



Review

Can plant–pollinator network metrics indicate environmental quality?

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ABSTRACT

Plant–pollinator interaction networks may be more informative than the diversity of species in the evaluation of the effects of environmental change. Considering that networks vary with the integrity of ecosystems, their changes may help to predict the consequences of anthropogenic impacts on biodiversity and ecological processes. This characteristic highlights its use as environmental quality indicator. However, to employ interaction networks as ecological indicators it is necessary to identify the most sensitive metrics and understand how and why they vary with environmental changes. This review aimed to identify, in empirical studies, which network metrics have been evidenced as being more sensitive to changes in environmental quality. We analyzed published empirical studies, that applied the network approach on environmental quality gradients. In addition to the network metric behavior, we studied the interactions between them and possible causes of their variation. The available empirical data indicated that degree, nestedness and connectance did not have a simple, linear or unidirectional response to habitat degradation. Conversely, the metrics interaction asymmetry, d' (reciprocal specialization index of the species) showed the most consistent responses to environmental change. The role of the species changed, ranging between generalists and specialists under different conditions. In addition, specialist species with morphological and behavioral constraints were lost in worse environmental quality situations. The identity of interacting species and their role in the network, with a further specification of groups and interactions most affected, are the properties with greater potential to indicate changes in environmental quality. Most of the available studies focused on metrics at the network level, but several studies and this review indicate that the patterns at the network level can be better understood in the light of metrics analyzed at the species level. Our results provide information that enrich the network analysis, highlighting the need to consider important features that are often neglected. Discussions and information compiled here are important for deciding how to look at empirical data and what to look for, as well as to indicate some caveats when interpreting data on plant–pollinator interactions with a complex network approach. Network metrics can be good indicators of environmental quality if the underlying ecological causes of the numerical changes are carefully analyzed.

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1. Introduction

Complex network approaches on plant-pollinator interactions encompasses the characteristics of species, their interactions, and the evolutionary processes generating the complexity of ecological relationships (Bascompte, 2007). Therefore, plant-pollinator interaction networks may be more informative than species diversity in the evaluation of environmental change effects. The conservation of these interactions may be more important for maintaining biodiversity and ecological services than preservation of species that are isolated in degraded environments (Forup and Memmott, 2005; Aizen et al., 2012). Considering that networks vary with the integrity of ecosystems (Montoya, 2008; Ferreira et al., 2013; Weiner et al., 2014), their changes may help to predict the consequences of anthropogenic impacts on biodiversity and ecological processes (Weiner et al., 2014). For instance, it is expected that networks will be simplified even before the local extinction of pollinator species (Aizen et al., 2012) suggesting their potential as environmental quality indicators.

Ecological indicators are selected by their functional relevance, ease of quantification and predictability (Heink and Kowarik, 2010). They enable the identification of changes in complex ecosystem processes in a simple, fast, reliable and early way (Dale and Beyeler, 2002). However, there are several challenges to overcome in order to employ interaction networks as ecological indicators to predict anthropogenic impacts. An important task is identifying the most sensitive metrics and understanding how and why they vary with environmental changes. Metrics such as nestedness and connectance are expected to indicate redundancy in the network interactions (Tylianakis et al., 2010). So that an increase in nestedness values, for example, could be interpreted as a good trend because it would increase assembly resilience (Tylianakis et al., 2010) as the asymmetry typical of nested networks would prevent cascade extinctions. However, nestedness increases could also result in network simplification by losing specialist-specialist interactions and/or increasing the proportion of super generalist interactions, and forming a cohesive, resilient, yet smaller, network. In a similar way metrics that are expected to indicate redundancy in the network interactions such as nestedness and Connectance (Tylianakis et al., 2010) could be better understood, if analyzed in conjunction with metrics that indicate complementarity of interactions such as H_2' and d' (Blüthgen et al., 2006).

The definition of conservation goals is another important topic which should be defined to support both the choice and the interpretation of network metrics. Conservation of the basic features of ecosystem functioning may not guarantee the conservation of native species diversity, and vice versa. Metrics that assess network stability and resilience, but disregard species composition, would not suffice if the goal is to conserve biodiversity. Therefore, understanding of what changes in the metrics indicate about biodiversity and ecological processes is important for their application in accordance with the conservation goals. This knowledge is also required to identify the desirable characteristics of a plant-pollinator network.

Empirical studies that investigate changes in plant-pollinator interaction networks under different conditions of environmental quality may bring with them important evidence regarding the application of interaction networks as ecological indicators. Such knowledge is essential for identifying which metrics should be analyzed under different environmental impacts and different conservation goals. This review aims to identify in empirical studies, which network metrics have been evidenced as being more sensitive to changes in environmental quality. We expect to identify candidate metrics that could be employed as indicators of network changes, with applications for biodiversity and ecological processes conservation.

2. Methods

We analyzed papers published up to December of 2016 that used plant-pollinator interaction network approaches on empirical data from gradients of environmental quality, impact or degradation. We searched on Web of Knowledge, Scielo and CAPES journal databases. The search was made with combinations of the key-words “environmental degradation”; “habitat loss”; “habitat fragmentation”; “interaction”; “mutualistic network”; “network”; “plant”; and “pollinator”. Papers supplementary material was also analyzed.

Metrics present in at least three of reviewed studies were selected. The metrics were classified as metrics based on unweighted links, which considered only the presence and absence of interactions, and metrics based on weighted links, which considered the frequency of interactions.

