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Review Article

Defaunation as a trigger for the additional loss of plant species in fragmented landscapes: considerations on the state of Espírito Santo, southeastern Brazil

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Abstract
Here we present a brief review on how the loss of fauna can cause a concomitant loss in plant diversity in the state of Espírito Santo, focusing on the context of current habitat loss and fragmentation and the importance of the mutualistic interactions between animals and plants. We discuss the main groups of fauna that are involved in pollination and seed dispersal, especially those that are found in the state of Espírito Santo. These ecological processes were selected due to their relevance for population dynamics and population genetics of plants. In Atlantic Forest, important pollinators include a variety of insects (especially bees), along with many species of birds and bats. Seed dispersers also include many taxonomic groups, from ants to large mammals. Each of these groups contribute in their own unique and complementary, rather than redundant, way. Habitat fragmentation causes a variety of problems for habitat integrity and the reduction of species diversity, and smaller fragments tend to support fewer species and smaller populations. As a consequence, pollinators and seed dispersers are lost or their activity is reduced, thereby reducing even further the reproductive success of the plants, leading to a vicious cycle of reduction of species diversity.
Key words: animal-plant interaction, fragmentation, habitat loss, pollination, seed dispersal.

Resumo
O presente trabalho apresenta uma breve revisão sobre como a perda de fauna pode causar a perda concomitante de diversidade vegetal no estado do Espírito Santo, considerando o cenário atual de perda e fragmentação de habitats e a importância das interações mutualísitcas entre animais e plantas. Foram considerados os principais grupos zoológicos envolvidos na polinização e na dispersão de sementes, especialmente aqueles com ocorrência no estado do Espírito Santo. Estes processos ecológicos foram selecionados devido à sua relevância na dinâmica e a genética populacional das plantas. Na Mata Atlântica, importantes polinizadores incluem uma variedade de insetos (especialmente abelhas), juntamente com muitas espécies de aves e morcegos. Os dispersores de sementes também abrangem muitos grupos taxonômicos, desde formigas até grandes mamíferos. Cada um desses grupos contribui de maneira única e complementar, mais do que de forma redundante. A fragmentação de habitats compromete a integridade do habitat e reduz a diversidade de espécies, ressaltando que fragmentos menores tendem a suportar menos espécies e menores populações. Como consequência, os polinizadores e os dispersores de sementes são perdidos ou sua atividade é reduzida, diminuindo ainda mais o sucesso reprodutivo das plantas, levando a um círculo vicioso de redução da diversidade de espécies.
Palavras-chave: interação animal-planta, fragmentação, perda de habitat, polinização, dispersão de sementes.

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Introduction

Espírito Santo is one of the four states in southeastern Brazil, being entirely inserted in the Atlantic Forest ecoregion. The colonization of the *capixaba* (the local name for the region and people from Espírito Santo) territory began in 1535, but the region was essentially unexplored economically until the half of the 19th century (Franceschetto 2014). Despite this delay in colonization, natural vegetation in the state suffered from an intense deforestation and forest degradation, and as a consequence of which natural areas are currently restricted to less than 13% of their original cover (FSOSMA & INPE 2016). Habitat loss and fragmentation, associated with hunting and other anthropic activities (*e.g.*, roadkills and introduction of exotic species), lead to the current situation of decline and loss of wildlife in Espírito Santo. A total of 753 species of plants (Simonelli & Fraga 2007) and 197 species of animals are threatened in the state, and 11 species of animals are already regionally extinct (Passamani *et al*. 2007). These numbers are based on assessments carried out in 2004 and therefore the flora and fauna of Espírito Santo are likely to be even more threatened today.

Currently, understanding how the loss of species may contribute to the loss of ecological interactions, and vice versa, in the state of Espírito Santo (and elsewhere) is limited due to the lack, and complexity, of studies of these effects. Nonetheless, some general patterns are understood, by which we can predict and recognize consequences of the loss of species and interactions. Thus, here we review the literature and place that in the context of Espírito Santo and the Atlantic Forest to explain how the loss of fauna can break down plant–animal interactions and result in the further loss of species and of interactions. We concentrate on the animals most often involved in pollination and seed dispersal and that are found in the state of Espírito Santo. We describe how different factors can cause vulnerability and local extinction of these animals, as well as their ecological functions and the plants with which they interact. This manuscript is organized in the following sections: Espírito Santo at the time of the early traveler naturalists, The process of occupation and Espírito Santo today, Plant-animal interactions, The Insects, The Birds, The Mammals, and Final Considerations.

Espírito Santo at the time of the early traveler naturalists

The eastern Brazilian state of Espírito Santo comprises a wide variety of native animals that fascinated and interested experts since the early traveler naturalists. Travel notes by prince Maximilian von Wied-Neuwied during his travels in Brazil at the beginning of the 19th century (in his writings "Viagem ao Brasil nos anos de 1815 to 1818") describe encounters with a great diversity of birds in his travels in where today lays the state of Espírito Santo, including gulls, herons and egrets, swallows, shorebirds, ducks, macaws, parrots and parakeets, toucans, woodpeckers, hawks, curassows and guans, trogons and brightly colored tanagers among many more. In addition, he also wrote about the frogs, sea turtles, caiman and snakes, a variety of species of monkeys, tapirs, deer, peccaries, porcupines, cats and manatees, as well as beetles and many kinds of butterflies, all within the state of Espírito Santo. Prince Maximilian also described a variety of environments and plant formations, including more than one type of forest, savannas (possibly areas of *restinga* - vegetation on sandy soils along the coast in Brazil, and *muçununga* - low forests on sandy soils far from beaches), native grasslands, swamps and lakes. These formations are encountered along the gradient from the coastal region to the highlands and mountains. The forests received most of his descriptive attention, which he described at great length as imposing and sombre, thick and beautiful or simply grand and magnificent, with majestic trees that gave refuge to the abundant and extraordinary diversity of animals (Wied-Neuwied 1942). For details on the vegetation of the state of Espírito Santo, see Garbin *et al*. (2017).

