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Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives

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Summary

The Brazilian Atlantic Forest hosts one of the world's most diverse and threatened tropical forest biota. In many ways, its history of degradation describes the fate experienced by tropical forests around the world. After five centuries of human expansion, most Atlantic Forest landscapes are archipelagos of small forest fragments surrounded by open-habitat matrices. This 'natural laboratory' has contributed to a better understanding of the evolutionary history and ecology of tropical forests and to determining the extent to which this irreplaceable biota is susceptible to major human disturbances. We share some of the major findings with respect to the responses of tropical forests to human disturbances across multiple biological levels and spatial scales and discuss some of the conservation initiatives adopted in the past decade. First, we provide a short description of the Atlantic Forest biota and its historical degradation. Secondly, we offer conceptual models describing major shifts experienced by tree assemblages at local scales and discuss landscape ecological processes that can help to maintain this biota at larger scales. We also examine potential plant responses to climate change. Finally, we propose a research agenda to improve the conservation value of human-modified landscapes and safeguard the biological heritage of tropical forests.

I. Introduction

Tropical forests are exposed to increasing levels of human-related disturbances, and in the near future, the last tracts of old-growth forests are likely to be converted into human-modified landscapes (Wright, 2005; Melo *et al.*, 2013a). Habitat loss and fragmentation, logging, fire and hunting, combined with emerging threats

from global climate change as a result of CO₂ emissions from fossil fuel consumption and regional shifts in precipitation, have caused an alarming loss of biodiversity, collapse of key ecosystem services and erosion of cultural heritage (Butchart *et al.*, 2010; Laurance *et al.*, 2012). Scientists are charged with understanding the response of tropical forests to human-generated disturbances at multiple biological and spatial scales and providing society with effective

guidance towards sustainability. Particularly critical is the potential role played by human-modified landscapes as key repositories of tropical biodiversity (i.e. conservation value) because, as noted by Schmitt *et al.* (2009) and Gardner *et al.* (2009), <10% of the tropical forest biome lies within strictly protected areas and the global network of protected areas has limited coverage. Accordingly, several new concepts have arisen, such as biodiversity corridors and climate-smart landscapes, all aiming to provide guidance for the effective management of human-modified landscapes (Harvey *et al.*, 2014).

The Brazilian Atlantic Forest hosts one of the world's most diverse tropical forest biota arising from its exceptional levels of species endemism (Mittermeier *et al.*, 2004), and its history of degradation describes, in many respects, the fate experienced globally by tropical forests. After five centuries of human expansion, most Atlantic Forest landscapes are archipelagos of small forest fragments surrounded by open-habitat matrices such as pastures and agricultural fields (Ribeiro *et al.*, 2009). However, in contrast to many developing countries that lack appropriate institutional capacity, Brazilian academics have long been devoted to describing the biodiversity of the Atlantic Forest and, more recently, to the conservation and research agenda suggested by modern paradigms, such as community homogenization as a result of the proliferation of native species and biodiversity-friendly landscapes (Tabarelli *et al.*, 2012a; Melo *et al.*, 2013a). This 'natural laboratory' has contributed to a better understanding of the evolutionary history and ecology of tropical forests and to determining the extent that this irreplaceable biota is susceptible to major human disturbances.

We present some of the major findings on the Atlantic Forest with regard to the responses of tropical forests to human disturbances across multiple levels of biological organization (from population to ecosystem level) and spatial scales, with a specific emphasis on plant species and their assemblages. First, we provide a short description of the Atlantic Forest biota, its relevance for ecosystem services and its historical degradation as natural landscapes continue to become human-modified landscapes. Secondly, we offer conceptual models describing how this biota is affected at the local scale by human disturbance and edge-related effects and how landscape processes can contribute to the persistence of species for a longer period of time in human-modified landscapes. Additionally, potential plant responses to climate change are examined. Finally, we discuss research challenges and examine some Atlantic Forest initiatives that will provide the required strategic knowledge to improve the conservation value of human-modified landscapes and safeguard the biological heritage of tropical forests.

II. The Atlantic Forest: a highly diverse, relevant and threatened forest

1. The oldest and richest South American forest

The Atlantic Forest originally covered > 1 450 000 km² of Brazilian territory, c. 17% of the total area of the country, ranging from 3°S to 30°S, from sea level to 2700 m above sea level and along > 3300 km of the Brazilian Atlantic coast (Fig. 1a).