The behavior of each metrics along the studied gradients was analyzed to assess their suitability as an indicator of negative environmental impacts on the network. For this, in addition to changes in the values of the metrics in response to different impacts and conditions, we also investigated the causes of variation and ecological significance such as the discussions and interactions with other metrics in each study.

3. Results and discussion

We found 18 papers (Table S1 in Supplementary material), in five categories of impacts or environmental conditions: plant species invasion (5 studies), land use intensity (6), habitat patch area (2), habitat restoration (4) and landscape degradation (2) (Fig. 1). One study was reported in two categories, because it analyzed two types of impact.

3.1. Network metrics

Nine network metrics were included in the analysis because they were calculated in at least three empirical studies (Table 1). Theoretically, metrics based on weighted links would be more accurate than those based on unweighted links (Ings et al., 2009). Weights based on interaction frequency precludes that rare and frequent interactions are considered as the same. However, few studies have directly addressed this question. Despite the theoret-

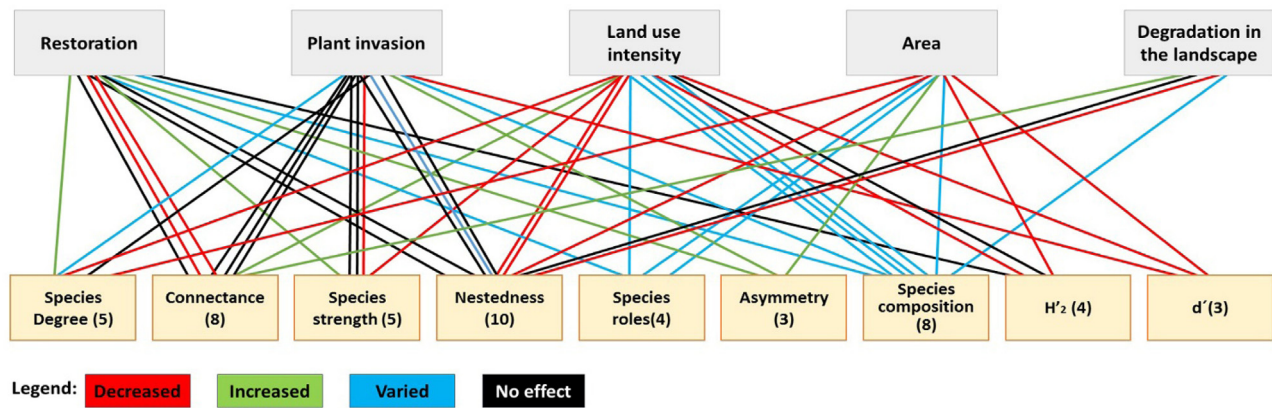


Fig. 1. Summary of articles describing the behavior of plant-pollinator network metrics' (beige boxes) in environmental quality gradients. The articles were categorized according to the type of quality gradient (gray boxes). The numbers in parentheses indicate the amount of metrics' results analyzed. Each line indicates whether the metrics decreased (red), increased (green), varied in the same study (blue) or did not change in the environmental quality gradient (black).

ical expectancy, [Corso et al. \(2015\)](#) found high correlation between the results of the same metrics calculated with weighted and unweighted links. In this study, four metrics were predominantly based on weighted links and three in unweighted links ([Table 1](#)). Metrics based on weighted links seemed to have greater potential as indicators than those which do not consider interaction frequency.

3.1.1. Interaction asymmetry

In the ecological context, interaction asymmetry indicates uneven dependency in the relationship among plants and pollinators ([Bascompte et al., 2006](#)). In asymmetric interactions a specialist plant relies strongly on a generalist pollinator, which depends weakly on that plant, or vice versa. Due to the higher proportion of specialist-generalist than specialist-specialist interactions, plant-pollinator networks are usually asymmetric ([Thébault and Fontaine, 2010](#)).

It is expected that interaction asymmetry increases resilience, when compared with symmetrical networks ([Ashworth et al., 2004](#)). Indeed, studies attribute the maintenance of specialist species in fragmented landscapes to their relationship with resilient generalists ([Newman et al., 2013](#)). It is a consensus, therefore, that the interaction asymmetry improves the coexistence of species over time, and facilitates the maintenance of biodiversity ([Bascompte et al., 2006](#)).

The three studies that used interaction asymmetry analyzed different environmental changes: introduction of alien species; decrease in habitat area; and a gradient from old forests to clear cuts (see [Table 1](#)). In these different contexts of environmental changes, interaction asymmetry increased due to the concentration of interactions by generalist species and loss of specialists-specialist interactions. Therefore, the increase of interaction asymmetry may indicate a loss of interactions between reciprocal specialists and an increase of generalist species with a greater ability to concentrate interactions. This happens despite the persistence of a core of interactions among “supergeneralists” ([Aizen et al., 2012](#)). In this way, interaction asymmetry shows similar behavior for different impacts, and sensitivity to the loss of interactions among specialists. Such interactions are considered important indicators of impact on the network ([Aizen et al., 2012](#)). In light of this, despite the few studies found, we suggest that interaction asymmetry is a good candidate as an indicator of the effects of changes in environmental quality, and, when compared to high quality reference sites in the same region, it is expected to achieve its highest interaction asymmetry values in the lowest environmental qualities ([Aizen et al., 2008](#); [Aizen et al., 2012](#); [Abramson et al., 2011](#)).