The Espírito Santo that Wied-Neuwied visited he described as having "delightful landscapes" and "such superb scenes and so rich with notable specimens" that "naturalists will have a long time to occupy themselves," with "the most varied and agreeable emotions" (Wied-Neuwied 1942). Even though the state was largely unpopulated at the time, plantations were already present (some of them extensive), especially of sugarcane, cotton, coffee, cassava and corn, that replaced the forests along the coastal lowlands, along with some cattle rearing. The forests in Espírito Santo were replete with a variety of high-quality hardwoods that were being exploited throughout the state for their lucrative lumber. In addition to this early deforestation and exploitation of forest resources, prince Maximilian wrote of hunting wild game for food deep in the forests, using gunpowder and lead with shotguns, occasionally with hunting dogs to take large game that tended to avoid men. He described several occasions in which the hunters returned home with bags or canoes nearly overloaded with game that was so abundant in the local forests (Wied-Neuwied 1942).

In 1860, the emperor Dom Pedro II visited the territory of Espírito Santo and he wrote briefly of his travels, with a little information on the flora. He wrote most about the natural environments (beaches, rivers, lakes) and fauna. Dom Pedro II wrote, for example, about the extraordinary birdlife he found in the state, describing species of colorful and beautiful plumages, aquatic birds, hawks and others (Rocha 2008). He also wrote about the hunting for animal skins, including caimans, tapirs, capybaras, deer, anteaters and jaguars (Rocha 2008).

The princess Teresa da Baviera, during a visit to Espírito Santo in 1888, also described the fauna and flora of the state (in her writings "Viagem ao Espírito Santo"). In addition to her interest in the fauna and flora, princess Teresa was fascinated by the habits and customs of the indigenous people of Espírito Santo, especially the *Botocudos* (indigenous groups of the Macro-Jê ethnic group, that pierced their lips and earlobes and inserted wooden discs with a diameter of up to 12 centimeters). She described her knowledge of nature as having been enriched by culinary experiences (animals that were hunted for food), along with what she was taught by the indigenous people and colonists (Baviera 2013). Princess Teresa wrote of dining on a wide variety of animals, including insects, fish, reptiles (caiman, snakes, lizards and sea turtle meat and eggs), birds (curassows and parrots, among many others) and mammals (spotted pacas, deer, tapirs and big cats, among others). Tapirs are emphasized and appeared to be the most appreciated meat by the colonists in some parts of the state. In addition to their meat, they were hunted for their hides as well, which was valuable at that time and used in a variety of applications (Baviera 2013).

These and other early traveling naturalists describe the beginning of the gradual and irreversible process that has lead up to the current situation of decline and loss of wildlife in the state of Espírito Santo. Habitat integrity and species diversity suffered from a variety of problems that were (and are) caused by habitat loss and fragmentation, and hunting that began with colonization and continues today.

The process of occupation and Espírito Santo today

Today, the landscape of Espírito Santo is much different from that explored by the traveling naturalists of the 19th century. The economy of the state continued to be dominated by sugarcane and cassava, until coffee became more important, beginning in the mid 1800s. Most of the settlements were located near the coast (did not extend beyond 20 km inland) and the state was essentially economically unexplored (Franceschetto 2014). At that time, agricultural, especially plantations for growing coffee, began to grow and spread westward (Loureiro 2006; Franceschetto 2014). Until that time, Espírito Santo was viewed by the Portuguese Crown as a barrier that limited access to the state of Minas Gerais and which helped prevent smuggling from that state (which was already important for mining gold and precious stones). Thus, before agricultural growth, the mountains, along with the forest cover and the indigenous peoples that resisted colonization, all contributed to the delay in occupation of the interior of the state of Espírito Santo (Loureiro 2006; Franceschetto 2014). Often, lumber extraction preceded the establishment of the coffee plantations that in turn grew even more to increase production, and were subsequently abandoned when the soil was no longer productive and which were replaced by pasture for the growing cattle industry. In some places, economic activity began with logging of high quality lumber and was followed immediately by extensive cattle production (Loureiro 2006). Espírito Santo continued its agrarian economy that was strongly dependent on the coffee monoculture until the late 1960s, when industrial activities began to increase in importance, along with silviculture (mainly eucalyptus) for the production of charcoal and cellulose for paper (Loureiro 2006).

As economic activities increased in the state with the drive for additional development, deforestation continued rapidly as any arable land in the natural environments was converted to agriculture, silviculture and livestock. This state that was original completely covered by the Atlantic Forest and its associated formations gave way to economic development. Less than 13% of the original natural areas remain, counting fragments larger than 3 ha, which now comprises forest (~11%) and non-forested natural areas (~2%), such as seasonally flooded areas (*várzeas*), *restingas* and mangroves (FSOSMA & INPE 2016). As the Atlantic Forest of Espírito Santo became more and more fragmented, most of the native fauna became confined to the ever-smaller and more isolated forest fragments. These smaller populations are beset by a variety of problems that reduce their chances of long-term survival along with that of the ecological processes of which they are often a very important part. In addition to those biological issues, climate change (changes in temperature, precipitation, albedo and local microclimate), in part caused by deforestation, has consequences for the remaining flora and fauna (Davies *et al*. 2001). The loss of animals due to poaching and roadkills, and the introduction of exotic species, among other anthropic factors, further aggravate the wildlife conservation scenario in Espírito Santo (*e.g.*, Passamani *et al*. 2007; Srbek-Araujo *et al*. 2014).

Plant-animal interactions

The first scientific research carried out with respect to plant-animal interactions is attributed to Joseph Gottlieb Kölreuter, around 1760, with the documentation of pollination service provided by several insects. He was followed by Christian Konrad Sprengel, in 1793, studying the relationship between plant fertilization and insects (Bascompte & Jordano 2014). Among other researchers, plant-animal interactions were also mentioned by Charles Darwin, a hundred years later, in his monumental "On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life". Darwin point out that plants and animals are linked together and form a web of complex relations (Darwin 1859). Today we recognize (aside from foraging, such as seed predation and herbivory) four kinds of animal-plant interactions that are multispecies mutualisms: 1) pollination, 2) seed dispersal, 3) protective mutualisms or harvest mutualisms (comprising protection of plants by arthropods, especially ants, in exchange for some product the plants provide), and 4) agriculture by humans (modified from Bascompte & Jordano 2014).

