HOW WELL DO WE UNDERSTAND LANDSCAPE EFFECTS ON POLLINATORS AND POLLINATION SERVICES?

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Abstract— Many studies in the past decade, mostly in temperate countries, have documented the effects of habitat loss and fragmentation on species richness, composition, and abundance and the behaviour of pollinators. Changes in landscape structure are considered to be the primary causes of the limitation of pollination services in agricultural systems. Here, we review evidence of general patterns as well as gaps in knowledge that could be used to support the development of policies for pollinator conservation and the restoration of degraded landscapes. Our results indicate a recent increase in the number of studies on the relationships between pollination processes and landscape patterns, with some key trends already being established. Many authors indicate, for example, that the spatial organization of a landscape has a great influence on the survival and dispersal capacity of many pollinators, as spatial organization affects resource availability and determines the functional connectivity of the landscape. Additionally, the shape, size and spatial arrangement of the patches of each type of natural environment, as well as the occurrence of different types of land use, can create sites with different degrees of connectivity or even barriers to movement between patches, which can deeply modify pollinator flows through the landscape and consequently the success of cross-pollination. However, there are still some gaps, such as in the knowledge of which critical values of habitat loss can lead to drastic increases in pollinator extinction rates, information that is needed to evaluate at what point plant-pollinator interactions may collapse. We also need to concentrate research effort on improving a landscape's capacity to facilitate pollinator flow (connectivity) between crops and nesting/foraging areas.

Keywords: Pollinator-friendly landscapes, conservation, land management, matrix, land use, agricultural systems, pollinator crisis.

INTRODUCTION

The past decade has seen a worldwide concern over pollinator decline (see COP 5 CBD section II decision v/5). This concern has sparked a remarkable increase in studies that identify threats to pollinators and quantify the impact of pollinator decline on pollination services in natural and agricultural systems. Most studies point to landscape changes resulting from intensive land use and leading to habitat loss and fragmentation as one of the primary threats to pollination services (Kremen et al. 2002; Steffan-Dewenter & Westphal 2008; Winfree et al. 2009). There is evidence that several crops are directly affected by changes in landscape structure, resulting in productivity loss that endangers both biodiversity and the stability of food production in the world (Steffan-Dewenter et al. 2005; Tscharntke et al. 2005; Chacoff & Aizen 2006, Carvalheiro et al. 2010; Isaacs & Kirk 2010).

Recent reviews indicate that pollinator loss in agroecosystems is faster in the tropics than in temperate regions. According to Aizen et al. (2009), agriculture has become more pollinator-dependent over time, and this trend is more pronounced in the developing world, which comprises almost all tropical regions, than the developed world. They propose that a shortage of pollinators will intensify the demand for agricultural land, a trend that will also be more pronounced in the developing world. Thus, the increases in total cultivated area needed to compensate for pollination deficits would be smaller in developed countries and larger in other parts of the world. This difference suggests a future increase in land conflicts in the tropics as well as the acceleration of deforestation processes and intensification of human pressure on natural tropical vegetation remnants, which has important practical consequences such as increased species loss and the subsequent deterioration of plant-pollinator networks, thus further weakening pollination services (Carvalheiro et al. 2011, Garibaldi et al. 2011). In this context, there is an acute need to quickly identify and overcome knowledge gaps regarding the interplay between landscape patterns and pollination processes and to directly apply new knowledge to the management of productive and sustainable landscapes.

Previous reviews and meta-analyses of pollination deficit focused on particularly relevant questions: i) the importance of changes in the abundance of foraging plants to bee

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conservation (Carvell et al. 2006, based on 14 datasets); ii) the effect of habitat fragmentation on plant reproduction (Aguillar et al. 2006, based on 54 studies); and iii) the relationship between the distance from natural or semi-natural habitats and pollination service (Ricketts et al. 2008, based on 23 studies).

Our present review is based on 219 studies, 166 of which specifically address effects on pollinators, including a broad range of questions about plant-pollinator interactions from an ecological landscape perspective. This survey was then summarized into a scientometric analysis that enabled the quantitative and qualitative evaluation of temporal trends in the knowledge produced in this research area beginning when this subject first appeared in the literature. Thus, our study presents the results of a broad literature review of the effects of landscape changes on pollinators and pollination services. Through this review, we sought to identify underlying patterns and gaps in knowledge as well as to help with the development of guidelines for research and conservation that could support new policies at the landscape level to minimize pollination deficits in areas degraded by intensive land use.

First, we present a brief description of the methods used for the literature review and data analysis. Next, we discuss the conceptual problems identified in the publications reviewed, which were related to landscape ecology, and the terminology standardization used in our study. Then, we present the most important general patterns observed and our primary findings. Finally, we note gaps in the existing knowledge that must be addressed by research programs aimed at meeting the demands for conservation and sustainable management of pollinators at the landscape level.