3.1.2. Nestedness

Nestedness describes a pattern where specialist species interact with a subset of the species with which the most generalized species interact ([Spiesman and Inouye, 2013](#)). For example, in a nested network, a specialist plant interacts with a subset of the floral visitor species of a generalist plant ([Bascompte et al., 2003](#)). Nestedness implies high cohesion among the species forming a core of interacting generalists to which the rest of the assembly is connected ([Bascompte et al., 2003](#)). This constitution allows, in the case of species loss, alternative routes in response to disturbances, reducing the cascade effect of secondary extinctions ([Bascompte et al., 2003](#); [Nielsen and Totland, 2014](#)).

With decreasing environmental quality, nestedness did not change in four, and decreased in five of the ten reviewed studies. Within the same study this metrics' behavior varied (increased and had no effect) with the impact of two alien plant species ([Bartomeus et al., 2008](#)). The possible causes of maintenance of nestedness with environmental degradation in [Devoto et al. \(2012\)](#) was not discussed by the authors. In the other three studies these maintenance was attributed to the high robustness of this metrics due to a reorganization of interactions ([Nielsen and Totland, 2014](#); [Padrón et al., 2009](#); [Vilà et al., 2009](#)). This reorganization may compensate for lost interactions, preventing disruptions that lead to extinctions ([Nielsen and Totland, 2014](#)). The fourth work indicating no effect on nestedness compared different levels of habitat loss in the surrounding landscape ([Spiesman and Inouye, 2013](#)). The authors observed that overall richness and abundance decreased with habitat loss. Also, nestedness was positively correlated with overall species richness and negatively correlated with plant species abundance. They argued that those opposite correlations had canceled out themselves, resulting in an absence of effect of habitat loss in nestedness. However, the article did not present a discussion on the ecological relations of those opposite effects to nestedness.

In four cases with different contexts of environmental quality, nestedness decreased in lower quality areas ([Burkle and Knight, 2012](#); [Burkle et al., 2013](#); [Vanbergen et al., 2014](#); [Moreira et al., 2015](#)). In [Vanbergen et al. \(2014\)](#) this result was independent of variation in species richness and the authors did not discuss the possible causes of nestedness decrease with environmental degradation. In the other three studies these results were attributed to the reduction in species richness (network size) and number of interactions performed (number of links) by the remaining generalist species by narrowing their diet breadth. Consequently, those changes could reduce functional redundancy among species, reducing resilience. Together, these factors contributed to the disruption of networks, which became less nested in more degraded areas. For

Table 1
Summary of observed trends in network metrics along environmental degradation gradients (from better to worse environmental quality) in five categories of impact or environmental condition. Calculation indicates whether the metrics are based on weighted or unweighted links. Question marks highlight data that are not unequivocal.

Metrics	Trend related to environmental degradation	Impacts or environmental conditions	Calculation	Reference
Interaction Asymmetry	Increased	Plant invasion	Weighted	Aizen et al., 2008
	Increased	Area	Weighted	Aizen et al., 2012
Species strength	Increased	Restoration	Weighted	Nielsen and Totland, 2014
	Increased	Restoration	Weighted	Nielsen and Totland, 2014
	Decreased (interaction strength)	Land use intensity	Weighted	Burkle et al., 2013
	Showed no relationship in the native plants (interaction strength)	Plant invasion	Weighted	Vilà et al., 2009
	There was no effect among the native plants, but in all areas of the strength of alien species was greater than the native	Plant invasion	Weighted	Bartomeus et al., 2008
	Exotic had greater strength than native in highly invaded sites	Plant invasion	Weighted	Aizen et al., 2008
H ₂ ' degree of specialization network-level	No effect	Restoration	Weighted	Devoto et al., 2012
	No effect	Land use intensity	Weighted	Weiner et al., 2014
	Decreased	Land use intensity	Weighted	Marrero et al., 2014
	Decreased	Area	Weighted	Burkle and Knight, 2012
d' of interaction specialization at the species level	Decreased	Land use intensity	Weighted	Weiner et al., 2014
	Decreased in the plant and pollinator, but the effect did not differ between aliens and natives	Plant invasion and Land use intensity	Weighted	Grass et al., 2013
Species composition	Decreased	Area	Weighted	Burkle and Knight, 2012
	modified	Land use intensity	–	Weiner et al., 2014
	modified	Land use intensity	–	Morales and Aizen, 2006
	modified	Area	–	Burkle and Knight, 2012
	modified	Degradation in the landscape	–	Spiesman and Inouye, 2013
	modified	Plant invasion and Land use intensity	–	Grass et al., 2013
	modified	Land use intensity	–	Burkle et al., 2013
Species roles	Modified	Restoration	–	Nielsen and Totland, 2014
	Modified/A generalist species may present as specialists and vice versa	Restoration	–	Nielsen and Totland, 2014
	Modified (diet breadth decreased)	Area	–	Burkle and Knight, 2012
	Modified	Area	–	Aizen et al., 2012
	Modified	Land use intensity	–	Burkle et al., 2013
Nestedness	No effect	Restoration	Unweighted	Nielsen and Totland, 2014
	No relationship	Degradation in the landscape	Unweighted	Spiesman and Inouye, 2013
	No effect	Plant invasion	Unweighted	Vilà et al., 2009
	Varied between increase/No effect	Plant invasion	Unweighted	Bartomeus et al., 2008
	No effect	Plant invasion	Unweighted	Padrón et al., 2009
	No effect	Restoration	Unweighted	Devoto et al., 2012
	Decreased	Area	Unweighted?	Burkle and Knight, 2012
	Decreased	Land use intensity	Unweighted?	Burkle et al., 2013
	Decreased	Degradation in the landscape	Weighted	Moreira et al., 2015
	Decreased	Land use intensity	Unweighted	Vanbergen et al., 2014
Connectance	No effect	Restoration	Unweighted	Nielsen and Totland, 2014
	No effect	Plant invasion	Unweighted	Vilà et al., 2009
	No effect	Plant invasion	Unweighted	Padrón et al., 2009
	No effect	Plant invasion	Unweighted	Aizen et al., 2008
	Increased	Degradation in the landscape	Unweighted	Spiesman and Inouye, 2013
	Increased	Land use intensity	Unweighted	Vanbergen et al., 2014
	Decreased	Restoration	Unweighted	Forup et al., 2008
	Decreased	Restoration	Unweighted	Forup and Memmott, 2005
Species degree	Increased in the Alien plant and decreases in native	Plant invasion	Unweighted	Aizen et al., 2008
	Decreased (species interactions/in a group of generalists)	Area	Unweighted	Burkle and Knight, 2012
	Increases in plant and pollinator	Restoration	Unweighted	Nielsen and Totland, 2014
	No effect in plant and decreased in pollinator	Plant invasion	Unweighted	Padrón et al., 2009
	Decreased	Land use intensity	Unweighted	Burkle et al., 2013