In this study, we will focus on pollination and seed dispersal to explain how the loss of fauna can break down these two important plant-animal interactions and result in the further loss of species (both plant and animal) in the state of Espírito Santo. These interactions were selected due to their relevance for 1) plant reproduction and maintenance of plant genetic diversity, affecting reproductive success and plant fitness through pollination (Paschke *et al*. 2002) and 2) seed germination and recruitment of seedlings, through seed dispersal that reduces density-dependent seed predation near the parent plant (Janzen 1970).

In addition to ecological relevance, pollination and seed-dispersal comprise a very wide diversity of organisms, both plant and animal, and the loss of these interactions will result in a substantial loss of biodiversity. For example, ca. 87% of angiosperms worldwide are pollinated by animals, and in the tropics increases to ca. 94% (Ollerton *et al*. 2011). Seed dispersal by animals is also extremely important, especially in tropical forests where more than 75% of trees species produce fruit whose function is to attract animals so that they disperse seeds (Howe & Smallwood 1982), including birds and mammals, as well as reptiles, fish and ants. Overall, in the Atlantic Forest about 65% of all woody plants are dispersed by vertebrates, as with endozoochory (after being consumed along with fruit, seeds are regurgitated or defecated), while in some places up to 90% are animal-dispersed, and so the loss of dispersers is likely to have far-reaching effects (Almeida-Neto *et al*. 2008). Plants that depend upon vertebrates for pollination and seed dispersal will suffer both ecological and evolutionary consequences due to the loss of fauna (genetic structure of populations can change, for example), and in addition can reduce or eliminate ecosystem services that these interactions provide (Galetti & Dirzo 2013). Defaunation of wildlife in tropical forests, therefore, can result in a cascade of deleterious consequences for the entire community which causes the reduction in species richness and greater dominance by a very few species, resulting in reduced biodiversity at all levels (Kurten 2013).

The Insects

Insect pollination is very widespread in angiosperms and thus pollination is the more important mutualistic interaction between insects and plants. A greater part of plant species in tropical forests are pollinated by insects, and several groups of insects stand out as pollinators, including Coleoptera (beetles), Diptera (flies), Hymenoptera (bees and wasps) and Lepidoptera (butterflies and moths; Kevan & Baker 1983; Roubik 1989; Bawa 1990).

The degree of specialization/generalization of the interaction between plants and insects is variable. It can be classified into four categories according to the functional groups of pollinators (beetles, syrphids, other dipterans, small bees, large bees, wasps, and butterflies/moths), as: monophily (exclusively pollinated by one functional group), oligophily (two functional groups, and one or both are the main pollinators), polyphily (three or more functional groups, but only one or two groups are the main pollinators) and holophily (a variety of functional groups pollinate indistinctly) (Freitas & Sazima 2006). Usually the number of functional groups of pollinators is strongly related to coevolution between certain groups of insects and plants - fewer pollinators, greater likelihood of coevolution (Roubik 1989).

Bees and wasps (Hymenoptera) are the most important insect pollinators as measured by number and variety of plant species pollinated as well as number and variety of hymenoptera involved (Bawa 1990), especially small and large bees (Kevan & Baker 1983; Roubik1989; Freitas & Sazima 2006; Senapathi *et al*. 2015). The majority of species in some common plant families are pollinated by bees in neotropical forests, including Burseraceae, Clusiaceae, Euphorbiaceae, Fabaceae (Leguminoseae), Flacourtiaceae (currently reorganized as other botanic families, such as Achariaceae, Samydaceae and Salicaceae), Lecythidaceae, Melastomataceae, Orchidaceae and Sapotaceae, including flowers of both the canopy and understory (Bawa 1990). Several species having monophily and oligophily are pollinated by bees (Roubik 1989; Freitas & Sazima 2006).

The orchid bees (tribe Euglossini) have long to extremely long tongues, and they visit a wide range of deep, tubular flowers that are not accessible to other bees (Dressler 1982). They are important pollinators that visit flowers to get their nectar, pollen, resin and (the males) to collect aromatic chemicals that they then convert to pheromones (Dressler 1982). Orchid bees are known to visit flowers of around 30 families in tropical and subtropical forests in Central and South America (Tonhasca Jr *et al*. 2003), including Apocynaceae, Bignoniaceae, Convolvulaceae, Gesneriaceae, Marantaceae and Rubiaceae, and they are the only pollinators of some neotropical Orchidaceae (Dressler 1982).

The *mamangavas* (bumble bees, genus *Bombus*, tribe Bombini; and carpenter bees, genus *Xylocopa*, tribe Xylocopini) are large and robust bees. They are generalists bees and visit flowers to collect pollen and nectar of a variety of families including Apocynaceae, Asteraceae, Bignoniaceae, Fabaceae, Melastomataceae, Myrtaceae, Passifloraceae, Rosaceae, Rubiaceae, Sapindaceae and Solanaceae (Marchi & Alves-dos-Santos 2013).

While we are more concerned with insect pollination, due to the ubiquitous nature of ants in tropical forests, they merit at least a mention. Some ants do clean and disperse seeds of several species of plants (Howe & Smallwood 1982; Pizo & Oliveira 2000), and other symbioses between ants and plants bear mention. Ants may defend plants against herbivory and defended plants often have structures in which ants may feed (extrafloral nectarines) and live. Extrafloral nectarines are present in over one hundred of Angiosperm families worldwide, and the families with the most species with extrafloral nectarines are Fabaceae, Passifloraceae and Malvaceae (Weber & Keeler 2013). Many species of plants apparently have adapted structures for the express purpose of being inhabited by ants, such as the two well-known examples of hollow stems occupied by ants in the genus *Cecropia* (family Urticaceae) and the hollow thorns of some Fabaceae (Hölldobler & Wilson 1990).

