Plant-pollinator interactions in ecosystems restoration

by

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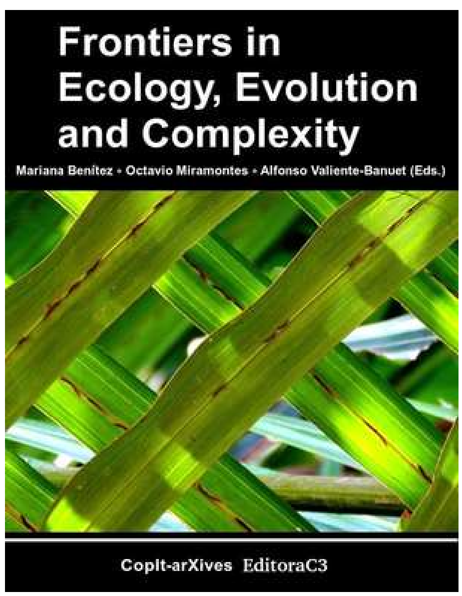

Contents

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1 Abstract

Measuring ecological restoration success is not simple, because the structure and composition of communities are very variable due to considerable fluctuations regarding soil nutrient levels, hydrology, and landscape, among others. Pollination is a process related to system sustainability and may be independent of the structural variation. Therefore, a failure to manage and promote pollinators could lead to decline or collapse in ecological restoration. Under any type of perturbation, plant–pollinator interactions disruption will depend on the level of specialization between a plant and its pollinators, on their abundance, and their sensitivity to land-use change. The proximity to natural landscapes can serve as an important support to pollinator communities in restoration activities. There is a vast amount of studies in pollination ecology but only a few addressed the question of plant-pollinator interactions as a tool to evaluate the success of restoration. Practical options aimed at restoring functional complementarity as resetting the maximum number of different functional groups or functional redundancy and resource use overlap can lead to different successional trajectories in the restored areas. Since different plant-pollinator communities might be regulated by different assembly rules there is still a vast amount of work to be done to understand the build-up of plant-pollinator communities in restored areas.

2 Resumen

Medir el éxito de la restauración ecológica no es sencillo, ya que la estructura y composición de las comunidades son muy variables debido a una considerable fluctuación en relación a los niveles de nutrientes del suelo, la hidrología, y el paisaje, entre otros. La polinización es un proceso relacionado con la sostenibilidad del sistema y puede ser independiente de la variación estructural. Por lo tanto, una falla en el manejo y promoción

de los polinizadores podría conducir a un fracaso en la restauración ecológica. Una perturbación significa una interrupción en las interacciones planta-polinizador y sus consecuencias dependerán del grado de especialización entre una planta y sus polinizadores, de su abundancia y de su sensibilidad a los cambios de uso del suelo. La cercanía a los paisajes naturales puede servir como un importante soporte para las comunidades de polinizadores en las actividades de restauración. Aunque hay una gran cantidad de estudios en ecología de la polinización, sólo unos pocos abordan la cuestión de las interacciones planta-polinizador como una herramienta para evaluar el éxito de la restauración. Opciones prácticas encaminadas a restablecer la complementariedad funcional, como el restablecimiento del número máximo de los diferentes grupos funcionales, o la redundancia funcional y la superposición de tareas en el uso de recursos, pueden dar lugar a diferentes trayectorias sucesionales en las zonas restauradas. Dado que las diferentes comunidades de plantas y sus polinizadores pueden ser reguladas por normas diferentes de ensamblaje, todavía hay una gran cantidad de trabajos por hacer para entender la construcción de estas interacciones en las zonas restauradas.

3 Introduction

The science of restoration ecology has experienced a major advance in the last 20 years, and numerous techniques have been proposed as tools to improve the biotic and abiotic properties of degraded systems [1–3]. Restoration goals usually emphasize structural aspects of biodiversity, such as species richness and abundance. Although several studies have found that structure influences function (e.g., [4, 5]), some processes related to system sustainability may be independent of the structural variation in healthy communities. These processes include trophic interactions, disturbance regimes, pollination and seed dispersal [6, 7]. Indeed, there is a growing concern about restoration dynamics [8] and the reintegration of interactions and processes in restoration programs [9, 10]. Moreover, there may be a considerable variation of the structural diversity of restored sites due to variations in soil nutrient levels, hydrology, and landscape context among others [11] and there are few studies bridging structural changes to processes [12, 13]. Hence, one of the challenges restorationists face is to maintain the self-sustainability of restored systems and to develop tools for assessing acceptable levels of variability among restored ecosystems.