example, an overall loss of 46% of interactions was reported over a 120 year period (246 of 532), and 51.5% of the number of species (54 of 109) affecting both, specialists and generalists (Burkle and Knight, 2012). These studies showed the decline in richness in two situations, leading to decreased nestedness. First in a short time, the decrease in richness was observed, mainly affecting the specialist

species, and leading to a narrowing of the niche of the remaining generalists (Burkle et al., 2013; Moreira et al., 2015). Second, in the long term, a more intense reduction of richness was observed, also affecting the generalist species (Burkle and Knight, 2012).

Bartomeus et al. (2008) observed that nestedness varied from no effect in areas invaded by species that facilitated the enhance-

ment of interactions between pollinators and native plants, and increased in the areas invaded by the species that usurped these interactions. In this case, the increase in nestedness was due to the disappearance of important links with native plant species and a centralization of interactions by alien species.

Regarding the influence of sampling, nestedness was one of the metrics that quickly attained an asymptote, a fact associated with high robustness to sampling effects (Nielsen and Bascompte, 2007). This feature has justified the use of this metrics as ecological indicators of changes in environmental quality, suggesting its use in environmental monitoring related to community stability conservation (Tylianakis et al., 2010).

Reviewed studies indicate that, although network nestedness exhibited different responses to changes in environmental quality, the explanations for these different responses are the same and are theoretically consistent. In this sense we can infer that the decline in nestedness is associated with the loss of species and interactions, or decreases in niche amplitude. On the other hand, increase of nestedness may be related to the concentration of interactions by generalist species. Cases of maintenance of nestedness with environmental degradation could be explained by compensations due to increases in species richness. The expectation that nestedness should increase as a result of environmental disturbance (see Tylianakis et al., 2010) is just one of the possible behaviors of this metrics, and was observed in only a minority of the studied cases.

Given this variation, a more appropriate analysis should consider which types of interactions are contributing to the changes in this metrics. Networks with a predominance of generalist interactions can be considered more resilient than similar ones that include more specialist–specialist interactions. However, this may not be a desirable condition, if what it is intended to be conserved is beyond the basic functioning of the systems. A purely mathematical analysis of the nestedness could, therefore, result in management actions that intensify anthropogenic impacts, if strategies are selected to increase nestedness or prioritize areas with higher values of this metrics, without careful attention being paid to the nature of the interactions.

We understand, however, that the empirical evidence does not support the adoption of a single standard behavior of this metrics as an indicator of environmental impact. We suggest that its faster stabilization is due to its central role in the structure of mutualistic networks, resulting from evolutionary interactions over the assembly development. Nestedness is one of the structural identities of plant–pollinator networks, absent only in conditions of great loss of interactions. This can partly explain a lower sensitivity to changes in nestedness with environmental degradation when compared to others in this review.

3.1.3. Connectance

In mutualistic networks, connectance is calculated by the division of the number of observed interactions by the number of possible interactions. The divisor is given by multiplying the number of species of plants and pollinators in the network (Blüthgen et al., 2008). Network connectance did not change in four studies, decreased in two studies and increased in one study due to the reduction of environmental quality. The explanations of the results in the four cases of absence of the effect differ between studies. In Nilssen and Totland (2014) the maintenance of connectance is justified by the increase in network size in areas of lower environmental quality and the robustness of the network to changes, in this case the structure of network is maintained due to a reorganization of the interactions. Aizen et al. (2008) argues that the lower connectivity of plant–pollinator native species was compensated by a greater connectivity of pollinators with exotic plant species. Padrón et al. (2009) attributed the absence of effect to analysis bias. They argued that the loss of the interaction would be less

expected than the decrease in its frequency. Such an effect would not be identified by the presence-absence matrix of interactions employed in their analysis. Therefore, they suggest that metrics based weighted links would be more accurate. Similarly, Vilà et al. (2009) attributed the lack of effect to sampling and impact intensity, reporting that the studied networks were small and sampled in areas with low intensity of alien invasion. The two studies in which connectance decreased compared old environments with young restored environments (Forup et al., 2008; Forup and Memmott, 2005). As a general trend, the increasing richness in older restoration areas reduced connectance. In Spiesman and Inouye, (2013) the connectance increased in a gradient of environmental degradation of the surrounding landscape. In Vanbergen et al. (2014) connectance (standardized by network size) increased with environmental degradation, but the authors did not discuss possible causes. In the three of these cases (Forup and Memmott, 2005; Forup et al., 2008; Spiesman and Inouye, 2013) either increases or decreases in connectance were attributed to variations in species richness.