MATERIAL AND METHODS

Database

The survey was carried out in late July 2011 in the Web of Science - Science Citation Index Expanded (http://portal.isiknowledge.com/), using the combination of the keywords 'Landscape AND Pollinat*'. The search was made with the filter 'topic' that searches for words defined in the title, keywords and in the body of the text. At a preliminary stage, we selected all articles that dealt directly with the effects of landscape changes on pollinators and pollination services. For analyzing the articles, a database was created that included a standardized list of the articles, which enabled compiling and quantifying the characteristics of those studies. This database is composed of 25 fields (Tab. 1) selected for the purpose of extracting information from each analyzed publication within a scientometric perspective, enabling us to measure and quantify the scientific and technological progress within this research topic.

From this database, chronological changes and other possible interrelationships between any fields could easily be extracted to perform exploratory analyses with the aim of identifying general patterns and the temporal evolution of worldwide trends in the scientific literature on the relationship between landscape structure and the availability of pollinators and pollination services. These trends were summarized into graphs and percentage analyses to allow a critical understanding of the knowledge accrued over the years. To facilitate the visual comparison of database fields with numerous categories, some graphs of chronological change are presented with the data clustered into quinquennial groups of surveyed works.

Conceptual problems and terminology standardization

The definition of concepts, and in some cases their standardization, is an important step in surveying scientific knowledge for environmental management purposes. The greatest problem with the inadequate conceptualization and standardization of scientific terms is the risk of attributing the effect of a certain entity to a similar but essentially different factor, which can make it difficult to understand the text or lead to mistaken conclusions.

Some of the analyzed articles clearly confounded the processes of habitat loss and habitat fragmentation. According to Fahrig (2003), this kind of confusion should be avoided because the consequences of those processes for biological conservation are essentially different, although they usually occur together in nature. This confusion is less frequent, but not absent, in papers from 2004 on.

Another controversial concept was the definition of a 'landscape matrix', a term that has been used in several ways in the landscape ecology literature. The most-used concepts define the matrix as a 'dominant unit of the landscape' (spatially or functionally) or as a 'set of non-habitat units' (Metzger 2001); both characterize the matrix as a landscape feature. However, in many of the studies analyzed in the present review, the word 'matrix' was frequently used without an explicit definition, for example, to mean the areas adjacent to the studied fragment, which could be better defined as context or type of fringing environments, depending on the situation. Many times, those definitions were unspecific, thus making direct interpretations difficult. The same problem was also identified for the concepts of patch, fragment, corridor and even landscape.

Hence, to avoid making mistaken conclusions derived from conceptual problems, we decided to standardize all of the technical terminology related to landscape ecology in accordance with the review by Metzger (2001) and also with the formal concepts of fragmentation and habitat loss proposed by Fahrig (2003). Therefore, in the present study, landscape is defined as 'a heterogeneous mosaic formed by interactive units, given that this heterogeneity exists for at least one factor, according to one observer and at a given scale of observation' (Metzger 2001). This concept is relatively broad, as it enables a wide variety of units/habitats of different sizes to be considered landscapes. However, it establishes minimum criteria for us to use to separate the landscape from its constitutive elements such as patches, corridors, edges and different types of environments.

This standardization was used to organize the structure of our database to eliminate a priori the conceptual confusion from some articles and to standardize our analysis. Hence, information from all articles was revised and

TABLE I. Information selected for the analysis and its respective categories. For all items we included also a category: 'information not mentioned by the author'. The items "Landscape context" and "Landscape approach level" were described following Metzger (2001) and Fahrig (2003).

Items for analysis	Categories
Publication year	–
Surname of the first author	–
Country of the first author	–
Journal title	–
Geographic location of the study area (country and geographic coordinates)	–
Ecoregion/climatic zone where the study was carried out	1. tropical (including subtropical), 2. temperate (including boreal)
Ecosystem	1. agriculture, 2. forest, 3. grasslands, 4. savannah, 5. desert, 6. urban, 7. agroforestry system (AFS)
The kind of landscape matrix was explicitly declared by the	1. yes, 2. No
Kind of matrix	1. natural, 2. silviculture, 3. agriculture, 4. urban
Landscape context	1. natural, 2. agriculture, 3. urban, 4. mixed
Nature of the study	1. empiric, 2. review, 3. meta-analysis, 4. modelling, 5. conceptual, 6. opinion, 7. editorial
Nature of the method	1. descriptive, 2. bibliographic survey, 3. observational (sampling), 4. experimental, 5. modelling, 6. meta-analysis
Nature of the objectives of the study	1. descriptive, 2. establishing relationships, 3. modelling, 4. review
Landscape approach level	1. landscape, 2. buffers, 3. patches, 4. intra-patches
Size of the study area (total sampling range)	1. up to 1 ha, 2. between 1 and 10 ha, 3. between 10 and 100 ha, 4. between 100 and 1 000 ha, 5. > 1 000 ha, 6. global, 7. not specified
Level of biological organization analyzed (unit mentioned by the author)	1. individuals; 2. populations, 3. communities
Study object	1. pollinator, 2. plant, 3. plant/pollinator interactions
Response variables described by the author	–
Independent explanatory variables described by the author	–
Type of relationship between the explanatory and response	1. directly proportional, 2. inversely proportional, 3. no relationship
Functional or taxonomic group studied	–
Sampling method	1. pan-trap, 2. trap-nest, 3. entomological net, 4. Focal observation, 5. counting of the frequency of visitors, 6. translocation, 7. baits, 8. others
Pollinator specialization as described by the author	1. generalist, 2. specialist, 3. not specified
Pollinator sociality	1. social, 2. solitary
Number of citations until July 2011	–

