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OPINION

In Euglossini we trust as ecological indicators: a reply to Añino et al. (2019)

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Abstract

Orchid bees have been considered as good ecological indicators of habitat disturbances but recently Añino et al. (2019. Sociobiology, 66: 194-197) highlighted reasons why the Euglossini role as indicators should be reevaluated. Despite agreeing with some points raised by them, we present an alternative view for the use of orchid bees as indicators. For us, the main problematic issues are: (i) the authors do not present a clear definition of ecological indicator, including its role as an indirect measure of the biota response to disturbed environments; (ii) they do not properly acknowledge the relative good taxonomic status of orchid bees when compared to the remaining bees; (iii) and they do not distinguish the use of particular Euglossini species as indicators in certain circumstances. In spite of some knowledge gaps, we argue that Euglossini are good candidates to be ecological indicators in tropical forests, maybe the best candidates among all the bees.

The need for ecological indicators

The need for organisms that rapidly indicate the complex anthropogenic habitat transformations is decisive in this fast-changing world. Indicators are living organisms that are easily monitored and whose status reflects or predicts the conditions of the environment where they are found (Landres et al., 1988; Siddig et al., 2016). Indicators can be separated into three categories corresponding to their main applications: (i) environmental, when responding to e.g. chemical compounds; (ii) ecological, related to disturbances such as habitat fragmentation, and (iii) as biodiversity estimators (McGeoch, 1998). A particular species can be considered an indicator, but taxa hierarchically placed above species are preferable because no single species should be expected to indicate an entire ecosystem condition, and also because many factors unrelated to the degradation of ecological integrity may affect the population status of an indicator species (Carignan &

Villeard, 2002). Several groups of invertebrates and vertebrates have been proposed as indicators based on established selection frameworks or on other justifications (Siddig et al., 2016). The criteria for selection of indicators have been extensively discussed in several papers and rely on the particular objective and scale of the measured disturbance (Landres et al., 1988; McGeoch, 1998; Carignan & Villeard, 2002; Siddig et al., 2016).

Reyes-Novelo et al. (2009) compiled the seven most common criteria for selection of ecological indicators and discussed their application to bees. The authors conclude that wild bees can be used as indicators, but further validation studies are necessary. Independently of the selection framework, bees have been used as ecological indicators especially for being a keystone group due to its main role as pollinator of wild and crop plants (Kevan, 1999; Garibaldi et al., 2013). The public concern about the decline of bees is increasing worldwide and the group can be considered as a flagship for conservation (Fortel et al., 2014).

A particular group of corbiculate bees, the orchid bees (tribe Euglossini), have been used as ecological indicators in the Neotropical region. There are about 230 species of Euglossini, distributed among five monophyletic genera (Moure et al., 2007; Ramírez et al., 2010). This group occurs from southern United States to Argentina, but most of its diversity is concentrated in Neotropical forests (Dressler, 1982; Roubik & Hanson, 2004). Much of the existing knowledge on these bees, especially that generated by structured inventories, was enhanced by the discovery and use of synthetic chemical compounds to attract adult males (Dodson et al., 1969). The justifications for the use of Euglossini as indicators are missing but can rely on their responses to fragmentation (e.g. Allen et al., 2019) and also on the relative good knowledge of their biology, taxonomy and distribution when compared with bees as a whole (Allen et al., 2019). Still, the presence and relative abundance of particular species such as *Eufriesea violacea* (Blanchard, 1840)*, Euglossa marianae* Nemésio, 2011 and *Eulaema nigrita* Lepeletier, 1841 have been considered as indicative of habitat quality (e.g. Tonhasca et al., 2002; Nemésio, 2009; Faria & Melo, 2012; Gonçalves et al., 2014).

Recently, Añino et al. (2019) highlighted some reasons why Euglossini should be reevaluated as indicators, based on criticisms contextualized under the seven established selection criteria reviewed by Reyes-Novelo et al. (2009). Here we argue against some aspects of their argumentation, concluding that this tribe meets the criteria to be considered as ecological indicator.

The seven selection criteria for ecological indicator applied to Euglossini

1. **The taxonomy of the group must be well known and stable so that the species can be identified reliably**. Añino et al. (2019) mention the lack of taxonomical security for the female identification of most species as the main problem, an argument also raised for criterion 2. In fact, Euglossini taxonomy is based almost entirely on males since they are consistently more abundant on museum collections (e.g. Nemésio, 2012a). This male dependency is caused by the use of chemicals for attracting and sampling individuals, an important aspect regarding the easiness of sampling (criterion 4). As virtually all Euglossini sampling protocols are based on chemical compounds to attract males, the ability to identify females is not necessary to the use of these bees as ecological indicators according to criteria 1, 4 and 6. In other words, Euglossini males are the candidates to be ecological indicators. On the other hand, orchid bees nesting biology and flower preference relies on female identification and the emergence of males is currently necessary to a proper species identification.