Based on this information we consider that the empirical results do not allow for simple inferences about the behavior of this metrics as a result of decreased environmental quality. The variation in the observed responses indicates, as suggested for nestedness, that connectance does not have a general, simple pattern of response to the reduction of environmental quality, as already indicated by Heleno et al. (2012). It is necessary to analyze this metrics with additional information to understand the specialist or generalist character of the interactions and their influence in connectance values. Connectance is emphasized as a characteristic that confers resilience (Tylianakis et al., 2010; Gilbert, 2009) and network stability (Bastolla et al., 2009). However it may be a result of a decrease in species richness and/or increase in the generalization of the network due to losses of specialist species. Therefore it does not, necessarily, represent greater environmental quality with regard to biodiversity conservation. In addition, connectance is sensitive to differences in sample efforts (Blüthgen, 2010). Given that we consider that the metrics connectance has important limitations, and should be interpreted with attention to its sampling effect and in light of other network metrics.

3.1.4. Species degree

Species degree is the number of interactions of each network node. The species degree of a plant, for example, is given by the number of pollinators with which the plant interacts. It has been interpreted as the simplest measure of specialization (Olesen and Jordano, 2002). Degree may refer to a single species or to an average across plant species, pollinator species, or all species in the network. Five studies presented species degree.

When analyzed at single species level or a subset in the network, species degree decreased with the reduction of environmental quality in four out of the five reviewed studies. In two studies on the impact of alien plants, species degree increased in alien species and was reduced in native–native interactions (Aizen et al., 2008; Padrón et al., 2009). In those papers, the authors emphasized the usurpation of interactions by alien species, which play a central role in the network, by having greater competitive potential and causing loss of interaction by native species. In Padrón et al. (2009), the degree decreased only in pollinator species. The authors attribute this result to a statistical effect due to low richness and high heterogeneity in plant degree. In Burkle and Knight, (2012) the decrease in degree occurred in the most generalist floral visitors, which interacted with fewer plant species in smaller habitat patches, narrowing their niche amplitude. In Burkle et al. (2013) the decrease in degree was explained by a massive loss of species and interactions including specialists and generalists. In this case, over 120 years the loss of species with many interactions decreased the

network degree. On the other hand, in Nilsen and Toltand (2014), the increase in species degree with the reduction of environmental quality occurred to plants and pollinators. This study refers to a disturbance gradient ranging from old forest to young forest and clear cuts. In this case, the increase in degree with environmental degradation was due to the rise of species richness in more disturbed areas, by the addition of generalist species.

In conjunction, the changes occurred due to a loss of interactions of native species under alien invasion; to a vast loss of specialist and generalist species under a long history of degradation; and to decreases in the average diet breadth of generalist species in smaller patches. Based on these findings, a decrease in the degree of generalist floral visitors is expected in degraded areas, but with an increase in the average level of generalization or degree of species of the entire network. These results converge at the same mechanisms of change in behavior of the species and reorganization of the network under different impact conditions.

For this reason, to interpret the degree as an indicator of environmental quality, it is necessary to consider whether the degree refers to plants and/or pollinators, and at which level, species or network. It is also important to consider the asymmetry in the interactions since it will indicate if species degree differs between both sides of the interaction, with important consequences for the interaction's resilience (Ashworth et al., 2004). Species degree is a simple and useful metrics. However, by averaging species degree, important information as interactions variation and distribution within the network are hidden. Therefore, average species degree is a measure with a low potential indicator when considered alone. Despite few empirical results, species degree at species level or degree distribution could be more informative than average species degree and should be the focus of greater attention.

3.1.5. Species strength

This metrics was found under different denominations (Table 1) and we adopted the most used, species strength. Species strength of species A in species B, is defined as the proportion of interactions between A and B in relation to the total registered interactions for A (Blüthgen et al., 2008). For example, if pollinator B interacted 5 times with plant A out of 20 interactions with any plants, the plant A interaction force on the pollinator B is 0.25 (25%). Thus species strength is given by the sum of dependencies of the species with which each species interacts and measures the dependence between species. Species strength is different from interaction asymmetry, as the latter is the difference between the dependence of a plant on a given pollinator versus the dependence of this same pollinator on that particular plant. Interaction asymmetry indicates the different dependency of two interacting species, while species strength indicates the dependence that the plants in general have in some particular pollinator (see Bascompte et al., 2006).

Species strength metrics was analyzed in five papers. In three of them, species strength presented no difference. However, it increased with declining environmental quality in Nielsen and Totland (2014), and decreased in Burkle et al. (2013). In the three cases of no effect, Vilà et al. (2009) and Bartomeus et al. (2008) compared areas invaded by exotic plant species with areas that were not invaded, while Aizen et al. (2008) compared areas with different incidences of alien plant species. The absence of effects in species strength refers to interactions among pollinators and native plant species. It was observed that exotic plants played a central role in the network, interacting with the largest number of pollinators. Exotic plants also had greater interaction strength on pollinators than native plants. Nevertheless, the authors report that the number of interactions between native species was maintained.