standardized according to the concepts used in Metzger (2001) and Fahrig (2003) and corrected in our data matrices by including standardized columns, which are presented in Tab. 1.

Another important aspect for properly assessing the studies was the minimum relevant information that should be reported in the publications, but that, in most cases, was omitted by the authors. Some of the missing information was, for example, the extent of the study area and the types of land uses surrounding the studied patches (Tab. 1). When that type of information was implicit in the article we made an effort to recover and explicitly include it in our analysis.

RESULTS AND DISCUSSION

General patterns

In the present review, we found 219 studies focusing on ecological landscapes and pollination processes. Those studies had primarily been published since 2001 (Fig. 1) in 60 journals. Thirty-five of those journals represented only one article, whereas the journal Biological Conservation published 25 of the analyzed studies (11.4%; Appendix II). In general, we observed a dominance of purely scientific journals specialized in ecology and conservation with barely any journals focusing on agricultural sciences, applied land management or food production technologies. This indicates that the relationship between landscape patterns and pollinator availability is not yet perceived as economically

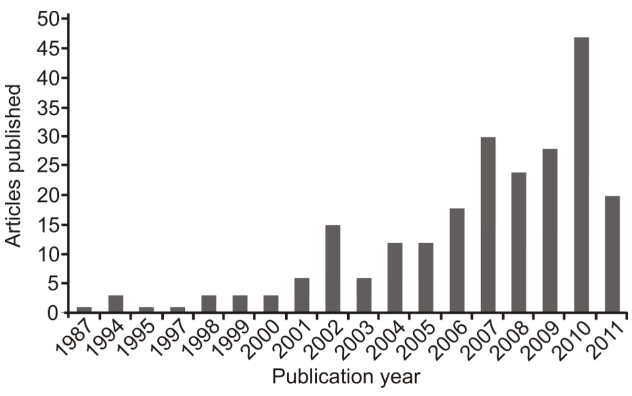

FIGURE 1. Temporal change of the number of articles that deal with pollinators and pollination services in the landscape until July 2011 (N = 219).

relevant outside of the biological and/or ecological sciences. Most studies were empirical/observational (166 studies; 75.8%), but some were reviews (29; 13.24%) that aimed to consolidate information, with a trend toward an increasing annual production of reviews (Fig. 2). We also identified nine modelling studies (4.1%), all from 2007 on.

The most frequently assessed biological organization levels were community (118 studies, 53.9%) and population (63 studies, 28.8%). Only 8 studies (3.6%) encompassed both communities and populations, and 7 studies (3.19%) focused on the behavioural responses of individual pollinators. From all 219 of the published studies initially selected by searching the online database, 166 (75.8%) directly addressed pollinators' response to landscape changes. Out of these 166 studies, 145 (87.3%) aimed to establish causal relationships between landscape patterns and pollinators availability, and 4 studies (2.41%) had merely descriptive approaches.

The first scientific study that explicitly analyzed the effects of changes in the spatial distribution of habitat on the activity of pollinator species was carried out in Brazil in the central Amazon (Powell & Powell 1987). However, between its publication and the year 2000, there was no meaningful increase in the number of studies on the relationship between changes in landscape structure and pollination processes, the literature being limited to only 15 (6.8%) papers in 13 years. It is worthwhile to highlight that among those publications are the empirical studies carried out by Aizen & Feinsinger (1994a; b) in Argentina, which used a community approach and reported a decrease in the richness and abundance of native pollinators in small and isolated fragments compared to continuous environments, with strong consequences for pollination. Those early studies can be considered the pioneers in establishing relationships between landscape structure, pollinator diversity and pollination processes.

It was only after 2000 that we could identify an increase in the number of papers on the effects of landscape structure on pollinators (Fig. 1). We found only 10 publications (6.2% of the 161 studies) between 1996 and 2000, whereas in the two subsequent quinquennia 51 (23.3%) and 151 (68.9%) papers were published, respectively. This increase was due primarily to the effort of work-groups from the United States, Germany and England (Fig. 3). This increase was most likely stimulated by the worldwide pollinator crisis identified in the previous decade (Buchmann & Nabhan 1996; Kearns et al. 1998), which created a scientific demand for an understanding of the causes of pollinator decline, particularly the decline of bee populations in the northern hemisphere.