In the case of euglossine males, identification keys are available for all the four genera, besides *Aglae* Lepeletier & Serville that is monospecific. The most intimidating scenario regards the genus *Euglossa* Latreille (ca. 120 species) that lacks a comprehensive revision. However, the situation is not the same for all the subgenus and species groups and some of them could almost be considered as "solved", mainly in some particular regions. We believe the best scenario is for the Brazilian Atlantic forest, whose entire fauna was studied in an extensive monograph (Nemésio, 2009), besides robust regional identification keys (e.g. Nemésio, 2011) and taxonomic papers focusing on particular species group of *Euglossa* (e.g. Faria & Melo, 2012; Nemésio, 2012b). These considerations are even more relevant when we consider that using some euglossine groups as indicators is much more feasible than using others (see criterion 4 and 6). So, the dependence of taxonomic keys would diminish in these specific taxa, making this problem much more treatable.

Finally, even with all the existing caveats on euglossine taxonomy, only a few other bee tribes (e.g. Anthidiini, Centridini, Emphorini, Eucerini, Meliponini, Tapinotaspidini) have such a good taxonomic knowledge accumulated to the Neotropical region as a whole, but other selection criteria were not fully addressed to these groups, especially criterion 6.

2. **Biology and lifestyle must be well known.** Lifestyles are rather uniform within bee tribes, however Euglossini comprizes solitary, communal, primitively eusocial nest builders and also cleptoparasite species (Michener, 2007). As pointed out by Añino et al., studies on several aspects of biology are lacking for most euglossine species. This is true, but it is not a particularity of these bees since this is an expected pattern for most invertebrates. Again, the comparison with the scenario for other tribes requires to realize that the biology of Euglossini can be considered as "well known", as, for example, the observation that about 10% of its species were recorded and studied with trap-nests (Costa & Gonçalves, 2019). Few other bee tribes have higher percentage of studied species. Still, there is a significant amount of information on the plants these bees visit for pollen, nectar, resin and aromatic compounds, besides nesting biology (including information on parasites), distribution of species along altitudinal gradients, etc. (synthesized mainly by Dressler, 1982; Ramírez et al., 2002; Cameron, 2004; Roubik & Hanson, 2004). An important issue (see criterion 1) regards that establishing meaningful links of the information on natural history for males and females critically depend on the correct identification of females (see Nemesio, 2012a). But even with this caveat, when existing biological data for Euglossini is compared with information for other bee tribes in the Neotropical region, perhaps only Centridini and Meliponini have similar overall knowledge.

3. **The group should be composed of well-defined and rich trophic guild that should be important in the structure and functioning of ecosystems.** As for the bees as a whole, Euglossini is a well-defined trophic guild of pollinators and matches very well with this criterion. The particular plant hosts for most species are unknown and we agree with Añino and colleagues that more attention should be given to this subject. However, we do not agree that the ability of some euglossine to thrive in the absence of its orchid mutualists (Pemberton & Wheeler, 2006) hampers their classification as

indicators, especially according to this particular criterion of selection. After all, how particular is this observation? And even though euglossine bees could succeed without orchids, they will need to visit plants to collect other resources. Also, a trophic narrow specialization is not necessarily a requisite to fit in this criterion.