It should be emphasized that these results did not imply an absence of impact on the pollination of native plant species, since there was usurpation of important interactions due to greater abun-

dance and generalization of the alien species (Aizen et al., 2008). The intensity and history of invasion were also relevant because it was possible that the absence of an effect on native species occurred only in the first stage of the invasion (Padrón et al., 2009; Bartomeus et al., 2008). Another important factor was the invasive species' characteristics, such as abundance of flowering, flower anatomy and phenology, which determine changes in their influence over the other species (Bartomeus et al., 2008). In this case, the apparent non-effect on species strength among native species, draws attention to the importance of addressing analysis on the network level. These could be able to identify the increased centrality of exotic species and the loss of interactions that are important for the native species.

The reduction of the interaction species strength in Burkle et al. (2013) resulted from the significant loss of species, including the most generalist over 120 years of environmental degradation. The authors argue that the extirpation of species resulted in the reorganization of the network so as to reduce the redundancy of interactions and nestedness. The increase of species strength described by Nielsen and Totland (2014) resulted from the increase of generalist interactions in the young forest.

As a general expectation, networks with species more dependent on each other may be more vulnerable to extinction cascade. On the other hand, low interaction strength between species could be indicative of network generalization by the loss of the more sensitive specialist–specialist interactions. We understand that because it indicates dependency between species, the analysis of this metrics may identify key species (network hubs), changes in species' roles in the network, and the loss of interactions. Information of this nature could direct conservation management by establishing target species and by predicting extinctions.

However, the data obtained did not have the consistency necessary to infer about the behavior of these metrics as a result of lower environmental quality. The interpretation of species strength as an indicator differs if the species affected play specialist or generalist roles in the network. Also we could not suggest the most appropriate condition or desirable values of interaction strength for biodiversity or ecological processes conservation.

3.1.6. Interaction specialization, degree of specialization or interaction selectivity at species level (d') and network-level (H_2')

The metrics d' and H_2' were proposed as representing “the degree of specialization of elements within an interaction network and of the entire network, respectively” (Blüthgen et al., 2006). The metrics d' , featuring specialization at the species level, is interpreted as the deviation of observed interaction frequencies from a null model in which all partners are used proportionally to their availability (Blüthgen et al., 2006). Complementarily, H_2' informs whether or not there exists high or low niche differentiation in the network and can be used to compare networks to describe which has more interactions between generalist or specialist species (Blüthgen et al., 2006). These metrics have been described as mathematically independent from the total frequency of observations due to standardization based on these totals. This feature avoids the influence of network size and sampling efforts, presented as connectance and nestedness (Blüthgen et al., 2006; Blüthgen, 2010).

The metrics d' (species level) declined in the three reviewed studies in which this metrics was calculated. Amongst the four studies analyzed, which calculated H_2' (network level), this metrics declined in two studies and did not change in two studies. In Weiner et al. (2014), in which H_2' did not change, the results for the degree of specialization at species level (d') varied with environmental quality.

The data indicated that H_2' , and more consistently, d' decreased as a result of different impacts. The main possible causes of this

decline suggested by the articles' authors were the decreased diversity of species; increased abundance of exotic plants (Marrero et al., 2014); reduced abundance of specialized plant–pollinator interactions (Grass et al., 2013); loss of specialist species; increased of generalist species (Burkle and Knight, 2012; Weiner et al., 2014); and loss of pollinator specialized in plant sensitive to environmental changes (Weiner et al., 2014).

Some authors have been interpreting the metrics H_2' as a measure of interaction selectivity rather than interaction specialization (e.g. Burkle and Knight, 2012). This is important, because for clear interpretation of H_2' metrics, it worth to be aware of two meanings that the word specialization encompasses. Among other ways a species can perform specialist interactions in all situations it exists because of evolutionary morphological or behavioral constraints (Ferry-Graham et al., 2002). Moreover, a species can change the number of interacting partners (diet breadth) in different environmental conditions, as a result of changes in its own and in its possible partners' abundance (Kunin, 1996; Fort et al., 2016). Those different interpretations of the metrics brings to our attention the importance of understanding why H_2' is changing, because the system is losing species that are always specialist or because species behaving as specialist at that situation are being lost or becoming more generalist. The reviewed articles did no distinguished between those cases, and we suggest that future studies try to separate those effects in H_2' interpretation because they can have different meanings as indicators.

This metrics' behavior in response to lessening environmental quality, and its avoidance of sampling and network size effects were features that make this metrics an important indicator of changes in the network. Another important feature was its possibility to identify specialization in both sides of the interaction. Included in the analysis was the interaction asymmetry, identifying different impacts of changes on plants and on pollinators. Information of this nature could be useful in management actions leading to decisions in which conservation measures may be more effective in maintaining functional redundancy in ecosystems, and regarded as being capable of increasing the assembly resilience (Weiner et al., 2014).

3.1.7. Species identity and their role in the networks

Interaction network approach is expected to offer more information than only species composition lists, a more traditional indicator of environmental impact. Network analysis is an advance, because species composition of plant-pollinator systems presents intrinsic spatial and temporal variation (Alarcón et al., 2008; Petanidou et al., 2008). It has been shown that the abundance of each species tends to be less stable over time than the overall abundance of the community or its functional groups (Blüthgen et al., 2016). However, land use intensity tends to affect the stability of entire communities over time, more intensely in higher trophic levels (Blüthgen et al., 2016).

In the reviewed studies, changes in the identity of interacting plants or pollinators were not as discussed as the network metrics. However it changed in a more consistent manner than any metrics. We found seven papers in which it was possible to analyze environmental changes effects on species composition. All of which evidenced changes in the composition of pollinator species interpreted by their authors as associated to changes in environmental quality.