Ants have a great interaction with diaspores of at least 30 families in the Atlantic Forest, such as Annonaceae, Arecacea, Euphorbiaceae, Melastomataceae, Meliaceae, Myristicaceae, Myrtaceae, Olacaceae, Sapotacea and Verbenaceae (Pizo & Oliveira 2000). Some species of small and medium-sized ants fed on and cleaning the fallen fleshy diaspores or occasionally transport very small seeds, and the large ants (subfamily Ponerinae) individually moved diaspores (up to 1 g, Pizo & Oliveira 2000). Even in cases where the dispersion by ants can be considered low, their importance tends to be significantly higher in the absence of primary dispersers (Brito-Kateivas & Corrêa 2012). Ants can sometimes also act as pollinators, through the adhesion of pollen to hairy structures in their bodies (Beattie 1985). Because the ant-plant interactions are often overlooked, the consequences of fragmentation for both ants and plants require further study.

Abundance and species richness of insects tends to decrease with reduction in area of the habitat and due to edge effects (change in microclimatic conditions), and small, isolated fragments may also lack habitat heterogeneity needed to support pollinator populations throughout the year (Bawa 1990). Some groups, such as the orchid bees, are dependent on well preserved forests and are vulnerable to the loss of suitable habitat, and often disappear in small fragments (Nemésio 2011). Ant species richness and composition are also influenced by fragment size and tree density, and some species are particularly sensitive to forest fragmentation (Leal *et al*. 2012). Many species and groups of pollinators (principally bees), as well as the plants they pollinate, are negatively affected also by agricultural intensification (including the use of agrochemicals), diseases, invasive species and climate change (Senapathi *et al*. 2015). Ecological changes, such as loss of pollinators, can lead to pollen limitation that then reduces reproductive success of the plants, causing a decline in seed production (Ashman *et al*. 2004). The bumble bees, for example, are facing population declines and consequent decrease in pollination service has already been documented around the world (Williams & Osborne 2009). Those factors all together result in the decrease on community stability by the disruption of mutualistic insect-plant interactions, highlighting the loss of one partner in species-specific interactions may lead to the extinction of the other (Bawa 1990). Ecosystem integrity in a future of environmental change is essential in order to maintain not only pollination services but also species diversity required to guarantee the functional redundancy and a range of reactions to environmental change (Senapathi *et al*. 2015).

The Birds

Habitat fragmentation can initiate a variety of snowball effects of changes in their animal and plant communities. For example, some species of birds are rapidly lost after fragmentation and some may quickly and others more slowly return upon forest recovery. Also, species loss and recovery are both functions of the size of the fragment and their distance from source populations as well as the autecology of the species of interest (Stouffer & Bierregaard 1995; Ferraz *et al*. 2003; Stouffer *et al.* 2011). Here we are concerned with the ways in which fragmentation can influence the bird assemblage which, in turn, influences the plant species that persist or invade the fragments. While an extinction debt occurs after habitat fragmentation, in which species loss continues over time (Tilman *et al.* 1994), we must recognize that the loss of plant species can depend on the dynamics due to a variety of interactions, including reduced seed dispersal due to the loss of frugivores as well as the addition of seed predators as well as reduced reproductive success due to the loss of pollinators.

The first step in understanding how fragmentation can result in the loss of important bird species that then contributes to plant extinction debts, requires understanding how habitat fragmentation is likely to influence, and reduce, bird populations. A reduction in bird populations implies both abundance and species richness. Also, considering that the contribution of birds to the maintenance of the plant community depends on the species of birds and their foraging habits, we must understand the dynamics of the different trophic groups, especially frugivores. Also, population dynamics depends on survival and reproduction rates of the various species involved (Martin 1995), and so we must look at how those dynamics will be influenced by forest fragmentation (Martin 1996).

Nest predation in natural settings is the cause of most reproductive failures (Ricklefs 1969; Skutch 1985; Roper *et al.* 2010). Thus, any changes in nest predation rates due to forest fragmentation should have importance influences on population growth or decline. Studies demonstrate that nest predation rates tend to increase in fragmented landscape, usually because predators from outside the fragment (such as feral cats, dogs, rats) find it easier to enter well into the fragment (Sherry 1986; Newton 1993; Kays & DeWan 2004; Obrien *et al.* 2008). Predation rate tends to be greater in tropical forests and birds may lose up to and more than ~90% of their nesting attempts due to predation (Roper 2005; Roper *et al.* 2010). Dynamics of reproduction and adult longevity may maintain a population, but if faced with even small changes in either reproductive success or adult survival, population decline may follow rapidly.

Small and medium-sized predators that are associated with humans (cats, dogs, rats) may often become more important with fragmentation because of the increase in edge and decrease in forest interior. Additionally, smaller natural predators can become more abundant due to the decline of the larger predators in fragments (Sodhi *et al.* 2004). Thus, species with relatively stable populations and that tend to suffer higher predation rates may be faced with greater predation rates, that then cause their population declines. For example, in Panamá, *Thamnophilus atrinucha* Salvin & Godman, 1892 (family Thamnophilidae, with several similar species in Espírito Santo) loses 89% of its nesting attempts to predation (Roper 2005). However, due to seasonality in eastern Brazil, the breeding season is probably much shorter in Espírito Santo and an increase in predation to similar rates is likely to cause population decline (Roper *et al*. 2010). The exact dynamics of fragmentation, edge effect and changes in survival and predation rates continue to be debated (Flaspohler *et al.* 2001; Lloyd *et al.* 2005, 2006; Rush & Stutchbury 2008; Bueno *et al.* 2012); nonetheless, evidence and logic suggest that small changes in survival and reproduction can have dramatic deleterious effects on bird persistence. Therefore, changes in species composition of fragments are expected as fragmentation increases and fragment size decreases.

