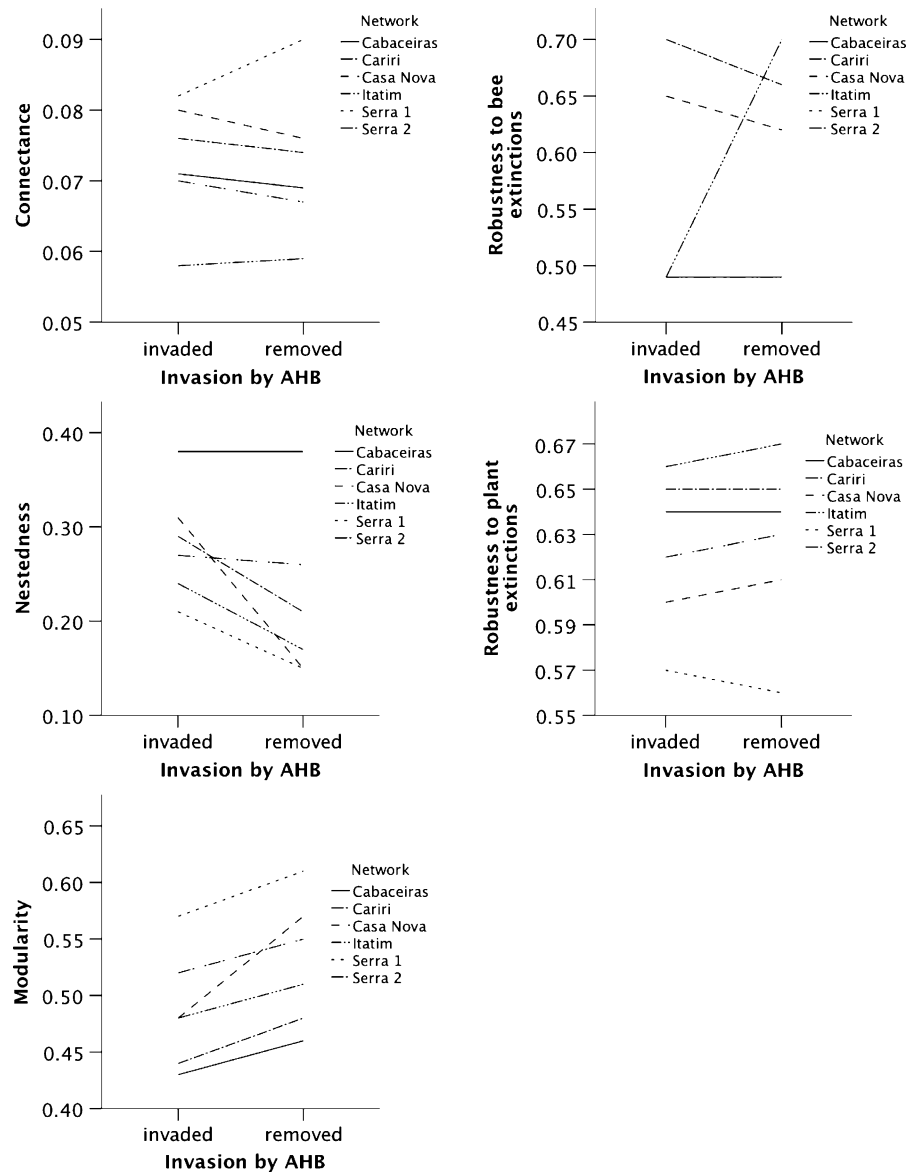
*lines* (links) represent nectar collection. Plants are represented as *triangles*, bees are represented as *circles*. The Africanized honeybee (B03) is represented as a *square*. Vertex size is proportional to the network functional role defined in the modularity analysis

of the AHB as a pollinator extends all over the world, and in most countries further studies on the natural history of its interactions with native plants are still needed (see an interesting debate in Aebi and Neumann 2011; Aebi et al. 2012; Ollerton et al. 2012). Furthermore, there is evidence that the AHB can replace native pollinators in small forest fragments (Aizen and Feinsinger 1994), which are the most common in northeastern Brazil, where most of the native habitats have been destroyed or fragmented (Myers et al. 2000). In small fragments the richness and abundance of native bees have been already reduced in most cases due to other independent factors, so the impact of AHBs in this case could be positive as this invasive bee could ensure that at least part of the native plants would be still pollinated (Aizen and Feinsinger 1994). In fact, Didham et al. (2005) suggested that in many cases invasive species are not drivers of ecosystem change, but also

passengers, and this seems to be the case in our study region, where most pressures on native species come from deforestation and fragmentation.