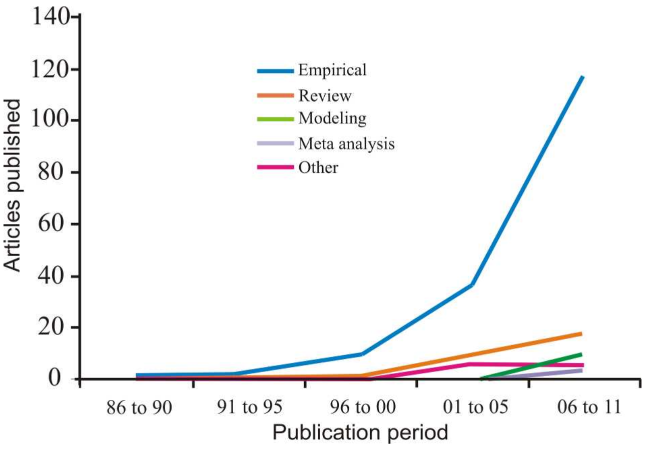

FIGURE 2. Number of studies of each type in 4-year time intervals from January, 1986 to July, 2011. (N = 219)

This temporal pattern of increasing publications was uneven between the climatic zones where the studies were carried out (Fig. 4). Our overall results indicated a clear trend toward an increase in the number of studies developed in temperate zones compared to tropical zones. Between 2001 and 2005, both climatic zones were similarly represented in terms of the number of publications with slightly more works carried out in tropical environments (16 studies in temperate regions and 19 in tropical regions). However, in the five following years (2006 to 2011), there was a great increase in the number of studies produced in temperate areas (79) that was not accompanied by an increased number of studies produced in the tropics in the same period (43). Among all 219 studies, most compared patches of the same landscape and few compared different

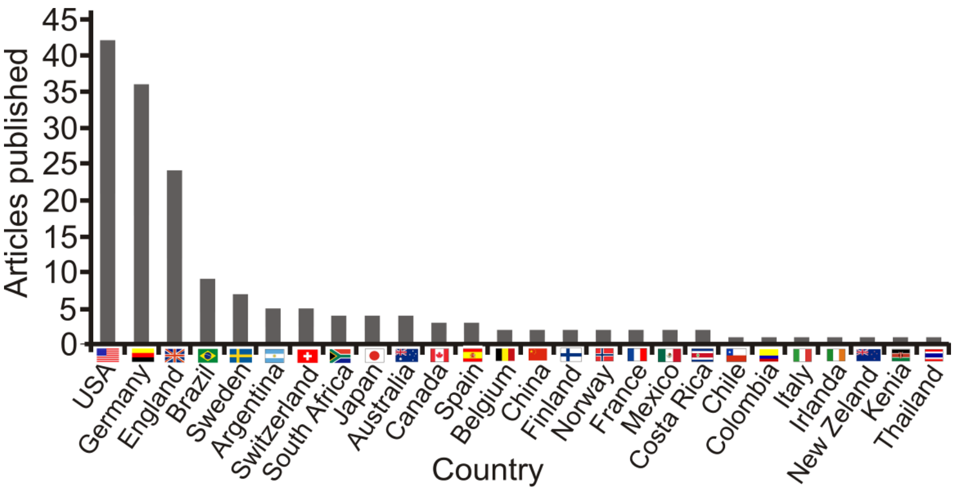

FIGURE 3. Country of the first authors of studies which are directly related to pollinators responses to landscape changes, revisions were excluded from this analysis (N = 146).

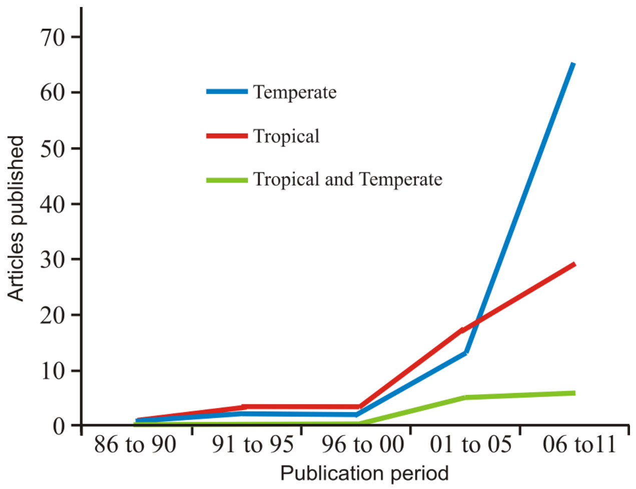

FIGURE 4. Overall number of studies produced in each one of the Climate zones by period (N= 219)