The Brazilian Atlantic Forest is most appropriately referred to as to a continuum of tree species distributions (Joly *et al.*, 1999; Oliveira Filho & Fontes, 2000) composed of five main types of forest – Dense Ombrophilous, Open Ombrophilous, Mixed Ombrophilous, Semideciduous Seasonal and Deciduous Seasonal (Fig. 1b). As proposed by Oliveira Filho & Fontes (2000), the definition of Atlantic forests should be as comprehensive as that of Amazonian forests, with rainfall distribution being the main factor differentiating between evergreen and semideciduous and deciduous forests. The north–south differentiation of both evergreen and semideciduous forests is strongly related to the combination of rainfall and temperature (Scudeller *et al.*, 2001), which is most evident in the Mixed Ombrophilous Dense forest of the southern states of Paraná, Santa Catarina and Rio Grande do Sul and across altitudinal gradients. The east–west differentiation is strongly related to gradients in seasonal rainfall as the distance from the ocean increases as well as temperature changes in mountainous areas (Salis *et al.*, 1995).

Although there is some controversy surrounding the exact age of the Atlantic Forest, it is still regarded as the oldest Brazilian forest (Rizzini, 1997). The Atlantic Forest consists of an assemblage of species that evolved from original forests dating back to when South America was connected to Africa 100 million yr ago, and more modern species resulting, for example, from expansions and retractions of the Atlantic Forest during the Quaternary (Brown, 1987; Behling & Negrelle, 2001; Bush & Oliveira, 2006; Behling & Pillar, 2007; Ledru *et al.*, 2007; Carnaval *et al.*, 2009).

As a result of its long evolutionary history, the biota of the present Brazilian Atlantic Forest is composed of Gondwana elements, such as members of the genera *Araucaria* and *Podocarpus* as well as some Proteaceae and Winteraceae species (Fiaschi & Pirani, 2009), together with both old (pre-Pliocene) and young (Pleistocene–Holocene) species (Silva & Casteleti, 2003). During its evolution, the Atlantic Forest also experienced periods of connection and biotic interchanges with other South American forests, such as the Amazon Forest, whereas periods of isolation may have led to allopatric speciation (Silva *et al.*, 2004; Ribeiro *et al.*, 2011). During the glacial periods of the Pleistocene, for example, moist forest refuges persisted in areas such as the Serra do Mar region, while the *Araucaria* forest expanded to southern Bahia State and connected to some areas of the colder forests of the Andes. Such a dynamic evolutionary history produced a distinct biota consisting of five well-defined species centres (Silva & Casteleti, 2003), with endemism rates ranging from 30% in birds to 44% in plants (Mittermeier *et al.*, 2004).

Our current knowledge indicates that this complex biome hosts a plant species diversity per unit area that is higher than that of the majority of the Amazon forests. Species richness, extremely high levels of endemism and the small fraction of the original forest covered led Myers *et al.* (2000) to rank the Brazilian Atlantic Forest among the top five biodiversity hotspots. In the southeast region, Thomaz & Monteiro (1997) recorded 443 tree species per hectare. Joly *et al.* (2012) and Eisenlohr *et al.* (2013), working along an altitudinal gradient in the Serra do Mar State Park, which is the largest continuous area of Atlantic Forest within a Protected Area, recorded tree diversity indexes as high as $H' = 4.48$. This biodiversity richness underscores the inclusion of the Atlantic Forest