The exact relationship of species changes over time with fragmentation is, of course, influenced by the niches of the species involved. Most studies about nesting success have included territorial, insectivorous species that are easier to study precisely due to their territoriality (Robinson *et al.* 2000; Duca & Gonçalves 2001; Wikelski *et al.* 2003; Roper 2005; Duca *et al.* 2006; Duca & Marini 2011, 2014; Marques-Santos *et al.* 2015; Lima & Roper 2016; Mathias & Duca 2016). While insectivorous birds may influence plant species through predation on herbivorous insects, plant dynamics will be more strongly influenced by birds that pollinate plants and that disperse seeds. Population dynamics are much less studied in frugivores (families Cracidae, Tyrannidae, Cotingidae, Pipridae and Thraupidae, with Turdidae somewhat of an exception) and pollinators (hummingbirds, family Trochilidae). Many of these species nest similarly to the more studied insectivores, and we must assume that predation on their nests will have similar trends in fragmented habitats. However, these groups comprise a wide range of autecologies and body size, all of which will have consequences on dynamics in fragmented environments. In general, large species tend to have slower reproductive rates and longer intervals between breeding attempts than the faster, smaller species (Robinson *et al.* 2010; Lovette & Fitzpatrick 2016).

Frugivorous birds comprise a wide variety of ecologies in eastern Brazil, beginning with the large curassows and guans (familia Cracidae) that may often be important seed dispersers (Terborgh *et al.* 1990; Marini 2001; Pimm *et al.* 2006; Kirwan 2009). Smaller frugivores include families that are common in Espírito Santo and are often birds of urban and rural regions. The Tyrannidae include the well-known *suiriris* (kingbirds and similar species, in the genera *Tyrannus* and *Myiarchus*) and the *bem-te-vi* (Great Kiskadee, *Pitangus sulfuratus* (Linnaeus 1766) and similar species) and a variety of lesser known understory and forest species. The Cotingidae tend to be extremely specialized in frugivory and include the *araponga* (bellbirds, genus *Procnias*) among others. The more omnivorous Tityridae (until recently considered Cotingidae) includes the *anambé* (tityras, genus *Tityra*) and *caneleiros* (genus *Pachyramphus*). The frugivore family Pipridae includes a variety of smaller species that form leks in which the males gather in groups to dance in fascinating coordinated cooperation to gain the attention of the females (genus *Pipra*, among others, and some species of smaller Tyrannidae also do this, and they tend to be frugivorous as well). Also omnivorous, the Thraupidae comprise a colorful family of birds, including the well-known *tiê-sangue* (genus *Ramphocelus*, and others). The well known *sabiás* (thrushes, family Turdidae) are omnivorous and extremely common and consume fruits of both native and exotic plant species (Ridgely & Tudor 1989a; Ridgely & Tudor 1989b). Thus, we find a wide range of breeding and social systems and feeding ecologies among several bird families, all of which will be influenced by forest fragmentation. We can divide these frugivores into two main groups: the larger birds including the curassows and guans, that may be very efficient seed disperses that tend to prefer forests and which will suffer from nest predation as well as poaching in fragmented landscape; the remainder being the smaller birds whose survival patterns in fragments are not easy to predict, but whose breeding patterns should be influenced by increasing nest predation in fragments. However, the smaller birds include the thrushes (*sabiás* in Brazil, family Turdidae) that have become associated with urban and rural landscapes and which seem to have characteristics that allow them to do well in anthropic settings (about which more below).

Large birds, such as the curassows and guans, also suffer from both predation and poaching (Michalski & Peres 2005, 2007; Barlow *et al.* 2006) and are likely to disappear rapidly from fragments (Harris & Pimm 2008). Because they are large, they can also consume larger fruits, often entirely, and thereby carry their seeds (disperse) longer distances where they will be defecated. Breeding rates tend to be relatively slow with extended intervals of parental care. Thus, potential population growth is relatively slow and after fragmentation is likely to decline. As a consequence, the species of plants that depend upon these dispersers may have no counterparts among the smaller frugivores of the forest, much like the extinct megafauna on a smaller scale (Janzen & Martin 1982). These birds also need relatively large areas to support stable populations (Sodhi *et al.* 2004; Bernardo *et al.* 2011). Thus, following fragmentation, reduced populations due to fragmentation will be followed by continuing population decline, which is likely to result in dispersal limitation for any species dependent upon these large birds (Freestone & Inouye 2006; Moore *et al.* 2008; Pinto & Macdougall 2010).

The extreme frugivores (family Cotingidae) tend to produce very small clutches and the bellbirds (*arapongas*, genus *Procnias*) only lay one egg per nest. Also, the young require a very long time interval to leave the nest and these two patterns together, perhaps due to frugivory, tend to result in very slow potential population growth (Snow & Goodwin 1974; Ingels 2008; Kirwan & Green 2011). The manakins (*dançarinos*, family Pipridae) only lay two eggs per nesting attempt, but may have several nesting attempts per year, and so their potential for population growth is greater than that of the bellbirds. Both of these birds families are very important seed dispersers because they often consume entire fruits and regurgitate or defecate the seeds (perhaps gaining a germination benefit in the process, Calviño-Cancela 2004; Daïnou *et al.* 2012) long distances from where they were consumed (Snow & Goodwin 1974; Kirwan & Green 2011). These species are also likely to decline in fragments, in part to the extinction debt (Tilman *et al*. 1994) that will result in the disappearance of some species of fruiting plants, as well as to slow reproductive rates coupled with increased nest predation. The tanagers (family Thraupidae) and flycatchers (Tyrannidae) include some species with similar life histories that will be affected similarly, resulting in a general decline in richness of seed dispersing species. Some species, nonetheless, seem to benefit from fragmentation.

Several species of tanagers and flycatchers, but especially the thrushes (family Turdidae), seem to benefit from fragmentation, perhaps because they have always been associated with marginal habitats. These species also tend to be omnivorous and consume a wide variety of resources (Ridgely & Tudor 1989a, 1989b; Sick 1993). Also, many species in this group are habitat generalists and are able to nest in a variety of settings. Reproductive rates are also more rapid among these species, and they may have more than one success per year (Marini *et al.* 2012; Marques-Santos *et al.* 2015). Unfortunately, also do their generalist habits, these species may often contribute to diversity homogenization (Elton 2000; Crooks 2004; Qian & Ricklefs 2006; Babak & He 2008; Croci *et al.* 2008; Winter *et al.* 2009; Gossner *et al.* 2016) because they consume fruits of exotic species as well as native species, dispersing seeds for both groups. As a consequence, due to the extinction debt, exotics may become much more abundant than native species. As the exotics become more abundant, omnivorous birds may benefit, while the more extreme frugivores may not, thereby further contributing to their decline as well as their role in the maintenance of the plant community.