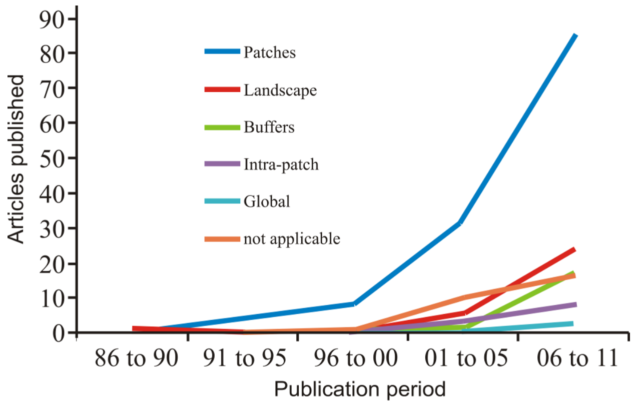

FIGURE 5. Temporal changes (number of studies/period) of the approach Level of the study (N= 219).

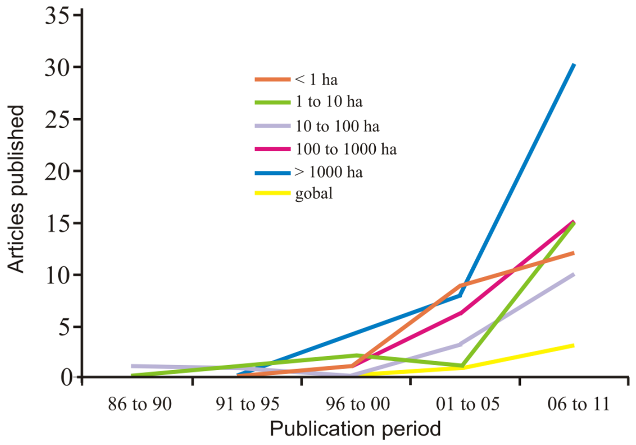

FIGURE 6. Temporal changes (number of studies/period) of landscape or patch size where the studies were carried out. Only those studies that specified patch or landscape size were considered. (N= 124).

landscapes, indicating that most of the available information is at the patch rather than the landscape level; this continued to occur in the last six years (Fig. 5). Only a few studies approached the problem at hand using whole landscapes as sampling units; about half of those studies used fixed distances around sampling sites (buffers) to assess how landscape structure affected pollinators. There was a noticeable increase in the number of publications using this type of approach after 2005 (Fig. 5). Additionally, we observed a large variation in the absolute meaning of patch size categories among studies, with no standardization of categories. The same patch size could be categorized as "large" in one study but "small" in another, even when the two studies addressed closely related organisms or processes. In addition, 77 studies did not provide any information on the size of the landscapes/patches studied. Out of the studies that provide information on habitat size (124), most (42) assessed patches or landscapes larger than 1 000 ha (Fig. 6).

We could also identify in our review a temporal change in the importance assigned to the inter-habitat matrix. References to matrix characteristics were scarce until 2005 (less than a third of articles) (Appendix III A). However, after 2006 the matrix began to be mentioned more frequently. In this period, the number of studies that did not cite matrix characteristics or left them implicit was very similar to the number of articles that commented explicitly about this matter. The proportion of studies that mention the matrix is also increasing among the full set of analyzed studies in the last decade (Appendix III A). This indicates a significant increase in interest in this aspect of the landscape, whose importance had already been noted in some existing publications (Clergeau & Burel 1997; Develey & Stouffer 2001; Rejinfo 2001). Among the 166 studies that focused on the relationship between the landscape and pollinators, most reported matrices composed of mixed, agricultural or natural environments (Appendix III B). The matrices composed of pastures, urban environments and silvicultures were few and represented similar numbers. After 2006, only a few empirical studies provided no information on the spatial context where the work was carried out.

Primary qualitative findings

In spite of the need for advancing the work of existing studies, some relationships could be clearly established in the surveyed literature. Many authors demonstrated that the spatial organization of the landscape has a great influence on the survival and dispersal capacity of many pollinator species, as spatial organization affects resource availability (Andersson et al. 2007, Jha & Vandermeer 2010; Cruz-Neto et al. 2011; Roulston & Goodell 2011) and determines functional connectivity, i.e., 'the capacity of the landscape (or landscape units) to facilitate biological flows' (Metzger 2001) in a given region (Steffan-Dewenter & Tscharntke 1999; Brosi et al. 2007). The shape, size and spatial arrangement of the patches of each type of natural environment as well as the occurrence of different types of land use can create sites with different degrees of connectivity or even barriers that impede animal movement through the landscape (Kreyer et al. 2004; Ekroos et al.

2008; Ricketts et al. 2008), which can strongly modify pollinator flows and consequently the success of cross-pollination (Gathmann & Tscharntke 2002; Goverde et al. 2002).