The relation of orchid bees and orchids are usually misunderstood and the importance of orchid bees as pollinators and/or flower visitors cannot be neglected. As pointed out by Roubik and Hanson (2004), orchid bees have been recorded foraging for nectar on flowers in 51 plant families, but how specific these interactions are among bees and plants have not been examined in detail. Studies focusing on the foraging behavior of some euglossine species have also revealed that a significant number of plants are visited by these bees. A high diversity of plants, 50 pollen types belonging to 20 botanical families, was used by females of *Euglossa cordata* (Linnaeus, 1758) for provisioning their brood cells (Ferreira-Caliman et al., 2018). These authors also discussed that even if their study have been carried out in an area where invasive plants were abundant, *Euglossa cordata* preferred to forage on native plants to collect floral resources. Silva et al. (2012) recorded that the flora visited by *Eulaema nigrita* is compound by 40 species from 19 botanical families, even if the species exhibited some preference for plants with poricidal anthers. And it should be highlighted that bees were collected during the flowering period of *Passiflora alata*, the main source of nectar for this bee where the study was carried out. Expressive numbers were also found for *Euglossa annectans* Dressler, 1982 (74 pollen types from 24 families, during a three-year fieldwork; Cortopassi-Laurino et al., 2009) and *Euglossa atroveneta* Dressler, 1978 (74 plant species detected in larval provisions of 51 nests during a single year; Arriaga & Hernández, 1998), in studies based on samples of larval provisions. All these data would allow the conclusion that *Euglossa* females may act as pollinators of many forest species (Cortopassi-Laurino et al., 2009). When pollen is collected from males, results are also relevant. In a study carried out in the Chocó region, Ospina-Torres et al. (2015) gathered pollen grains attached to the body of 352 males of at least 22 euglossine species, and found that these males were associated to 84 plant species, but dependent of a small group of them. They also discussed a nested pattern in this relation, as several specialists bees and plants have interacted with a small group of generalists (both bees and plants). Extreme mutualisms appear not to be the main pattern on plant-pollinator interactions, as interactions seem to be much more asymmetrical (e.g. Olesen & Jordano, 2002). Some particular evidence from euglossine x euglossophilous plants also suggests so (e.g. Borrell, 2005). And all the matter on orchid bees becomes even more important if we consider that this tribe comprises 20-30% of the total bee species in various Neotropical forests (see Roubik & Hanson, 2004). We believe that studies focusing on the plants visited by those species with greater potential to indication (see criterion 6)

should be prioritized, as a way to attack this impediment in a faster and more targeted manner.

4. **Organisms should be easily captured, manipulated and observed; the study of the group should not jeopardize its conservation.** It was noted by Añino and collaborators that the chemical compounds facilitate the collection of male orchid bees, a practical resource especially in rapid assessments of indication programs. The relative easiness to sample males should be considered as a positive aspect that enables the use of the group as indicator despite the uncertainty about females frequency (see Nemesio, 2012a). Bees as a whole are sampled in flowers with hand-nets or caught with bowl traps, a hard task in tropical forests, and none alternative bee group has a particular sampling method so efficient as the scents are for euglossines.

The hand-netting (an active sampling method) and bait-traps (a passive method) are two methods for capture, and while the first is considered more effective (Nemésio & Vasconcelos, 2014), traps allow a higher number of replications, which maximizes the sampling effort (Knoll & Penatti, 2012). The sufficient replication is a guideline to biological sampling in environmental licensing studies (Ferraz, 2012), favoring the use of bait-traps. The highlighted problem with hand-netting is the bias caused by the skills of the collector, an issue that can be avoided by a training phase (but see discussion on Nemésio, 2012a). The attraction of orchid bees to baits, allied to the overall size of these bees, makes the sampling easier when compared to hand-netting bees in flowers under active search. In the case of bait-traps, Sydney and Gonçalves (2015: p. 35) concluded that "alternative baited trap designs do not have much influence on the richness and abundance parameters (except for the landing platform), thus making most studies directly comparable". Still, performance of bait-traps should be replicated in other landscapes for validating the prediction of Sydney and Gonçalves (2015).

With regards on collection jeopardizing euglossine conservation, there are no studies focusing on the actual impacts of samplings on the populations of orchid bees (Nemésio, 2012a).

5. **The geographical distribution of the group should be broad, including different habitats, allowing the use of a variety of experimental designs and comparisons.** Orchid bees present a broad geographical distribution along the New World, occurring from southern United States to Argentina (Michener, 2007). The southern limit of their distribution is not so well defined, with a record of a species of *Euglossa* near Buenos Aires (Martín García Island; Roig-Alsina, 2008). Regarding the western limits in Southern America, Trans-Andean distributions seem to be restricted to lower latitudes (e.g. Dick et al., 2004), but the extension of geographical distributions within genus and species widely varies (see Roubik & Hanson, 2004). We conclude that the distribution of orchid bees is broad enough to consider this criterion as applicable to the group. However, it is important to highlight that the abundance and richness of Euglossini is greater on tropical forests of Central and South America than

on the northern and the southern portions of their distribution (Michener, 2007), restricting where they (and which species) can be effectively sampled in indication studies.

We agree with Añino et al. (2019) that understanding the distribution of orchid bees is a complex matter. But, again, in a comparative way: are there so many other groups of bees with so predictable distributions? Is this a reason to set aside any possibility of using bees or orchid bees as indicators? We believe that one of the main questions in Añino and colleagues' argumentation, the lack of definition of a specific scale and context for indication, is particularly important for this criterion. One species, regarded as a promising indicator in a specific context, is not necessarily an indicator in other. Previous authors agreed that the spatial scale should be always evaluated when selecting an indicator (Carignan & Villeard, 2002; Siddig et al., 2016).