The threat to plant communities through the loss or decline in their seed dispersers is clearly an important threat for tropical forests as a consequence of forest fragmentation. However, an equally important process may be less obvious and that is of the pollinating species that help maintain genetic diversity of plant populations. Hummingbirds (*beija-flores*, family Trochilidae) comprise a diverse group of birds with one thing in common - they all visit and pollinate plants. Many species of hummingbirds migrate and local migration may often occur as the timing of flowering changes among the many species of plants that they visit (Wethington & Russell 2003; Arizmendi & Ornelas 2007). Mostly due to their small size, hummingbirds are poorly studied and the impact of their pollination on plant reproductive success is hard to estimate. However, the very strong coevolutionary patterns of the New World Hummingbirds (Cotton 1998; Zanata *et al*. 2017) suggest that hummingbirds have been extremely important in the evolution and diversity of tropical plants. The state of Espírito Santo has about 33 species of hummingbirds that range in size from ~2–9 g, with short to long bills and that inhabit a variety of habitat types (Ruschi 1982; Ridgely *et al.* 2015). Despite their species diversity and behavior as pollinators, the difficulty of studying how plants depend on their pollinators has impeded the understanding of the importance of hummingbirds for the persistence of the plants they pollinate. Also, because hummingbirds are so small and often difficult to detect within forest, how fragmentation influences their own populations remains unknown. Nonetheless, the existing evidence suggests that plants benefit from the plant hummingbird association, but that hummingbirds themselves may be less affected by fragmentation if fragments are larger than 10 ha and relatively near much larger forest fragments (Borgella *et al.* 2001; Martín González *et al.* 2015).

The Mammals

The ability of any species to withstand landscape modifications is determined by how much habitat is loss, how isolated the resultant fragments are and how strong is the rupture in biological and interspecific interactions of which the organisms play a part (Fischer & Lindenmayer 2007). In general, mammals are susceptible to habitat fragmentation and its effects on the species depend on not only size and degree of isolation of the fragments, but also the spatial arrangement of fragments in the landscape (Andrén 1994). Even species that are very mobile can suffer from the effects of isolation in very fragmented landscapes, and it is unlikely that isolated, relatively small (few hectares) fragments can maintain mammal populations (Andrén 1994). Thus, the composition of the matrix (the area between fragments), along with the dispersal capacity of the species of interest, its ability to move from one fragment to another or to live in the matrix, are elements that will define the vulnerability of that species to fragmentation and habitat loss (Fischer & Lindenmayer 2007).

Mammals with restricted geographical distributions, low population density, low reproductive rates, large body size and that occupy higher trophic levels tend to be the most vulnerable to extinction (Purvis *et al*. 2000). For the ecosystem, the consequences of species loss will depend upon redundancy of the species in the system. Where a variety of species serve the same function, the loss of any one element may not be immediately apparent, but when few or no species are redundant, the loss of the keystone species can then cause an important loss in functional diversity (Petchey & Gaston 2002). This pattern is especially important for larger species (Brose *et al*. 2017). Larger mammal species tend to interact (consume, predate, disperse) with a larger number of plant species and, consequently, the loss of the large mammal can result in the simplification of trophic networks (Brose *et al*. 2017).

Here we will discuss only bats and medium to large-sized mammals because both groups are known to play important parts in plant-animal interactions in tropical forests, especially pollination and seed dispersal. The medium to large-sized mammals, in addition to their precarious position in forest fragments, are also subject to poaching, adding additional pressures that can drive them to local extinction in the Atlantic Forest (Chiarello 1999; Galetti *et al*. 2009; Sousa & Srbek-Araujo 2017).

Bats

Bats (order Chiroptera) form a very diverse group and which, because of their food habits, have ecological functions that are fundamental to the maintenance of plant communities (Charles-Dominique 1986; Fenton *et al*. 1992; Fleming & Sosa 1994). Bats and plants have a very strong interaction and when bats consume fruits, nectar or pollen, they provide seed dispersal and pollination in exchange for the nutrients the plants provide. Thus, the association between many plants and bats is often exclusive, and some plant species have clearly coevolved with bats for seed dispersal (chiropterocory) and pollination (chiropterophily, Hilje *et al*. 2015).

Bats are among the most efficient mammalian seed dispersers (Fleming & Sosa 1994), in part because they are the only truly volant mammal and in part because they are so abundant and varied in their use of resources and habitat within any landscape (Estrada *et al*. 1993). It is estimated that a 145 g bat can disperse thousands of seeds in a single night (Esbérard 2000), often carrying seeds large distances from the parent plant (Morrison 1980; Charles-Dominique 1986). The size of seeds that bats disperse varies widely. Smaller seeds are dispersed by endozoochory (ingested and eliminated with feces) while larger seeds are dispersed by stomatochory (carried to a feeding perch where the bat will consume the fruit pulp and drop the seed).

Bats in the family Phyllostomidae, especially those in the subfamilies Stenodermatinae, Carolliinae and Rhinophyllinae, are specialized in frugivory in the neotropics (Reis *et al*. 2007; Lima *et al*. 2016). In the Atlantic Forest of the state of São Paulo these bats are known to disperse seeds of at least nine genera of native plants in eight plant families (Passos *et al*. 2003). In Espírito Santo, bats disperse at least 20 native plants in 15 genera and 13 families (Zortéa & Chiarello 1994; Pedro & Passos 1995; Lima *et al*. 2016). Families dispersed by bats in the two states include Araceae, Clusiaceae, Curcubitaceae, Moraceae, Piperaceae, Solanaceae and Urticaceae (Zortéa & Chiarello 1994; Pedro & Passos 1995; Passos *et al*. 2003; Lima *et al*. 2016). Additional families dispersed by bats include Rosaceae, in the state of São Paulo (Passos *et al*. 2003), and Humiriaceae, Lauraceae, Fabaceae, Malpighiaceae, Myrtaceae and Passifloraceae, in the state of Espírito Santo (Zortéa & Chiarello 1994; Lima *et al*. 2016). The first records of bats (*Artibeus lituratus* (Olfers, 1818)) carrying fruits of the *muçunungа*-endemic *Humiriastrum mussunungense* Cuatrec were noted in Espírito Santo (Lima *et al*. 2016). *Muçununga* is a forest formation unique to sandy soils in the Atlantic Forest in the northern Espírito Santo and southern Bahia.