It is also widely known that higher proportions of natural or semi-natural environments in the landscape enable the maintenance of pollinator species that would otherwise go locally extinct with the suppression of the native vegetation (Laurance et al. 2002; Lennartson 2002; Taki & Kevan 2007; Hadley & Betts 2009). Although many types of crops are able to provide food to many pollinator species (Westphal et al. 2003; Albrecht et al. 2007; Holzschuh et al. 2008; Klein et al. 2008), food is not the only resource needed for pollinators' survival. In addition to food, animals need adequate sites for nesting and reproduction (Steffan-Dewenter & Tschanrtke, 1999; Knight et al., 2009). For many pollinator species, those sites are found more frequently in natural environments (Gathmann & Tscharntke. 2002, Westphal et al., 2003, Dixon, 2009) composed of primary vegetation or as the result of natural regeneration or restoration initiatives (Goverde et al. 2002; Kremen et al. 2007).

Many studies demonstrated that reductions in the size and number of natural remnants in the landscape can have deleterious effects on many species (e.g., Beier et al. 2002; Kremen et al. 2004; 2007, Cortes-Delgado & Perz-Torres 2011; Cruz-Neto et al. 2011). As large patches tend to have higher environmental diversity, they usually maintain more diverse communities of pollinators than smaller patches (Aizen & Feinsinger 1994b; Tscharntke & Brandl 2004). In fact, Steffan-Dewenter et al. (2001) postulate that the number of visitors to a flower in sites with intensive agricultural management in central Germany increases significantly in landscapes with more types of semi-natural environments, which characterizes them as more complex in comparison to landscapes dominated by monospecific crops. Those studies reinforce the importance of preserving native vegetation patches with enough area to maintain several pollinator species in the landscape, particularly in the case of specialist species restricted to only a few habitat types (Tscharntke & Brandl 2004; Tscharntke et al. 2005). However, the minimum size needed for native vegetation patches to ensure the survival of those pollinator species and the conservation of their pollination services is uncertain and most likely differs for different ecosystems and species (Aizen & Feinsinger 1994a; Kremen et al. 2004; Ricketts et al. 2004; Tscharntke et al. 2008).

In addition to the extent of natural environments, several authors indicate that the distance between patches has been one of the primary factors to affect the long-term maintenance of many species (Wiens 1995; Lennartson 2002; Smith & Hellmann 2002, Lander et al. 2010). This occurs because variations in the distances between habitat remnants change the landscape's connectivity, which can restrict the movement of individuals through the landscape and the establishment of new populations. Large inter-patch distances may also directly affect the accessibility of floral resources for individuals, threatening the floral visitors' populations. Studies indicate that the abundance and richness of native pollinators may increase significantly as the distance to natural environments decreases, which also affects agricultural production (Steffan-Dewenter & Tschanrtke 1999; Greenleaf & Kremen 2006, Klein 2009; Tscharntke et al. 2011). In the state of Minas Gerais in southeastern Brazil, for example, De Marco & Coelho (2004) reported that the proximity of crops to native vegetation resulted in a 14.6% higher coffee production compared to farms further from native vegetation. Similar results were observed in Indonesia (Klein et al. 2003) and in Costa Rica (Ricketts et al. 2004). In some cases, these variations in the landscape structure can even lead to behavioural changes in native pollinators (Osborne et al. 1999; Goverde et al. 2002), affecting their interactions with other species. In North American landscapes, for example, it was observed that the proximity of natural vegetation patches to sunflower crops increases the number of native bees, which compete with exotic bees (*Apis mellifera*). This surplus of pollinators leads to a more efficient cross-pollination process, incurring higher seed production (Greenleaf & Kremen 2006).

In addition to proximity to natural habitats, the matrix surrounding native vegetation patches, which is usually composed of different types of crops and agricultural management regimes, also exerts a strong influence on the behaviour and local maintenance of pollinators (Osborne et al. 1999). What has been established in the literature, primarily from the early 1990s on, is that the isolation level of native habitats and crops depends on the interaction between the pollinators' biological characteristics and the hostility of the matrix, resulting in both negative and positive effects depending on the species (Jules & Shahani 2003; Tscharntke & Brandl 2004; Ricketts et al. 2008; Brittain et al. 2010; Carvalheiro et al. 2010; 2011). Indeed, some studies have indicated that the characteristics of the matrix are an essential factor in the maintenance of a landscape's functional connectivity, with some pollinator species even benefiting from some agricultural activities (Westphal et al. 2003; Klein et al. 2007). Based on a compilation of 22 years of research in fragmented landscapes in the Amazon, Laurance et al. (2002) concluded that, due to the existence of a wide variety of responses to fragmentation, the inter-forest matrix can maintain high species richness, even leading to an increase in beta diversity in fragmented landscapes. However, because species that avoid the matrix tend to be the first to go extinct after fragmentation (Jules & Shahani 2003; Westphal et al. 2003; Tscharntke & Brandl 2004, Cussans et al. 2010; Kamm et al. 2010), we believe that the maintenance of a high diversity of native pollinators in the landscape requires that both the matrix and the surrounding natural habitats be sufficiently diversified.