Ecological science has devoted over the recent years a large effort to understand some aspects of ecosystem processes such as nutrients cycling and climate regulation. Interactions among species, including its effects on other species' populations, are less well known. The pollination of flowering plants is an emblematic example: approximately 90% of flowering plant species rely on biotic pollination for reproduction and genetic viability maintenance [14]. Although important for population maintenance, relatively few plant-pollinator interactions are absolutely obligate and most are more generalized [15].

These interactions also face a high level of variability in time and space [16, 17]. This is an important point because some researchers have suggested that pollination restoration may be independent of the taxa of pollinator involved [10, 18], but long-term data to address this is lacking. Due to their effect on plant reproduction and genetic flow, the failure to manage and promote pollinators could lead to a decline or failure of ecological restoration efforts [19]. Besides that, plant–pollinator interactions may not re-establish automatically themselves in communities undergoing restoration management, because pollinators establish populations only once their habitat requirements have been met. For example, in addition to food resources, bees require nesting sites and nesting materials (e.g. [20, 21]). These features make pollination a useful functional bio-indicator for comparing restored communities to reference communities. However, ecological restoration of plant–pollinator interactions has had few recent experimental studies [10, 12, 18, 22]. This deficiency in the knowledge to restore pollinator capability represents a major drawback in restoration programs, particularly in regions where specialist invertebrate and vertebrate pollinators exist, such as in global biodiversity hotspots [23]. In this chapter we will first review the effects of human disturbances in pollination and the role of landscape in the restoration of plant-pollinator webs. Then we will review recent experimental studies on plant-pollinator interactions in restoration and finally we will address some steps in ecological restoration that may improve the relation plant-pollinator.

4 The role of anthropogenic perturbations in pollination

Under any type of perturbation, plant–pollinator interactions disruption will depend on the level of specialization between a plant and its pollinators, on their abundance, and their sensitivity to land-use change [24–26]. Generalist plants tend to be more protected against the loss of any particular pollinator than highly specialized plants due to the risk of a reproductive failure [25, 27]. These asymmetries may buffer against species loss in mutualistic networks [28] and appear to be the norm in plant-pollinator networks [29]. Even considering pollinator redundancy in a network, shared traits by pollinators may imply shared sensitivity to anthopogenic changes, as it was reported to some functional groups of bees whose abundance declines with climate changes [30]. Plant attractiveness and rewards for pollinators may be potentially influenced by perturbation because it alters the amount of light, water and nutrients received by plants [31]. These environmental modifications may alter the number and size of flowers or the amounts and qualities of pollen and nectar produced by them. These changes in turn may affect the behavior of pollinators and the pollen transfer and plant reproductive success (reviewed in [32]).

Landscape fragmentation

The interactions in fragmented habitats are mainly affected by changes in the abundance of populations [33]. However, relatively few studies have directly measured changes in species interactions in fragmented landscapes and have consistently found that species interactions involving predators, parasitoids and pollinators are frequently more severely affected by fragmentation than host–herbivore interactions [26, 34–41]. Actually, the increase in fragmentation is expected to reduce the functional diversity [42] and to promote the erosion of reproductive traits in small fragments as observed in tropical rain forest remnants [43]. Evidence of nonrandom loss of interactions with decreasing fragment size was found in 12 pollination webs from isolated fragments in Argentina, ranging from tens to thousands of hectares [26]. Species with low interaction frequency and more specialized are subject to a higher risk. Besides that, there are structural changes in the networks associated to fragmentation, as for example changes in the central role of generalist species depending on fragment size.

