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What do we know about the effects of landscape changes on plant–pollinator interaction networks?

Patrícia Alves Ferreira[a,1], Danilo Boscolo[b,*], Blandina Felipe Viana[a,1]

[a] Federal University of Bahia – UFBA, Biology Institute, Rua Barão de Geremoabo s/n, 40170-210 Salvador, BA, Brazil
[b] Federal University of São Paulo – UNIFESP, Rua Prof. Arthur Riedel, 275 – Jd. Eldorado, 09972-270 Diadema, SP, Brazil

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ABSTRACT

Biotic interactions play an important role on the organization and persistence of biodiversity. Unnatural modifications of landscape structure such as habitat loss and fragmentation can isolate populations and disrupt biological communities, affecting species survival and altering the complex set of relationships between plants and pollinators. Plant–pollinator interaction networks have characteristics such asymmetry and nestedness that may influence the stability and robustness of networks to landscape changes. Species in mutualistic networks might respond to landscape modifications with a sudden collapse at critical habitat destruction thresholds. In this work we review general trends in the scientific literature related to the effects of landscape changes on plant–pollinator networks. For this, a survey in Scopus and Web of Knowledge databases was conducted in May 2011 using all seven possible combinations of the terms “pollinat*” with the terms “landscape”, “habitat loss” and “network”. We found 155 papers and 92% of those showed significant effects of landscape changes on pollinator diversity and plant reproductive success. Approximately 50% of all analyzed papers showed effects of agriculture intensification as a result of increases in the conversion of natural areas into agricultural crops on plant–pollinator interactions. Landscape modifications affected cross-pollination and the sexual reproduction of plants largely because of reduced diversity and availability of pollinators due to increased habitat isolation and reduction of floral resources and nesting areas in the remaining available habitat. An integrated approach concerning the effects of modified landscapes on natural ecosystems regarding how these variations can affect the stability and robustness of pollination networks can be extremely useful for conservation of plant–pollinators interactions, with positive overall consequences for conservation of plant, pollinators and pollination services in natural and agricultural ecosystems.

1. Introduction

Biodiversity is more than a collection of species. Networks of biotic interactions involving predation, parasitism and pollination play an important role on the organization and persistence of biodiversity (Fortuna and Bascompte, 2006; Bascompte, 2009). In addition, biotic interactions may affect the resilience of ecosystems to landscape modifications (Montoya, 2008). Because of that, studies including information on ecological networks often allow a better assessment of the possible effects of habitat changes on biodiversity loss (Forup and Memmott, 2005; Montoya, 2008; Sabatino et al., 2010). These studies have great potential to assist in the conservation of biodiversity (Jongman, 2004).

Plant–pollinator networks consist of a special type of ecological network with specific characteristics, such as asymmetry of interactions, with specialist species frequently interacting with generalists and nestedness (Bascompte, 2009). These networks structural attributes may influence the stability and robustness of interactions and network responses to changes (Bascompte et al., 2003). Nestedness and asymmetry generate cohesive network cores which may help withstand species loss, since the most linked species play a central role in the network stability (Bascompte et al., 2003; Bascompte, 2009). For that reason plant–pollinator networks could be more resistant to negative effects of landscape changes (Ramos-Jiliberto et al., 2009; Olesen and Jordano, 2002; Memmott et al., 2004, 2005; Petanidou et al., 2008; Vilà et al., 2009). Species in mutualistic networks might also respond to landscape modifications with a sudden collapse at critical habitat destruction thresholds (Fortuna and Bascompte, 2006). Kaiser-Bunbury et al. (2010) showed that there must be a strong impact

* Corresponding author. Tel.: +55 11 33193300; fax: +55 11 40436428.
E-mail addresses: patybio13@yahoo.com.br (P.A. Ferreira), danilo.boscolo@unifesp.br, danilo.boscolo@gmail.com (D. Boscolo), blandefv@ufba.br (B.F. Viana).
[1] Tel.: +55 71 3283 6554; fax: +55 71 3283 6513.

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on networks stability when more than half of the most connected species is lost and most network cores can no longer be supported. At these critical values the extinction of pollinators may abruptly increase, leading to the disruption and collapse of plant–pollinator interactions (Viana et al., 2012).

