**Discussion**

Until today many efforts have been made trying to understand how species interactions shape traits evolution, however most studies have focused on a pair of species. Recently, both empirical and theoretical studies have paid more attention on the role that multispecies interaction networks play in shaping trait evolution (*e.g.* Andreazzi et al., 2017, Moré et al. 2018). Guimarães et al (2017), for example, using a mathematical model and numerical simulations, showed that in multiple-partner mutualisms, such as pollination and seed-dispersal, indirect coevolutionary effects play a great role in shaping species traits throughout ecological networks. Nevertheless, most of this studied used a fixed network structure and did not consider other aspects, such as genetic components. Our model, by considering ecological dynamics, mating preferences and genetic components, give a step towards in the comprehension of the drivers of multispecific coevolution dynamics an community assembly in mutualistic networks.

**The evolution of convergence and complementarity in mutualistic network**

Previous studies have argued that evolutionary convergence is the product of multispecific coevolutionary processes (’diffuse coevolution’) (Janzen, 1980; Thompson and Cunningham, 2002; Jordano et al., 2003; Bascompte and Jordano, 2007) and, therefore, convergence events are molded by similar ecological (or niche) selective pressures. Using a model of ’phenotype differences’, Nuismer et al. (2012) have shown that for weak coevolutionary selection, trait values in animal and plant species can be highly variable and non-convergent, but trait values of animal and plants species can have high complementarity. However, strong coevolutionary selection decreases variation in the trait values of animal and plant species, increasing convergence and, simultaneously, decreasing complementarity (i.e. correlations between traits of interacting species are weakened). Using a different approach, Guimarães et al. (2011) showed that trait convergence may in part emerge as a consequence of selection for a complementarity trait between the plants and animals. Similar to our model and in contrary to Nuismer et al (2012), Guimarães et al (2011) considered not only coevolution (i.e. evolution driven by other forces not related to mutualistic interactions), but also a different source of selection, which was a background evolution

By adding other selection pressure to the dynamics, being either a background (Guimarães et al. 2011) or a sexual selection (this study), it was possible to observe the evolution of both convergence and complementarity in the community. On the contrary, by considering only coevolution, Nuismer et al. 2012 results showed the  evolution of convergence and complementarity by coevolutionary selection to be unlikely. In fact, others non-selective forces underlying trait dynamics seem to produce convergence. For example, Stayton (2008) simulated evolution along phylogenies according to a Brownian motion model of trait change and demonstrated that convergence is always expected in a given phylogeny and that rates of convergence can be higher when clades are diversifying under only the influence of genetic drift. Furthermore, other types of constraints in the production of variation can also lead to convergence. If the variation produced is limited, then unrelated species are likely to produce the same variation, which may then become fixed in the population by genetic drift (Stayton, 2008; Losos, 2011). Additionally, developmental constraints may also explain the convergence of traits by … (Solé et al., 2002; Lynch, 2007; Losos, 2011). Nevertheless, either the role of developmental constraints or genetic networks in determining convergence in species-rich mutualistic networks has yet not been explored. For example, the tinkering of traits by evolutionary forces largely affects developmental pathways (e.g. gene regulatory networks) (Solé et al., 2002). Developmental pathways are not static but can diverge through time randomly without  substantially affecting the phenotype (Wagner, 2008). This concept, also called developmental system drift (DSD) (True and Haag, 2001), might play an important role in the evolution of convergence in morphological traits and it should be considered as another process where drift can act (Ohta, 2002), for example, by random wiring in gene regulatory networks. Based on a method that excludes cases of the development of a similar trait in related but distinct species descending from the same ancestor, our results show that additional constraints, such as dispersal limitation and assortative mating, limit the production of variation and lead consistently to convergence in distinct lineages in  species-rich mutualistic networks.

Evolutionary complementarity is also consistently observed in our results but with a larger variation than convergence. Complementarity is argued to be the main result of tight coevolution between mutualistic species by mechanisms, such as trait-matching (e.g. corolla length-proboscis length) (Jordano et al., 2003). There is empirical (Anderson and Johnson, 2008, Thompson et al. 2013) and theoretical evidences (Gomulkiewicz et al., 2000; Fernandes et al., 2019) for coevolutionary hot spots (Thompson, 1999), which suggests that local selective regimes can promote the coevolution of traits (Gomulkiewicz et al., 2000; Ferdy et al., 2002; Gomulkiewicz et al., 2003; Jordano et al., 2003; Bronstein et al., 2006; Thompson and Cunningham, 2002; Thompson, 2009; Jones et al., 2009). In contrast, our results show that medium levels of complementarity can emerge from relatively non-selective forces and constraints occurring at several levels, and geographic limits to encounter partners and disperse, to the genetic and morphological  constraints on producing viable offspring. In addition, our model fitting shows our predictions fit well to the observed plant-hummingbird complementarity across a broad range of complementarity threshold values (see Figure 6).