Increases were observed in the abundance of some groups of species, while others had their number reduced. In two of these studies, changes occurred even when species diversity indices (Weiner et al., 2014) and the network topology did not change (Nielsen and Toltand, 2014). The increase in abundance of some pollinator groups may conceal the loss of other groups in analysis that take into account only the network structure metrics. On the other hand, analysis taking into account only species diversity

would not be sufficient to represent critical changes in communities and ecosystems processes (Blüthgen et al., 2016).

Some studies advocated that species composition should be complementary to analyzes of network structure (Tylianakis et al., 2010; Geslin et al., 2013; Kaiser-Bunbury et al., 2010). We agree with them because metrics such as degree of specialization, interaction specialization, interaction asymmetry and strength of interaction are better interpreted in the light of possible drivers at the level of species or species groups. In addition, changes in species composition allow for the identification of unapparent impacts when the focus is only on topology. Network structure's robustness to changes in its species composition or species role would conceal these impacts (Nielsen and Toltand, 2014). Another important factor is the possibility to understand the influence of species' characteristics in network topology in order to identify which metrics may be more representative of changes at species level. Species identity is therefore an important variable, able to indicate which groups can be benefited or harmed by anthropic impacts.

Similarly to composition, changes were observed in the role of species in four papers in which it was possible to make this analysis. However, only one paper had made a systematic analysis, classifying seven types of interaction, ranging from specialists to super generalist (Nielsen and Toltand, 2014). The conclusion of this paper was that changes occur in the role of species because they can become more or less generalist. These changes could be seen in different studies under diverse denominations. Aizen et al. (2012) wrote about "decreasing frequency and degree of generalization of many of the most ubiquitous interactions", Burkle and Knight, (2012) referred to the "decreased diet breadth" of generalist species in smaller areas. Burkle et al. (2013) mentioned "decreased fidelity" in the plant-pollinator relationship and increases in interactions by more specialist species.

Intrinsic temporal variation in species composition and their role in the network have been empirically evidenced as part of the system, conferring higher robustness and resilience to plant-pollinator interactions (Alarcón et al., 2008; Petanidou et al., 2008). Four studies attributed part of the variation in species role to the differences in environmental quality rather than to intrinsic temporal fluctuations. Despite the short duration of most studies, spatial replication is expected to represent some of this within-treatment intrinsic variation. However, the spatially correlated temporal variation due to climate should be addressed in long term studies.

Changes in species roles in the network seem to be related not only to the characteristics of pollinator or plant species, but are also an emergent property of the established interactions. Those interactions went beyond morphological compatibility and pairwise relationships (Herrera, 1987). Foraging behavioral decisions based on energetic gain and cost resulted from the evolutionary history of species, historical formation of the assemblies, abundance of resources, competition and physical factors such as microclimate variations and landscape connectivity (Rathcke, 1983; Feinsinger, 1987; Kunin, 1996; Cranmer et al., 2012). Changes in the role of species allow for network reorganization, conferring greater resilience. On the other hand, the less redundant reciprocal interactions between specialists become more vulnerable to environmental changes. Therefore, changes in the role and composition of species, when analyzed from the perspective of networks, could allow for the identification of the groups and interactions that are most affected by environmental degradation, providing a combined analysis of threats to biodiversity and ecosystem processes. Despite few empirical studies addressing species' roles changes in plant-pollinator networks it seems to have potential indicating environmental quality or at least to explaining patterns in network structure, and deserves more attention.

3.2. Metrics and the resilience of the undesirable state

Metrics expected to indicate greater resilience such as interaction asymmetry, nestedness and connectance presented, in some studies, higher values in areas with worse environmental quality (Table 2). This result indicates an apparent contradiction, because or those metrics do not indicate greater resilience, or worse quality areas are more resilient than better quality ones. The possible causes attributed to observed trends on those metrics indicated that the network may be more resilient in worse areas. However, in all cases, changes in those metrics were attributed to simplifications of network structure (Table 2).

Resilience could be defined as “magnitude of disturbance that can be tolerated before a system moves into a different region of state space and a different set of controls” (Carpenter et al., 2001). In

addition, alternate stable states are possible and the management effort aims at increase the resilience of the desirable stable state and to reduce the resilience of the undesirable ones (Carpenter et al., 2001). What seemed to happen in most of the environmental gradients reviewed is an increased in the resilience of the simpler state, with less species and interactions, undesirable for biodiversity and function conservation. Therefore, as in other applications (Newton, 2016), in plant–pollinator network approaches we should not consider the increase the values of metrics which indicate resilience as our conservation goals. It is important to define clearly the concept of resilience and the desirable stable state of the system (Carpenter et al., 2001; Newton, 2016).

In order to interpret those apparent contradictions most of the studies discussed the possible causes of metrics behavior by accessing the observed changes at species levels, based on specialist or

Table 2
Summary of the effects of metrics related to reduction in environmental quality, their respective causes and our expectations about the consequences to the resilience and biodiversity conservation of the system based on the studies' results. The expected effect in the resilience is sometimes achieved by a change in the state of the system, generally by its simplification.