Climate change

Climate change is responsible for a variety of responses in natural systems, including changes in species distribution, abundance and phenology [44]. Because these changes may affect both partners in pollination interactions, phenological changes may not be concordant [30, 45]. There is a reported advance in bee emergence [30], hummingbird immigration [45] and flowering [46] in temperate areas associated with global warming. Despite that, Memmot et al. [47, 48] found few research papers that specifically investigate pollination networks and persistence facing climate change. Climate change also may lead to partial or total asynchrony between pollinator life cycles and flowering phenologies that may result in a breakdown of pollination mutualisms in the case of obligate pollination systems [49, 50]. Less seasonal systems might be expected to support a higher asynchrony due to the longer growing season and longer phenological cycles than more seasonal systems. This can be expected because population-level flowering asynchrony results in higher plant reproductive success due to a reduction in competition for pollinators, an increase in the number of mates due to temporal changes in mate availability and a reduction on the effective population size [51]. Changes in abundance and asynchrony may be especially critical to short-lived species, but long-lived or migrating species can be very sensitive to climatic changes since they depend for longer on their partners' abundance [50, 52].

5 The role of landscape in pollination

The proximity to natural landscapes that may support pollinator communities is an important component of pollinator activity [53]. Agro-ecosystems with more natural or semi-natural habitats are often more pollinator-species rich [41, 54, 55]. On the other hand, restoration of pollinator communities may have the potential added benefit that pollinators deliver service to crops and native plants beyond the restored site, adding a direct value to the restored habitat [55, 56]. The presence of natural landscapes in fragmented habitat matrices is expected to affect the ability of pollinators to migrate and establish and, as a result, it is expected also to affect restoration capability [23]. Some taxa, less agile or less distributed, may be especially susceptible [23].

It is not known how ecological corridors may adequately support pollinator migration to restored sites. The responses to corridors are taxa-dependent [57]. Eventually a landscape intervention may require the establishment of corridors [57] or pollinator-friendly agri-environments [58] involving key resources: (i) species that provide a major nectar or pollen source, (ii) bridging species (plants that provide resources over resource-limited times) and (iii) magnet species (plants with attractive flowers associated with species with unattractive or small flowers; [59].

6 Experimental studies on plant-pollinator interactions in restoration

Even that there is a vast amount of studies in pollination ecology, only a few have addressed the question of plant-pollinator interactions as a tool to evaluate the success of restoration [60]. In the English heathlands, it was showed that although two ancient and two restored meadows were structurally very different, there were no significant differences between restored and reference meadows in plant or insect species richness, in the proportion of flower species visited by insects, in the numbers of pollen grains being moved by flower visitors, or in the number of links per species [10]. In these heathlands, Forup et al. [22] compared the complex network structure between restored heaths and ancient heaths. They found that four restoration projects established successfully heathland plants and pollinator communities and was stable after 14 years. The key pollinators were the same on ancient and restored sites after 11 years and were also the most abundant flower visitors 14 years after restoration. Another important result was that heathland restoration sites may not need to be immediately adjacent to intact habitat to be successful, since species composition was not related to distance from ancient sites. This may be due to the fact that in their study, the functional important pollinators are mobile, abundant and able to traverse other habitat than heathland (honeybees, *A. mellifera*, and bumblebees, mainly *B. terrestris/lucorum*), which are traits related to a higher regional abundance and so they may buffer against local loss [61, 62].

Bee and plant communities at restored at mid-successional stage riparian sites along the Sacramento River in California, United States were compared to remnants of riparian habitat within the same region [18]. Restored riparian habitats presented richness and abundance of native bees equal to that found in close remnants of riparian habitat. Connectance of bee–plant interaction networks in restored riparian habitats was similar to that of remnant riparian habitats and the proportion of native plants receiving visits by bees at restored sites. However the compositions of the bee communities at restored sites were different from those at remnant riparian habitats, with a lower redundancy of

Figure 1: *Placidina euryanassa* (Nymphalidae: Lepidoptera) visiting flowers of *Acnistus arborescens* (Solanaceae) in a restored area of Southern Atlantic Forest, Paraná, Brazil. Photo kindly provided by Jana M. Tesserolli de Souza.

pollinators in restored areas. The author argues that restoration of pollination may be achieved with a different species composition from those of reference sites, but the lack of pollinator redundancy may result in a lower robustness in restored areas.