 With our new approach, we were able to reproduce most observed patterns of convergence and complementarity in a plant-hummingbird community. Observed convergence values were close to those predicted by the model for the hummingbird community, but we predicted a higher value of convergence in the plant community than those observed in the empirical plant community. According to previous models, fewer convergence events could be indicative of weak coevolutionary selection processes acting on the plant species. Although this is a possible explanation for our overestimation of convergence, we think that our convergence estimates may have been biased by the fact that we could not consider all the plant species of the community (≈ 50%) only around 60% of the hummingbird species. To the best of our knowledge, our study is the first to quantify and compare convergence and complementarity values from an empirical dataset with model predictions.

**A new approach to calculate convergence**

One prominent problem in the literature is how to quantify convergence. This problem is probably related to the lack of a rigorous or precise definition of convergence (REFS). Previous studies proposed different ways of doing this, but their measurements of convergence do not consider phylogenetic relatedness. For example, Guimarães et al. (2011) measured convergence as “the mean pair-wise difference between traits of species at same trophic level” considering all the species of the guild, whereas Nuismer et al. (2012) calculated the variance as a proxy to predict convergence (i.e., large values weak convergence whereas small values of the variance may indicate strong convergence). The main problem with these measurements is that they ignore phylogenetic relatedness and, consequently, they tend to overestimate convergence events. In most definitions convergence is an evolutionary pattern in which “similar phenotypes evolve *independently* in multiple lineages” (Stayton, 2015). Thus, it is essential to consider phylogenetic distance to correct for shared and, therefore, dependent evolutionary history. By using a new approach to measure convergence, which considers phylogenetic relatedness and phenotypic similarity, our model shows that in the absence of abiotic selection trait convergence and complementarity always evolve, but with little and large variation, respectively.

**The emergence of mutualistic network structure**

Nuismer et al. (2012) explored the connection between convergence and complementarity to nestedness patterns in mutualistic networks. They showed that coevolutionary selection tend to decrease nestedness and it generates even more strongly antinested networks when coevolutionary selection  increases by favoring the emergence of reciprocal specialization. In contrast, nestedness values were very high in our model, as it is in real mutualistic networks. Previous neutral models (*e.g.*  ), by taking into account ecological drift, produced high values of nestedness, which suggests that random interactions and species abundance distribution (’neutral forbidden links’ (Canard et al., 2012)), are determinants of the structure of mutualistic networks. Connectance values obtained from our simulations are close to the predictions of other neutral network models (Canard et al., 2012, …? ). However, compared to real mutualistic networks with similar diversity. our connectance values (C = 0.5) are higher than the reported webs (C = 0.28) (Olesen and Jordano, 2002). Interestingly, Nuismer et al. (2012) found that only assuming coevolutionary selection forces also leads to an increase in connectance. This means that both basic genetic and ecological processes, and coevolutionary selection can increase connectance in mutualistic networks. The question is why observed mutualistic webs have a lower connectance than those predicted by our model and previous models. We conjecture that this difference in connectance values might be due to different types of forbidden links (i.e. biological constraints impeding plant-animal interactions), such as phenology (Encinas-Viso et al., 2012; Olesen et al., 2008) or environmental fluctuations that were not explicitly included in our approach.

**Conclusion**

In summary, our results show the emergence of convergence, complementarity and nestedness following basic genetic and ecological processes. Our predictions fit well to the observed plant-hummingbird complementarity and hummingbird convergence. In contrast to previous studies, we found highly nested values in agreement with empirical mutualistic networks (Bascompte et al., 2003). Our results suggest that diversification dynamics combining ecological (demography and dispersal limitation), population genetics (mutation, recombination, assortative mating and drift) and morphological constraints may form the basic processes producing the key patterns of mutualistic networks, from trait convergence and complementarity to connectance and nestedness in mutualistic networks.