Landscape changes caused by habitat loss and fragmentation have become a central issue in conservation biology (Haila, 2002; Fischer and Lindenmayer, 2007). Decreasing habitat availability at the landscape level can isolate populations and disrupt the structure of biological communities, directly affecting species survival and interactions. These processes can alter the complex set of relationships between plants and pollinators (Fortuna and Bascompte, 2006), promoting higher rates of plant self-fertilization and consequent inbreeding depression due to reduced success of animal driven cross-pollination (Lennartsson, 2002). This can lead to important changes in both presence and relative abundance of different reproductive traits of plant species, resulting in reduced functional diversity of plant communities in natural areas (Girão et al., 2007).

In this paper we aimed to search for general trends in the scientific literature dealing with the effects of landscape changes, including habitat loss and fragmentation on plant–pollinator interactions. We asked what is known about the effects of landscape changes on plant–pollinator interaction networks and inquired how agriculture intensification with increased conversion of natural areas into crops can affect plant–pollinator interactions. Overall, we want to understand if there is enough knowledge available to efficiently design plant–pollinator friendly landscapes with positive effects for the conservation and management of plants, pollinators and pollination services in changed habitats.

2. Procedures

We conducted a survey of the scientific literature in May 2011 using all seven possible combinations of the terms "pollinat*", "landscape", "habitat loss" and "network" in the Web of Science and Scopus databases. From the search results we selected all articles which dealt with the effects of landscape modifications on pollinators, plants and/or pollination. We did not include in the analysis papers that exclusively evaluated the responses of plant–pollinator networks without any explicit mention to the effects of landscape change. We performed exploratory analyses to identify general patterns in the scientific literature regarding the effects of habitat modification on plant–pollinator interactions. In cases where the same study measured more than one variable, we considered all response variables separately.

Many studies analyzed in the present review used some terms without an explicit or specific definition, what could make proper interpretations difficult. Definition of concepts and their standardization is also an important step when surveying scientific knowledge for environmental management purposes as attributing the effect of a certain term to a similar but essentially different factor can make it difficult to understand the available information and may lead to wrong conclusions. Therefore, to avoid the drawbacks derived from conceptual problems, we standardized all technical terminology related to landscape ecology in accordance with Metzger (2001) and Fahrig (2003), as suggested by Viana et al. (2012), and normalized papers analyzed according to the categories previously defined (Table 1).

3. Overview

We found 155 papers that evaluated directly or indirectly, explicitly or implicitly, the effects of landscape modifications on plant–pollinator interactions. Overall, 92% (143 papers) showed significant effects of landscape changes on the diversity, frequency and movement patterns of pollinators and/or on the diversity, reproductive systems, reproductive success and productivity of plants. Most effects were relative to changes of the spatial distribution of landscape elements (65%). About one quarter of the analyzed papers reported effects of landscape composition, specially the proportion of land covered by different types of environments (Supplementary material 1).

One of the most frequently observed patterns was that pollinators diversity is affected by habitat loss and fragmentation (Liow et al., 2001; Darvill et al., 2006; Nates-parra et al., 2008; Winfree et al., 2009; Quintero et al., 2010), mostly due to increased isolation of habitat patches (Greenleaf and Kremen, 2006; Brosi et al., 2007; Zurbuchen et al., 2010) and also because of reduced landscape complexity caused by environmental simplification (Steffan-Dewenter et al., 2001; Bartomeus et al., 2010; Hoehn et al., 2010; Holzschuh et al., 2010). From the pollinators point of view, loss of landscape complexity usually lead to the reduction of floral resources and nesting areas in the remaining available habitat patches, impairing population survival and reducing their overall diversity (Potts et al., 2003; Klein et al., 2004; Brosi et al., 2008; Jha and Vandermeer, 2009; Goulson et al., 2010). Reduced diversity was observed mainly for bees (Ahrne et al., 2009; Jauker et al., 2009; Hoehn et al., 2010; Quintero et al., 2010), the worldwide most important pollinators (Roubik, 1995), but also for other pollinator groups such as birds (Breitbach et al., 2010) and bats (Quesada et al., 2003, 2004; MacSwiney et al., 2007; Willig et al., 2007).