The services provided by pollinators include the pollination of native plant species in patches of natural vegetation as well as the pollination of crops in agricultural areas. The magnitude of the effect of habitat fragmentation on plant reproduction in natural vegetation remnants was analyzed by Aguilar et al. (2006) based on 54 studies. These authors observed that reductions in patch size and increases in the isolation of natural habitat fragments have generally negative effects on pollination and on fruit and seed production in the native species studied. Among the effects that we compiled from our survey, the most evident are related to the size of the native vegetation remnants where pollinator populations live. In small native vegetation fragments, plants tend to receive limited pollination services and exhibit lower fruit and seed production (Donaldson et al. 2002; Brys et al. 2004; Kolb 2008; González-Varo et al. 2009; Taki et al. 2010). Moreover, we found studies demonstrating that fragmentation and habitat loss can lead to a dramatic simplification of pollinator interaction networks due to a decrease in the availability of specialized and rare pollinators (e.g., Donaldson et al. 2002; Brosi et al. 2007) For instance, the loss of some pollinator groups such as birds, flies and non-flying mammals impaired pollination and consequently the reproduction of several plant species in some fragments of the Brazilian Atlantic forest (Lopes et al. 2009). As a result, second growth forest patches developed plant assemblages with a higher frequency of species and individuals that are pollinated by generalist vectors with approximately 30% lower functional diversity of pollination interactions in comparison to continuous mature forest areas (see Girão et al. 2007; Lopes et al. 2009; Cruz-Neto et al. 2011).

Furthermore, in our review, we also observed that self-incompatible species, which depend completely on pollinators for sexual reproduction, are the most susceptible to habitat fragmentation (Aguilar et al. 2006; Girão et al. 2007; Lopes et al. 2009; Tabarelli et al. 2010; Cruz-Neto et al. 2011). With these results, we suggest that fragmentation promotes a remarkable change in the relative abundance of certain reproductive attributes of Atlantic forest trees and that it largely reduces the reproductive functional diversity of tree assemblages. Therefore, in fragmented landscapes, it is likely that small fragments and narrow forest corridors, both dominated by edge effects (Murcia 1995), are not sufficient on their own to conserve the complete diversity of life histories of trees and their mutualists (Lopes et al. 2009).

Regarding agricultural landscapes, Aizen et al. (2009) estimated that in the absence of pollinating services rendered by animals, world agricultural production might decrease by up to 8%, with clear social and economic impacts. According to these authors, worldwide agricultural production has historically increased at a rate of approximately 1.5% per year, and there is no evidence of global variation in the productivity of species that are dependent on vs. independent of pollinators (Aizen et al. 2009). However, we found several studies showing evidence of the effects of the composition (i.e., which ecosystems are there and in what proportion) and disposition (i.e., how those ecosystems are distributed in space) of landscape elements on agricultural production (Klein et al. 2003; De Marco & Coelho 2004; Ricketts et al. 2004, Gemmill-Herren & Ochieng 2008, Phalan et al. 2011), which indicates that unplanned changes in landscape pattern can reduce the productivity of pollinator-dependent crops.

Knowledge gaps to be explored

All of the information discussed above highlights the importance of areas of natural vegetation for the maintenance of pollinator species and their associated flora. Based on our results, we suggest that, in general, agricultural landscapes must be interspersed with natural and semi-natural vegetation patches for the maintenance of proper pollination services in native and human-made environments. Obviously, variations among different ecosystems and species and their interactions with their surroundings must be considered. The relationship between landscape structure and pollinator survival and behavioural responses is a very complex subject that has only recently begun to be revealed (Bélisle 2005). Therefore, to advance our knowledge of those relationships and understand how the composition and configuration of the landscape affects plant-pollinator interactions, more studies are needed that address the diversity of pollinators and population attributes (such as density fluctuations and survival) and can explain changes in diversity and behavioural attributes (such as mobility and foraging patterns) that could modify the efficiency of individuals as pollinators.

That type of research is particularly needed for tropical ecosystems, where the recent increase in the number of studies has been lower than in temperate regions and where the higher diversity of plants and pollinators impedes a more thorough knowledge of these systems. Due to the high worldwide importance of those regions for the production of food and primary agricultural goods, more attention should be given to the development of knowledge of pollinators and pollination processes in complex tropical landscapes. High-diversity tropical regions are usually located in developing countries, which commonly have limited funds and specialized personnel with which to conduct high quality environmental research (e.g., Stocks et al. 2008). International scientific cooperation could reinforce national research programs.