The most commonly observed genera of fruits being consumed by bats include *Ficus*, *Cecropia*, *Piper*, *Solanum* and *Vismia* (Mikich *et al*. 2015). Some bat genera seem to be strongly associated with particular groups of plants, such as *Artibeus* spp. with *Ficus* and *Cecropia*, *Sturnira* spp. with *Solanum*, and *Carollia* spp. with *Piper* (Pedro & Passos 1995; Passos *et al*. 2003; Mikich *et al*. 2015). This specialization is apparently associated with resource partitioning in which similar sympatric species avoid or reduce competition thereby allowing species coexistence (Marinho-Filho 1991). These plant species are often associated with secondary succession in disturbed or damaged areas, and bats tend to disperse seeds during flight into altered areas (seed rain), thereby contributing to forest regeneration (Charles-Dominique 1986; Martins *et al*. 2014). In Espírito Santo, 60% of bat-dispersed plant species are of early successional stages, three genera of which are pioneers and another six are from early stages of secondary succession (Lima *et al*. 2016). Bats can also disperse seeds of exotic species (Zortéa & Chiarello 1994; Lima *et al*. 2016), thereby contributing to plant invasions and species homogenization (*e.g*., Qian & Ricklefs 2006; Winter *et al.* 2009). For example, in Espírito Santo, *Artibeus* spp. disperse seeds of exotic plants in the families Arecaceae, Rosaceae (Zortéa & Chiarello 1994), Fabaceae (Lima *et al*. 2016) and Sapotaceae (A.C. Srbek-Araujo, unpublished data).

Some bats are also effective pollinators (Fleming & Sosa 1994) and the neotropical Phyllostomidae, subfamily Glossophaginae, include species specialized for pollination. These species tend to have morphological adaptations for feeding in flowers, including an exceptionally long tongue and a long snout (Silva & Peracchi 1995). Other Phyllostomidae species are less specialized, but also visit flowers and may be occasional pollinators as well (subfamilies Stenodermatinae, Sazima *et al*. 1999; and Phyllostominae, Silva & Peracchi 1995). A variety of plants are pollinated by bats (Sazima *et al*. 1982; Sazima & Sazima 1988; Silva & Peracchi 1995; Sazima *et al*. 1999; Arias *et al*. 2009; Ramírez *et al*. 2015), many of which evolved flowers that favor pollination by bats (Howell 1974). Flower adaptations that favor bats including nocturnal anthesis (flower opening), white or light colored petals in flowers located towards the ends of branches and oriented in such a way as to facilitate bat visits and contact with pollen, as well as having particular odors and production of larger amounts of pollen and nectar (Howell 1974; Ramíres *et al*. 2015).

Studies of plant species pollinated by bats are still few in the Atlantic Forest. Nonetheless, bats in the subfamily Glossophaginae have been found to pollinate at least 19 plant genera in this biome (Nogueira *et al*. 2007). In the state of São Paulo, for example, 16 species in 10 genera and 10 families were pollinated by bats (Sazima *et al*. 1999). Among the more important pollinating bats are *Glossophaga soricina* (Pallas 1766) that is important in pollinating two Atlantic Forest endemic plants, *Dyssochroma viridiflorum* (Sims) Miers (an epiphytic Solanaceae) and *Pitcairnia albiflos* Herb (a rare bromeliad of the Tijuca Forest in the state of Rio de Janeiro) (Nogueira *et al*. 2007).

Fragmentation is usually accompanied by the loss of bat species, including dispersers and pollinators, because some species of bats are very sensitive to loss of habitats and often may not visit isolated forest patches (Fenton *et al*. 1992; Fuchs *et al*. 2003). For these species, the matrix between fragments becomes an effective bat filter (Cosson *et al*. 1999). Thus, smaller bats and those of the forest interior are even more sensitive to fragmentation and their loss or isolation in fragments can have demographic consequences for the plants they visit and disperse (Cosson *et al*. 1999). As pollinators, it has been shown that at least one species of bat-pollinated plants produced a lower fruit set (number of fruits per flower produced in each tree) in fragments than in continuous populations, suggesting that the loss of or reduction in pollinator activity can often reduce the fitness of their host plants (Fuchs *et al*. 2003). Additionally, in continuous populations, progeny had lower levels of relatedness due to greater outcrossing or more sires (Fuchs *et al*. 2003). Thus, fragmentation can simply make it harder for plants to be found by their bat pollinators, thereby reducing reproductive output of those plants which then becomes a vicious cycle.

Medium and large-sized mammals

Among the medium and large-sized mammals that were or are common in the Atlantic Forest and important for plant-animal interactions, are primates (family Atelidae: genus *Alouatta* - howler monkeys, and genus *Brachyteles* - muriquis, formerly wooly-spider monkeys; and family Cebidae: genus *Sapajus* - capuchin monkeys), medium-sized rodents (family Dasyproctidae: genus *Dasyprocta* - agoutis; and family Cuniculidae: *Cuniculus paca* (Linnaeus, 1766) - spotted paca), squirrels (family Sciuridae: genus *Guerlinguetus*) and ungulates (order Artiodactyla, family Tayassuidae: *Pecari tajacu* (Linnaeus 1758) - collared peccary, and *Tayassu pecari* (Link 1795) - white-lipped peccary; and the order Perissodactyla, family Tapiridae: *Tapirus terrestris* (Linnaeus 1758) - lowland tapir). Some species in the order Carnivora, especially in the families Canidae (dogs and foxes) and Procyonidae (coati, kinkajou and raccoon), also often consume fruits and disperse seeds. These mammals act as primary and/or secondary seed dispersers, some of which may often be seed predators as well (Gautier-Hion *et al*. 1985; Kurten 2013). Additionally, the rodents are also important for their habit of scatter-hoarding or caching seeds (Gautier-Hion *et al*. 1985; Kurten 2013), which effectively disperses the seeds in a variety of different places, often leading to germination. Medium and large-sized mammals often defecate the ingested seeds mixed with various amounts of fecal matter, which may create an ideal environment for germination, aside from the possible benefits of seed processing by passing through the gut of the animal.