Landscape modifications also affected cross-pollination and the sexual reproduction of plants largely due to reduced diversity and availability of pollinators (Parra-Tabla et al., 2000; Dick et al., 2003; Aguilar et al., 2006). Reduced plant population density and number of pollen donors available in landscapes may also cause disruption of pollination processes (Fuchs et al., 2003; Uchiyama et al., 2009), which changes the selection pressures of floral traits, modifying the set of reproductive strategies of whole plant communities (Lopes et al., 2009). Plant population density changes may have deep effects on the amount (Fuchs et al., 2003) and quality of plant progeny (Cascante et al., 2002; Lennartsson, 2002; Lowe et al., 2005; Eckert et al., 2009).

We also found that 77 studies (approximately 50% of all 155 analyzed papers) showed effects of landscape changes caused by agriculture intensification on plant–pollinator interactions as a result of increased conversion of natural areas to agricultural crops (Kremen et al., 2007; Steffan-Dewenter and Westphal, 2008). Approximately 75% of these studies advocated that landscape changes affects the diversity, movement and frequency of pollinators, and 36% the diversity, reproductive systems, reproductive success, resources and productivity of plants.

Nevertheless we found only one paper explicitly assessing the effects of landscape changes from the perspective of complex networks of plant–pollinator interactions. Hagen and Kraemer (2010) observed significant structural differences of plants and floral visitors networks in structurally diverse landscape mosaic within forest, forest edge and farmlands in Kenya.

Overall, in our review we noted that most available studies focused mainly on the effects of landscape modifications on pollinator diversity and/or plant reproductive success. Nevertheless, there are some studies which indicate that nested and asymmetric mutualistic networks tend to be reasonably robust and resilient to most landscape changes (Olesen and Jordano, 2002; Memmott et al., 2004, 2005; Petanidou et al., 2008; Ramos-Jiliberto et al., 2009; Vilà et al., 2009). Theoretical, empirical or manipulative studies about mutualistic networks answers to landscape changes could reveal important information for the maintenance of these networks, and specifically of plant–pollinator interaction networks under modified environments.

Table 1
List of categories used for organizing and analyzing the selected papers found in May 2011 using all seven possible combinations of the terms "pollinat*" with the terms "landscape", "habitat loss" and "network" on Web of Science and Scopus.

Variables	Categories	Descriptions
Year		
Authors		
Journal		
Study location		
Climatic region	Tropical Subtropical Temperate	
Ecosystem	Agriculture Forest Savanna Desert Agro-forestry Urban	
Matrix	Agriculture Natural Savanna Forest Agro-forestry Urban Mix	
Landscape	Agriculture Natural Savanna Agro-forestry Mix Urban	
Study type	Empirical Revision Meta-analyze Modeling Theoretical	
Methods	Descriptive Observational Experimental Literature survey Modeling Meta-analyze	
Objectives	Descriptive Establish relations Explicative Modeling Review	
Approach level	Landscape Patches Buffer	
Sample unity	Individuals Population Community	
Study object	Plant Pollinator Interaction	
Dependent variables	Plants diversity	Plants richness and abundances
	Plants reproductive systems	Plants reproductive traits as self compatibility
	Plants reproductive success	Fruit and seed set
	Plants productivity	Crops production
	Floral resources	Nectar and pollen available in the system
	Pollinators diversity	Pollinators richness and abundances
	Pollinator's visits frequency	
	Pollinators movements	
Independent variables	Patches area	
	Patches isolation	
	Landscape composition	How landscape elements are spatially distributed
	Landscape configuration	Which are the landscape elements available
	Matrix	
	Edge	
	Floral resources	
Variables relationship	Positive Negative Unrelated Differences No differences	