Starting from a broader perspective, the complexity of plant-pollinator systems and the broad spatial scale necessary for studies of landscape ecology indicate that larger research teams and greater cooperation are needed to compare landscapes rather than patches within the same landscape, the more frequent approach. One aspect that is strongly highlighted in the literature is the risk that the processes of fragmentation and reduction of habitat area pose to the conservation of pollinators and the maintenance of pollination services worldwide. Lennartson (2002) states that the processes of habitat loss and fragmentation can lead to abrupt qualitative changes in landscape structure, limiting the survival and movement of pollinators. Those processes may result in species extinctions due to threshold dynamics, deeply affecting the viability of biological populations and communities beyond a certain degree of habitat loss (Andrén 1994; Metzger & Décamps 1997). Local extinctions could lead to the disruption of plant-pollinator interactions with unpredictable consequences for the maintenance of biodiversity and environmental services (e.g., Steffan-Dewenter & Tscharntke 1999; Girão et al. 2007; Brosi et al. 2008; Lopes et al. 2009; Tabarelli et al. 2010). The identification of those thresholds and their implications is of extreme importance for the conservation of natural environments. To properly conserve biological diversity and its associated processes, habitat loss should never reach such extinction thresholds (Radford et al. 2005). Public policies and legal enforcement should be substantially based on scientific knowledge and precautionary principles to guarantee that the status of the landscape remains well above these modification-inducing levels. To do this, it is necessary to determine which critical values of habitat loss can lead to drastic increases in pollinator extinction rates so that we can evaluate at what point plant-pollinator interactions may collapse. However, determining such values for each region is an extremely difficult task, as this most likely varies among systems. Ideally, conservation strategies should be grounded in research conducted in the same region or in areas with similar ecological characteristics.

Similarly, we should concentrate efforts on acquiring the necessary knowledge to improve the landscape's capacity to facilitate pollinator flow (connectivity) between crop areas and nesting and foraging habitats. However, due to huge interspecific variations in pollinators' capacity to use and move between landscape components such as natural vegetation corridors or large extents of anthropogenic environments, our search for new techniques for integrated landscape management must aim at the maintenance of not only structural but functional connectivity between environments. In this way, it would be possible to ensure effective pollen flow and, consequently, fruit and seed production. Therefore, it is essential that we understand how pollen is dispersed, and to do so we must investigate the factors that affect pollinator mobility. However, to complete this task, methodological and technological obstacles must be overcome. Because most pollinators are tiny animals such as bees, most telemetry equipment is still too large or heavy to be carried by individuals. This hinders the direct assessment of movement behaviour in the landscape and consequently most of the presently available information on this subject comes from indirect observations and/or deductive conclusions based on basic biology. Nevertheless, new technologies have been developed in the last decade, such as harmonic radars for honeybee-sized animals (Osborne et al. 1999) or radio-tracking for bumble bees (Hagen et al. 2011), which will enable important developments in our understanding of pollinator spacing behaviours in coming years. The development of better individual tracking technologies will inevitably lead to more detailed studies on pollinator movement through the landscape, which together with the knowledge already available in the literature will lead to the development of better tools and guidelines for the management and design of landscapes with highly efficient ecosystem services, also ensuring the long-term conservation of pollination services in agro-natural systems.

The integrated management of landscapes based on scientific knowledge can compensate for global habitat loss (Ricketts et al. 2004; Tscharntke & Brandl 2004), as structurally complex landscapes with good habitat connectivity have proven to be more efficient in the maintenance of species diversity (Tscharntke et al. 2007). Additionally, simple changes in agricultural management such as the restricted use of pesticides and the sowing of species used by pollinators along crop edges can result in important improvements in landscape quality (Kremen et al. 2004, Gabriel et al. 2010; Carvalheiro et al. 2011; Krauss et al. 2011; Kovács-Hostyánszki et al. 2011).

Furthermore, for the integrated management of landscapes to become a reality for land use planning, in addition to incentives for excellent scientific research in areas related to the topics discussed herein (which will provide a technical basis for decisions on land use), public policies are needed to stimulate the following: 1) incentives for the creation of land use categories that enable pollinator flow and enhance pollen flow and the sexual cross-reproduction of native and cultivated plants in agrosystems and their surroundings; 2) the natural regeneration or restoration of pollinator-friendly habitats in sites where those environments have been degraded; 3) the monitoring of plant species that provide feeding and nesting resources for pollinators; 4) the conservation of key elements such as habitat patches and corridors that support the structural and functional complexity of the landscape; 5) population increases in managed native pollinator species in the vicinity of crops, thus ensuring their access to floral resources; and 6) planned reforestation at a regional scale, using multiple native species that will serve as resources for pollinators and that must be positioned in such a way as to improve pollen flow in the landscape.

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APPENDICES

Additional supporting information may be found in the online version of this article:

APPENDIX I. List of articles selected for analysis

APPENDIX II. Graphical representation of the number of analyzed articles published per journal

APPENDIX III. Graphical representation of the temporal changes of studies that mention the matrix (A) and matrix type (B).

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