Larger frugivorous mammals are not simply redundant in terms of their importance for seed dispersion with respect to bats and birds. These mammals often eat larger fruits and those with tough pericarps that are not accessible to other seed dispersers. The rodents with their specialized incisors and the primates with their visual acuity and ability to manipulate can harvest kinds of fruits that birds and bats cannot. Also, ungulates can swallow larger seeds rather than crush all them with their molariform teeth. Additionally, some of the larger mammals tend to remove a larger number of seeds and, due to the size of their home ranges, they disperse seeds over larger distances (Fragoso *et al*. 2003; Bueno *et al*. 2013). Seed dispersal by medium and large-sized mammals is variable quantitatively, qualitatively and spatially, and is influenced by gut passage time, defecation frequency, defecation behavior (*e.g.*, latrine use), pattern of movement, habitat use and social organization (Bueno *et al*. 2013). Thus, seed dispersal is complementary rather than redundant among medium and large-sized mammals (Bueno *et al*. 2013), and complements patterns of birds and bats. For example, tapirs and muriquis have distinct seed dispersal effectiveness and disperse a variety of plant species, some of which are dispersed by both or by one or the other (Bueno *et al*. 2013). According to compiled information from a literature review, tapirs are known to disperse seeds from at least 34 plant families (76 species), muiriquis disperse 55 families (220 species) and their overlap includes 24 families (29 species) (Bueno *et al*. 2013).

Several plant families are dispersed by medium and large mammals and include the important families Anacardiaceae, Arecaceae, Annonaceae, Celastraceae, Chrysobalanaceae, Euphorbiaceae, Fabaceae, Lauraceae, Malphigiaceae, Melastomataceae, Moraceae, Myrtaceae, Rubiaceae and Sapotaceae, along with many others in the Atlantic Forest (Hilje *et al*. 2015; Bueno *et al*. 2013). Thus, the loss of larger mammals can completely change the dynamics of dispersal for many species in these (and other) families, thereby potentially altering community composition and genetic structure of the populations. Also, the absence of large frugivores may result in greater seed predation rate (up to five times more) due to the predation by small rodents (Galetti *et al*. 2015). Although small rodents can disperse seeds, they are responsible for consuming about 64% of all seeds in non-defaunated sites, and more than 98% in defaunated areas (sites where large mammalian herbivores were extirpated, Galetti *et al*. 2015).

In Espírito Santo, larger frugivores have declined in abundance and often disappeared completely from many forest fragments and therefore, most of the state. For example, red-rumped agoutis (*Dasyprocta leporina* (Linnaeus 1758) were once common throughout the state, and are still relatively common in some protected areas, but they have disappeared from many smaller fragments and elsewhere are in decline or are less abundant than they once were (Chiarello 1999). A similar, but more extreme, trend is found in the spotted pacas (Chiarello 1999) and they remain one of the most favored illegally-hunted prey in Espírito Santo (Chiarello 1999; Sousa & Srbek-Araujo 2017). The northern muriqui (*Brachyteles hypoxanthus* (Kuhl 1820)), found only in the mountainous regions, today is restricted to two protected areas and very few small fragments on private land in the state (Mendes *et al*. 2008). Lowland tapirs, once found throughout the state, are restricted to only three regions in the north (Flesher & Gatti 2010), two of which include the last populations of the white-lipped peccary in Espírito Santo (Chiarello 1999). Larger mammals clearly face a much greater challenge to their continued survival in the state, and all suffer from forest fragmentation, habitat loss and poaching. The impact of their decline as seed dispersers for the many plant species associated with them is very difficult to predict. Nonetheless, the loss of large frugivores is of such importance that the ecosystem services they provide are failing and probably already lost in many places. Long-term consequences of the loss of these mammals will include changes in forest structure and species composition.

Final Considerations

The wide variety of animals that interact with plants include many species that are likely to be important pollinators and seed dispersers, and that will suffer (and are likely to already have suffered) from habitat loss and fragmentation and poaching in the state of Espírito Santo. In this context, patterns of a vicious cycle in the reduction of species diversity in forest fragments are clear. The fragmentation itself, which loses species simply due to the extinction debt process (Tilman *et al*. 1994), results in fewer plants, making distances between individuals and populations them larger. The matrix that is formed between fragments may not be traversed by pollinating or seed dispersing animal species, enhancing the isolation of plant populations. In turn, because smaller fragments also support fewer animals, pollination and dispersal are simply reduced because of few numbers of animal agents. Reduced pollination and seed dispersal result in lower reproductive success of those plants. Once the plants become rarer due to that reduced reproductive success, the animals that visit them will also have a smaller resource base that will then limit their own numbers. At the same time, exotic plants in the matrix may be favored by these changes, and will be visited by the more flexible pollinators and frugivores that will then favor the differential reproductive success of the exotic plants. As a result, community homogenization is expected, where the resultant fragments are dominated by very few plant species (some likely to be exotic) and the very limited number of pollinator and seed-dispersing species that can be supported by them (Elton 2000). We are going to experience a synergistic decline in fauna and flora components, with the simplification of biological communities and the loss of ecosystem services provided by animals and plants.

We recommend that studies be carried out to map the ecological interactions between animals and plants in Espírito Santo (and elsewhere), to better understand the consequences of and synergy between their losses, to extend what is known beyond general theoretical patterns. Conservation efforts must reduce the impact of fragmentation before the harm is irreparable, and to restore interactions when possible to recover the original complexity and diversity in the state of Espírito Santo and in the Atlantic Forest as a whole.

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