We found several indications that landscape modifications affect plant–pollinator interactions by reducing the abundance and diversity of pollinators (Steffan-Dewenter and Tscharntke, 1999; Kremen et al., 2002; Chacoff and Aizen, 2006; Fujimori et al., 2006), which leads to lower seed production (Brudvig et al., 2009; Nazareno and Carvalho, 2009; Lander et al., 2010; Vesk et al., 2010). Deforestation can also affect plant reproductive processes by changing the foraging behavior of pollinators and consequently the quality of plant gene flow (Ghazoul and McLeish, 2001). In general the diversity of floral visitors and the frequency of observed visits decreased with increasing the distance to natural habitats (Chacoff and Aizen, 2006). The richness and abundance of flying floral visitors, for example, dropped more than 80% over a distance of 500 m from natural habitat in tropical and subtropical agro-forestry systems (Carvalheiro et al., 2010). Additionally, bees usual foraging distances, which depend on maximum efficiency foraging strategies, are smaller than their maximum measured flight distance, indicating that nearby areas can function as key habitat structures to preserve bee populations (Zurbuchen et al., 2010).

Trees with limited distribution and reduced genetic variation were more likely to go extinct in the face of landscape changes (Hamrick, 2004). Seed production may be affected by reduced amount of pollen transfer between flowers (Schmucki and Blois, 2009), but plants which can produce fruits by self-fertilization are usually favored in landscapes where plant individuals are isolated and pollinators and pollen flow is reduced or improbable (Pinto-Torres and Koptur, 2009). Composition of plant communities in landscapes, which have experienced severe fragmentation can be modified in favor of species pollinated and dispersed mainly by passive processes such as wind pollination and with detriment of species that are pollinated and dispersed by animals (Regal, 1982; Ghazoul and Shaanker, 2004).

A stochastic individual-based simulation model developed by Keitt (2009) suggests that as landscapes are changed and native habitat is removed, plant–pollinator systems tend to be altered and even small disturbances may cause plant–pollinator interactions collapse within the remaining habitat patches in fragmented landscapes. Keitt (2009) suggested that extinction thresholds for plant–pollinator interaction systems may occur at about 50–60% of habitat loss, when pollinators and plants generalist species start to disappear from communities. But not only habitat loss can cause the disruption of pollination interaction networks. According to the model developed by Kaiser-Bunbury et al. (2010), there must be a strong impact on networks stability when more than half of the most connected species is lost, which causes a sudden and rapid collapse of the total strength of the networks. These complementary results indicate that there is a pungent need to set which are the critical values of habitat loss that can increase pollinators' extinction up to the point where natural plant–pollinator interaction networks may collapse (Viana et al., 2012). However, strictly defined values may not really exist, with each case being unique. Also, empirical field studies concerning ecological networks often lack replication and these different responses associated with plants and pollinators make their results difficult to be understood (Dupont et al., 2009). In addition, both sides of the mutualistic interaction must be assessed in order to properly predict pollinators' extinction chances and plant reproductive vulnerability to landscape changes (Ashworth et al., 2004).

Moreover, studies about habitat fragmentation which focused solely on the differences of biodiversity patterns of non-fragmented versus fragmented landscapes are generally inadequate to represent the gradual effects of habitat changes. Nevertheless, this approach is still the more frequently used in empirical fragmentation studies (Ewers and Didham, 2006). On the other hand, simulations based on real landscapes and species with distinct life histories have been useful to increase our comprehension about the relationships between landscape dynamics and biodiversity (Burel et al., 1998). Approaches that take into account continuous measures of landscape changes along gradients of habitat degradation could be more thoroughly used to evaluate the effects of gradual habitat modifications on plant–pollinator interactions.

Agriculture intensification and conversion of natural to urban environments also changes natural habitats features, affecting plant and pollinators diversity (Ahrne et al., 2009; Frankie et al., 2009; Bommarco et al., 2011), pollinators community composition (Carre et al., 2009), pollinators floral visits behavior (Ricketts et al., 2008) and may influence plant reproductive success (Priess et al., 2007; Kim et al., 2006). Additionally, conventional agricultural management which uses large crop areas, insecticides, herbicides and exotic pollinators may also negatively influence local plant–pollinator interaction networks because of environmental simplification and resources reduction for pollinators, consequently lessening the availability of pollinators for plants (Klein et al., 2007; Jha and Vandermeer, 2010). These changes may have important implications for pollination processes, with important effects even for crop production (Richards, 2001), as pollinators are important for more than 75% of the world's most important agricultural plants species (Klein et al., 2007).