This relative high importance of the AHB in the studied networks was corroborated by the analysis of its influence on network parameters. The effect of the AHB on nestedness was the strongest observed, reaching an extreme decrease of 50% when this species was removed from the Casa Nova network. As nestedness is considered as a resilience-increasing topology (Bascompte and Jordano 2007; Bastolla et al. 2009), an invasion by AHBs could potentially enhance the stability of the pollination system, although we observed no effect on robustness in our study. Regarding connectance, our findings differ from those obtained by Aizen et al. (2008), who studied other pollination systems and observed that connectance of the subnetwork formed by native bees and plants dropped significantly as the level of invasion by exotic

**Fig. 2** In most networks, the simulated removal of the Africanized honeybee from native bee-plant networks led to a decrease in nestedness, an increase in modularity, and no effect on connectance and robustness to extinctions. Differences between each original studied network (invaded) and its modified version without the AHB (removed) were tested with paired *t* tests for connectance ( $p = 0.68$ ), nestedness ( $p = 0.04$ ), modularity ( $p = 0.009$ ), robustness to the extinction of bees ( $p = 0.81$ ), and robustness to the extinction of plants ( $p = 0.45$ )



bees increased. In our study, connectance was consistently low in all networks and it was unaffected by the AHB. One probable explanation for this result is that on average connectance was much lower in our studied networks than in the pollination networks studied by Aizen et al. (2008), and they were also lower than values reported for two other Caatinga bee-plant networks (Biesmeijer et al. 2005). Therefore, nectar collection and pollination interactions between bees and plants in the Brazilian Caatinga may be more specialized at community level than previously thought.

However, as already discussed, because the AHB is not always an effective pollinator (Goulson 2003a; Ollerton et al. 2012), it remains unclear whether those changes in nestedness and modularity have actually positive or negative consequences. On the one hand, as the AHB monopolizes interactions with native plants (as observed for an invasive plant by Lopezaraiza-Mikel et al. 2007), its impact is probably negative, as native flower visitors are considered as more efficient than exotic species for pollinating native flowers (see the discussion in Ollerton et al. 2012). This is especially true if we consider that the AHB tends to



be harmful to self-incompatible plants, as it visits many flowers of the same individual plant in a single foraging bout (Dupont et al. 2004). On the other hand, if the AHB is indeed an effective pollinator of some plant species, then its impact may be positive for them, as this invasive species may replace lost native pollinators and enhance cohesiveness and stability of the pollination network. Therefore, it is important for future studies in the Brazilian Caatinga to assess the legitimacy and effectiveness of the AHB as a pollinator of native species, as the quality of a pollinator at the population level is a key to evaluate its ecological functional role at the network level.

In summary, our findings suggest that the AHB changes network structure profoundly and becomes a very influential species in several native pollination systems. We suggest that the net effect of the AHB on the local pollination networks studied may be negative, as it is improbable that this highly generalistic bee species pollinates all native plants effectively. Therefore, the monopolization of interactions by the AHB at the network level may create a structure that seems more cohesive from the topological perspective, but which is of poorer quality, considering the pollination services delivered by this invasive species. All in all, these local pollination networks may look healthier, but be in fact dominated and degraded by the AHB. Conservation plans targeted at the whole pollination service (as suggested by Walker 1992) should take into account that exterminating the AHB from local communities may not be the best action, as those bees are deeply integrated into local networks, and may be important in local communities where native bees have already been extinguished by other factors, such as habitat loss and fragmentation. Studies on the quality of the AHB as a pollinator of native plants of the Caatinga are urgently needed to assess the net effect of this invasive bee on local pollination networks.

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