In Mauritius island, restored areas may benefit from controlled removal of alien species, with an increase of native plant abundance, pollinator richness, floral abundance and pollinator visitation rates, resulting in a higher redundancy in pollinators [63]. Much less is known for tropical forests. Phenological coupling among plants and pollinators had a major effect on interactions establishment in plant-pollinator networks in restored sites of a tropical rain forest in Southern Brazil [13]. Concordant to that, at restored areas with four different ages (4, 5, 6, 7 years) in tropical rain forest in Southern Brazil, herbs and shrubs were very important food resources at the beginning of the restoration because they increase the supply of resources in areas where pioneer tree species take two to ten years to start the reproductive phase [64]. Herbs and shrubs were generalists plants able to establish interactions with specialists or rare insects (see Figures 1 and 2) [64]. Besides that, the structure of plant-pollinator networks in restored sites of this tropical rain forest was related to structural changes, canopy height, tree diameter variation, basal area and understory density [13]. Restoration of pollination network structure for a temperate forest was also affected by structural changes, such as tree diameter variation and tree density [12]. These structural effects on pollination networks may be directly related to flower resource availability to pollinators (as in [63]), as well as other non-food resources [12, 13].

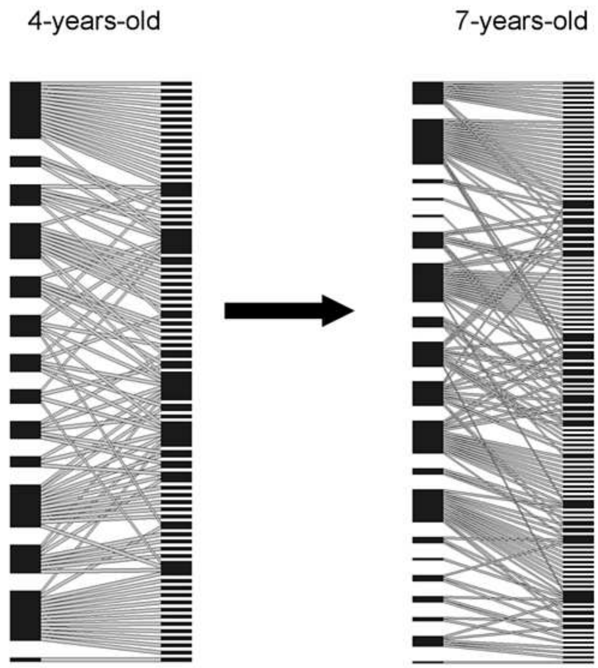

Figure 2: Plant-pollinator networks in four-years-old (left) and seven-years-old (right) restored areas of Southern Atlantic Forest, Paraná, Brazil. Data kindly provided by Ana Júlia Donatti

7 How to restore the pollination interactions in a degraded area?

Increase in network interaction diversity and interaction evenness seems to be good indicators of a healthy successional process including those in restored areas [12, 13, 65]. Some authors argue for a higher redundancy to increase the stability of restored areas which may be achieved in species-rich communities [18, 63]. Practical choices aiming to restore functional complementarity, the maximal number of different functional groups, or functional redundancy, overlap in resource use, may result in different successional trajectories in restored areas [12]. More studies are also needed on restored systems involving butterfly and bird pollination networks. Functional traits can be used to access the process involved in the assembly of plant-pollinator communities [66]. The balance between neutral or niche-based processes changes along the successional process [67] with a growing importance of niche-based factors in older forests. At least in successional areas, the structure and interaction frequency of tropical hummingbird networks are better explained by neutral factors in early successional sites and by niche-based factors in late successional areas [68]. This calls for attention for the need to understand how functional traits are related to community assembly rules in restored areas. At the same time, there are recent developments in ecological theory [69] that would impact many aspects of ecosystem restoration. These developments include concepts and methodologies from complex systems and network theory. Many important questions in restoration such as how to measure its success can be now reviewed from the point of view of non-linear dynamics where an important conclusion is that even under almost identical initial conditions, the outcome of the restoration could lead to a new ecosystem different from the previous undisturbed one [70]. However, this is in no way discouraging. Better understanding of ecological interactions such as pollinator-plant relationships seen as complex networks would help in unprecedented ways the practical goals of restoration.

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