The value of ecosystem services promoted by standing forest patches for agriculture and other human-made systems is still little known. Ricketts et al. (2004), however, estimated that the actual costs of reduced pollination services are probably higher than previously expected. Spatially explicit land use change simulations clearly indicate that most of the ecological and economic values of natural habitats can potentially be saved over the coming decades if the remaining patches are preserved within agricultural landscapes (Priess et al., 2007). An approach which integrates agricultural areas, natural habitats and planned urban ecosystems may improve pollination services efficiency in these ecosystems. The maintenance of natural habitats surrounding agricultural areas may improve pollination services in the crops while the conservation of native pollinators may also be important for pollination of wild plants species. (Goulson et al., 2008; Hannon and Sisk, 2009; Hennig and Ghazoul, 2011).

Alternative management practices, such as organic farming (Andersson et al., 2012), and urban gardens (Ahrne et al., 2009) had positive effects on pollinator diversity at different landscape scales (Gabriel et al., 2010; Jha and Vandermeer, 2010; Van Rossum, 2010). However, Winfree et al. (2008) pointed out that the heterogeneity of habitats surrounding crops could be more important than the farm management system for maintaining the diversity of native bees. For example, the resource mass production offered by some crops can also promote the maintenance of pollinating bee species (Walther-Hellwig and Frankl, 2000). The proximity of natural areas to crops can facilitate pollination due to the higher diversity of pollinators in natural habitats, where they can find proper nesting sites and appropriate supplementary resources in times of scarcity (Ricketts, 2004; Klein, 2009; Lonsdorf et al., 2009; Tscharntke et al., 2011), allowing high seed-set and more stable reproductive success of both native and cultivated plants (Dick et al., 2003; Greenleaf and Kremen, 2006). Landscape heterogeneity and connectivity can also increase pollinator diversity and plant reproductive success (Van Rossum, 2010). Proximity of natural habitats, green areas in urban landscapes, proper environmental management and pollinator-friendly landscape arrangements can promote the conservation of pollination services in natural, urban and agricultural systems (Marshall and Moonen, 2002; Zhang et al., 2007; Klein et al., 2008; Ricketts et al., 2008; Brudvig et al., 2009; Keitt, 2009; Brittain et al., 2010; Jha and Vandermeer, 2010; Van Rossum, 2010; Hennig and Ghazoul, 2011; Viana et al., 2012).

4. Conclusions

Deforestation can affect the reproductive processes of plants by causing changes in the abundance and foraging behavior of pollinators and, consequently, the quality and quantity of plant gene flow (Ghazoul and McLeish, 2001). The maintenance of heterogeneous landscapes can increase local and regional biodiversity and possibly maintain ecosystem services (Morreale and Sullivan, 2010). The consolidation of knowledge concerning ecological processes such as pollination at the landscape level are of extreme importance for the management of natural areas with the aim of conserving ecosystem services (Tscharntke and Brandl, 2004; Nazareno and Carvalho, 2009; Olschewski et al., 2010). Overall, the papers we analyzed showed that it is possible to consider the creation of landscape designs which could maintain pollinators diversity (Priess et al., 2007; Goulson et al., 2008; Hannon and Sisk, 2009; Jauker et al., 2009; Hennig and Ghazoul, 2011), as well as plants and pollination services. However, we found only one paper (Hagen and Kraemer, 2010) which empirically analyzed the effects of landscape changes on plant–pollinator networks. Remaining papers studied the effects of landscape changes on pollinator diversity and/or the reproductive success of plants without directly assessing its consequences to the stability of pollination networks. This indicates that there still exist a profound need to increase scientific efforts on the study of landscape changes consequences on plant–pollinators networks structures and stability. An integrated approach concerning the study of the effects of modified landscapes on natural ecosystems and how these variations can affect the stability and robustness of pollination networks may be extremely useful for conservation of plant–pollinators interactions, with positive overall consequences for conservation of plant, pollinators and pollination services in natural and agricultural ecosystems. We believe that studies of interaction networks on landscapes perspective may provide important information and understanding of the best strategies for plant, pollinators and pollination conservation.

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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.2012.07.025.

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