Metrics	Behavior related to disturbance	Possible causes of observed behavior	Resilience	Biodiversity Conservation
Interaction Asymmetry	Increased	Loss of specialist–specialist interactions	Increased in a simplified state	Decreased
Species strength	Decreased	Significant loss of species	Increased generalism by simplification	Decreased
	Increased	Increase of generalist interactions due to the addition of generalist species	Increased resilience	Increased
	No effect	Characteristics of the invasive species, network analysis method, unknown invasion intensity	Unknown	Unknown
H ₂ ' degree of specialization network-level	Decreased	Loss of specialist	Increased resilience of a simplified state	Decreased
d' degree of specialization species level	Decreased	Reduced the abundance of specialized plant–pollinator interactions, loss of specialist species; increase of generalist; loss of pollinator specialized in plant sensitive to environmental changes	Unknown	Decreased
Species composition	Modified	Increase of abundance of some groups of species and reduction of others; loss or addition of specie.	Increased resilience of a simplified state	Decreased
Species roles	Modified	Reorganization of interactions in the network. Species became more or less generalist.	Increased resilience of a simplified state	Unknown
Nestedness	Decreased	Loss of species and interactions, or decreases in niche amplitude	Decreased resilience of both more complex or simplified state	Decreased
	No effect	High robustness of this metrics due to a reorganization of interactions; compensations of lost interactions by increases in species richness and abundance, especially of generalist species	Maintenance of resilience of a more complex state because of addition of species, including exotic generalists.	Decreased
Connectance	Increased	Centralization of interactions by alien species and loss of native interactions	Increased resilience of a simplified state	Decreased
	Decreased	Increased species richness	Decreased resilience of a more complex state	Increased
	No effect	High robustness of this metrics due to a reorganization of interactions; compensations of lost interactions due to increases in species richness and/or abundance, especially of generalist species; network analysis method, unknown invasion intensity.	Maintenance of resilience of a more complex state because of addition of species, including exotic generalists.	Unknown
Species degree	Increased	Decrease in species richness and abundance.	Increased resilience of a simplified state.	Decreased
	Decreased	Loss of interactions of native species under alien invasion; massive loss of specialist and generalist species; decreases in the average diet breadth of generalist species	Decreased resilience	Decreased
	Increased	Increases in species richness of generalist exotic species and loss of interactions among native species	Increased resilience in a simplified state	Decreased

generalist grouping of species or interactions. The complementary information at species level and the integrated analysis of network size, interaction asymmetry, H_2' , plus the changes in species compositions and their roles in the interaction are necessary to choose the better stable state to conserve.

4. Conclusion

The elaboration of this review highlighted some challenges in finding general patterns from specific studies on plant-pollinator interaction networks. Sometimes it was difficult to know exactly which metrics were calculated and discussed. If paper's focus was not on the metrics' behavior and they were not directly presented in the paper and supplements, it was necessary to understand the metrics' behavior through the authors' interpretation. The scarce empirical data available is recent and variable, both in the impact category studied as much as in the metrics evaluated. These factors hinder comparisons and conclusions about a given metrics for use as an indicator of changes in the network as a result of habitat degradation. In this review, we analyzed each metrics grouping for the different impact categories. The network response may differ among impact categories, but there is not yet enough data to detect those possible differences. For that reason we did not directly address this question. We also could not address the question whether plant-pollinator networks composed by fewer species (lower sized) would respond differently to environmental quality changes than those with larger sizes. The establishment of databases considering the interactions and their frequencies will allow for a more standardized analysis and for more informative conclusions regarding the use of network metrics as indicators of environmental quality.

High temporal and spatial variation is known for some plant-pollinator assemblages. That intrinsic variation may change network structure and metrics, making it necessary to understand the magnitude of intrinsic variation to attribute a particular effect to environmental quality. Well designed replicated studies allow for estimating such effects separately. However, spatially synchronic effects such as responses to climatic variation need long term studies to be understood.

There is now an expectation that the basic structure of the network would be relatively robust to environmental changes (Nilsen and Totland, 2014; Padrón et al., 2009). The available data indicates that the network tends to reorganize towards a simpler stable form, maintaining the system basic functioning, but with losses of biodiversity. In 74% of the cases evaluated in this review (37 of 50 results of the network metrics in Table 1), it was possible to identify variations in structural metrics under different conditions of environmental quality. Discounting possible publication bias, it seems that network structure is not as robust as expected. It is important, in this discussion, to identify the magnitude of change accepted by the predictions of robustness. In cases of environmental degradation, for instance, plant-pollinator interaction networks may still be more nested than random networks, but nestedness may vary compared to reference areas with better environmental quality.

The usage of network metrics as indicators requires predictable responses to changes in environmental quality. The available empirical data indicated that species degree, nestedness and connectance did not have a simple, linear or unidirectional response to habitat degradation. Conversely, the metrics interaction asymmetry, d' (reciprocal specialization index of the species) showed the most consistent responses to environmental change. The role of the species changed, ranging between generalists and specialists under different conditions. In addition, specialist species with morphological and behavioral constraints were lost in worse environmental quality. Those changes in diet breadth and local extinctions changed

the values of those metrics. The identity of interacting species and their role in the network with a further specification of groups and interactions most affected are the properties with greater potential to indicate changes of environmental quality. Most of the available studies focused on metrics at the network level, but several studies and this review indicate that the patterns at the network level can be better understood in the light of metrics analyzed at the species level.

Our results provide information that enriches the network analysis, highlighting the need to consider important features that are often neglected. Discussions and information compiled here are important in deciding how to look at empirical data and what to look for, as well as to indicate some caveats when interpreting data on plant-pollinator interactions with a complex network approach. Network metrics can be good indicators of environmental quality if the underlying ecological causes of the numerical changes were carefully analyzed.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2017.03.037>.

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