In the case of particular species indicating disturbances, a simple example comes from *Euglossa fimbriata* Moure, 1968. Within the Atlantic Forest this species could be assumed to be rare in the deep interior of the forest (Nemésio, 2009), suggesting a kind of negative relation with forested areas. On the other hand, in a different context, the Brazilian Cerrado, the species shows a clear tendency to be positive related to the savanna proportion in the landscape (Moreira et al., 2017). Even if these statements could both suggest a general relation with more open areas, the potential of the species as indicators is clearly different in these two specific contexts. Considering the spatial scale for indication, it could also help to define how broad a species distribution has to be for being a useful indicator. For spatially restricted contexts, species with restricted distributions could even be more appropriate. We also point that, whenever possible, eventual shifts between the historic and the current distribution of species should be considered to state their roles as bioindicators. *Euglossa marianae* could be used as an example, as its historic distribution is regarded to be much broader than the current. Old records presented by Nemésio (2009) [as *Euglossa analis*], Nemésio (2011) as well as Faria and Melo (2012), state that the species used to occur from southern Bahia to northern São Paulo state, mostly in litorean areas. Several recent inventories carried out within this region (e.g. Ramalho et al., 2009), in forest fragments with very distinct sizes, have shown that the species is currently found only in fragments larger than 3,200 ha, with most records from preserved fragments larger than 6,000 ha (see discussion in Coswosk et al., 2018).

Añino and colleagues also claimed the impossibility of accurately defining the distribution ranges of many species as they (i) are not attracted by chemical baits, and (ii) are able to fly long distances to find the baits, moving across different habitats. Dealing with the point (i) is much simpler: these species should not be considered in bioindication, in the same way as those presenting a striking geographical structuration in scent preference, and in this latter case, the use of the species should be restricted to the spatial context where this issue is controllable. The point (ii) is knotty, especially if the bioindication uses parameters of euglossine assemblages, as the existence of directional artificial stimuli from scents could homogenize euglossine assemblages (see Milet-Pinheiro & Schlindwein, 2005; Ramalho et al., 2013; Coswosk et al., 2018). However, the existence of such a directional stimuli could be, in theory, even reinforcing the possibility of using orchid bees as bioindicators. Considering the example of *Euglossa marianae* (and also other species from the *analis* species group) within the Brazilian Atlantic Forest, even though they are able to fly long distances to reach the baits, these bees continue to be strongly associated to the inner sites of large forests (Tonhasca et al., 2002; Nemésio & Silveira, 2006; Coswosk et al., 2018).

6. Species should tend to specialize in a particular habitat, so that they are sensitive to habitat degradation and regeneration. We believe this is a decisive criterion for indicator selection. Añino et al. mentioned two main problems, (i) population stability and rare species hampering the interpretation of the responses of orchid bees, and (ii) studies showing none or positive responses to disturbances. In the case of population stability, the authors cited the study of Roubik (2001), conducted in a natural area that was not subject to intense disturbance. But this example can be taken as indicative that populations do not oscillate that high under undisturbed conditions, an important background to orchid bees selection as indicators. It would then be necessary to advocate the realization of studies focusing on the population stability of species in disturbed environments, in order to allow the necessary comparisons, before simply discarding the possibility of using orchid bees as indicators. We agree that rare species individually could not be good indicators of disturbance since their abundance can be expected to naturally fluctuate and they can be expected to disproportionately respond to habitat fragmentation (see Ramalho et al., 2013). But in this specific case, using assemblages of several species could tend to minimize the effect the presence of particular species.

The unexpected relations between Euglossini diversity and fragmentation mentioned by Añino et al. should be contextualized. Botsch et al. (2017) found that while the abundance and species richness of orchid bees were not different in fragmented and contiguous forest, the community composition and evenness really were, and one of their conclusions was "these results demonstrate the conservation value of continuous forest, given the differences in community composition between continuous forest and fragments, greater community evenness in continuous forest, and a trend toward greater β-diversity" (Botsch et al., 2017: p. 639). Robust evidence on this matter was recently provided by Allen et al. (2019), which stated that euglossine bees can be useful as indicators of the impacts of human disturbance. They even suggested (p. 752) that "orchid bee abundance is a simple measure that can be monitored by conservation managers without the need for much analytical expertise or even species identification. Although this should not be used in isolation, it could serve as a useful warning flag of negative impacts of disturbance".

We also evaluate that Añino et al. have not assessed the matter of using particular Euglossini species as indicators of disturbance. Two examples are *Eulaema nigrita* and *Eufriesea violacea*, if the first is commonly considered as an indicator of habitat perturbation, while the latter is an indicator of habitat quality in fragments of Atlantic Forest in southern Brazil (Gonçalves et al., 2014). But it is important to highlight here the question of the spatial scale/ context (see above), as there is no evidence of the effects of habitat disturbance on *Eulaema nigrita* in the Brazilian Cerrado (Silva & de Marco Jr, 2014). We discussed above the role of *Euglossa marianae* as an indicator of large preserved forests in the Brazilian Atlantic forest (Nemesio, 2009; Faria & Melo, 2012). This species is still a good indicator in another context, although quite related to fragment size, the edge effects. Two studies carried out in large fragments of Brazilian Atlantic Forest (Nemésio & Silveira, 2006 [as *E. analis*]; Coswosk et al., 2018) brought evidence showing that this species avoids the edge of the forest. Additional discussion on other candidates for indication is presented by Nemésio (2012a).

All these examples have shown that even with their great potential to exploit resources due high fight capacity (Pokorny et al., 2015), orchid bees species are able to respond to alterations in habitats.

7. The group must have species with potential economic importance. The main economic importance of bees regards pollination. As far as we know there is no reported case of Euglossini as the main pollinator of crop plants, differently from other bee groups (Giannini et al., 2015). There are some records on the importance of orchid bees as the main pollinators of Brazilian nut (*Bertholletia excelsa*, Lecythidaceae) (Mori & Boeke, 1987; Maués et al., 2002), pollinators of mangaba fruits (*Hancornia speciosa*, Apocynaceae) (Oliveira et al., 2014) and minor pollinators of passion fruit (*Passiflora* spp., Passifloraceae) (Gaglianone et al., 2014). However, the indirect effect of pollination service on natural systems should not be discarded. The long known extraordinary flight ability of euglossine bees (e.g. Wikelski et al., 2010), allied with their trapline foraging behavior (e.g. Ackerman et al., 1982), make these bees an important element for promoting outcrossing among plants with natural low densities (Janzen, 1971).

Euglossini are good ecological indicators

The selection of an ecological indicator is subject to the study purpose and related parameters such as spatial extent and habitat predictors, and no specific group can be considered a universal indicator (Siddig et al., 2016). These parameters are variable under different scenarios and should be stressed before or even after the use of indicators, when interpreting the results. We believe that it is possible to assume that orchid bees collectively match the seven selection criteria and should be considered as ecological indicator of disturbances in tropical forests. The main reasons that support their use are the ease

of sampling, established taxonomy and sufficient knowledge of the most general patterns regarding the responses to disturbances. One can argue that these criteria may not be fully addressed by the tribe, but (i) biological knowledge is never to be considered as complete; (ii) not necessarily all criteria should be completely matched; and (iii) the relative knowledge on euglossine bees, when compared to alternative candidates within wild bees, can be a desirable proxy for selection. Still, particular species can also be secondarily used to indicate habitat alterations and they could also be subject to the seven selection criteria. For example, taxonomy (criterion 1), that can be problematic in the case of cryptic species and/ or some particular species groups (e.g. the *Euglossa cordata* group).

In Brazil the installation of enterprises or activity potentially harmful to the environment such as highways, hydropower plant and mining, must undertake environmental licensing with a preparation of environmental studies. The practical choice of indicators deals with the enterprise kind, the preliminary assessment, and the need for informative groups including particular species and higher taxa (Ferraz, 2012), and this choice is made by the inspection agencies and the consultant companies. Terrestrial invertebrates are important groups to be assessed especially in enterprises regarding vegetation suppression. In Amazon and Atlantic forests orchid bees have already been used as indicators in such environmental studies together with other groups such as ants and frugivorous butterflies. In the specific case of approval of new dams, empirical evidence suggests that these bees should be considered in environmental studies before approving such enterprises (Storck-Tonon & Peres, 2017). Academic researchers should be aware of the pros and cons of the use of the group as ecological indicators since they have the qualifications to be competent consultants in environmental studies (Silveira et al., 2010).

The points raised by Añino et al. (2019) are certainly relevant and we agree with some of them. However, the present rebuttal offered an alternative view for the use of orchid bees as ecological indicators. We wonder to continue the debate they have proposed about the use of orchid bees as ecological indicators and all opinions should be respectfully considered. Anyway, the debate is a healthy way to contextualize the existing data and searching for a solid basis for euglossine-based indication, centered in scientific evidence.

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Contributions of authors

RBG and LRRF equally contributed to the arguments presented here and wrote the final version together.

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