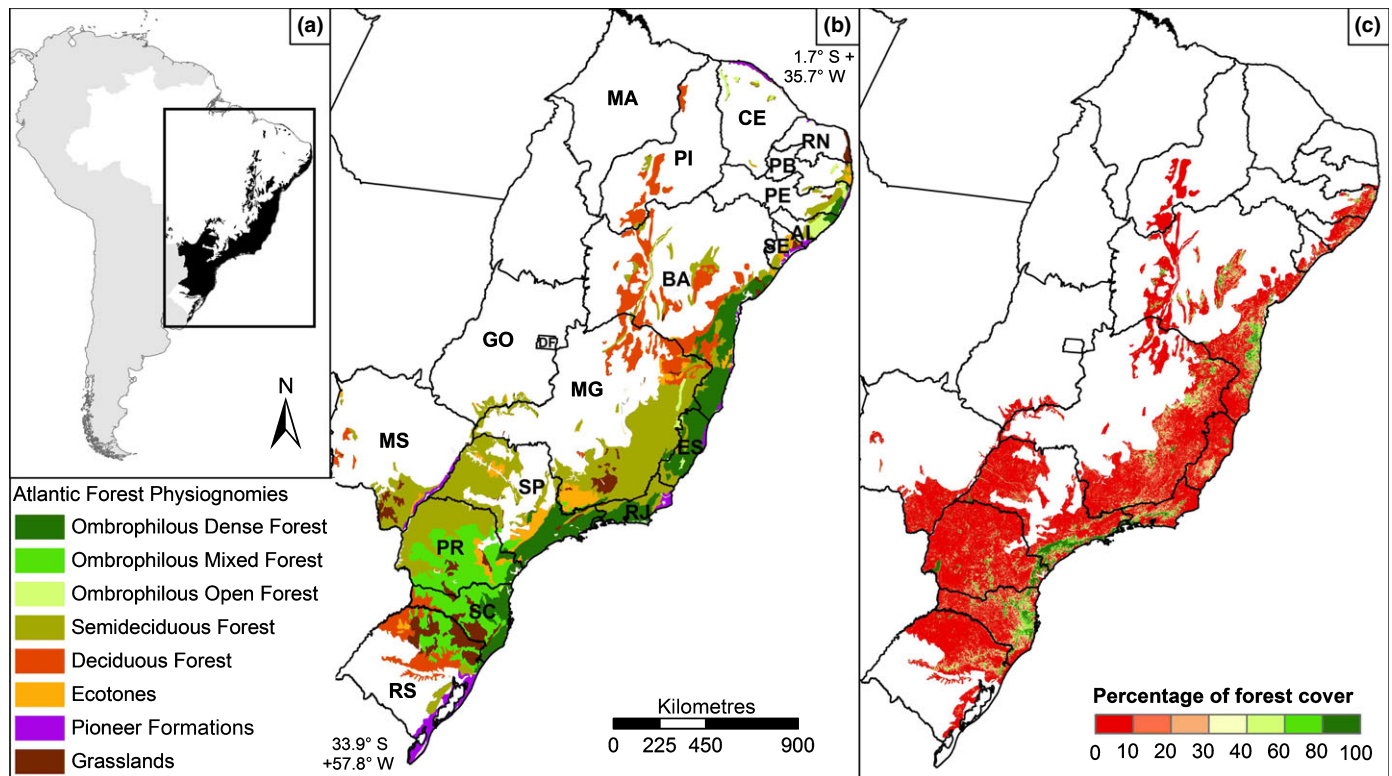


Fig. 1 Maps showing the original spatial distribution of the Atlantic Forest domain (a, in black), the main vegetation physiognomies that compose this domain (b), and the remaining forest cover in 2008 (Ribeiro *et al.*, 2009), represented in cells of 256 ha (c). Abbreviation of Brazilian states in (b): MA, Maranhão; PI, Piauí; CE, Ceará; RN, Rio Grande do Norte; PB, Paraíba; PE, Pernambuco; AL, Alagoas; SE, Sergipe; BA, Bahia; GO, Goiás; DF, Distrito Federal; MG, Minas Gerais; ES, Espírito Santo; RJ, Rio de Janeiro; SP, São Paulo; MS, Mato Grosso do Sul; PR, Paraná; SC, Santa Catarina; RS, Rio Grande do Sul.

South-East Reserves on the list of World Natural Heritage Sites by UNESCO (The United Nations Organization for Education, Science and Culture; <http://whc.unesco.org/en/list/893>).

The diversity of plants provides conditions for the development of uncountable interactions with microorganisms, both in the rhizosphere and in the phyllosphere. Using a sample of three individual trees from nine different tree species, Lambais *et al.* (2006) estimated that each tree species carried 95–671 bacterial species, 97% of which were unknown, which would yield *c.* 2–13 million new bacterial species in the Atlantic Forest.

2. Ecosystem services provided by the Atlantic Forest

The importance of the Atlantic Forest goes beyond the maintenance of its rich and diverse biota. The Atlantic Forest also provides a broad set of relevant *ecosystem services*, that is, the direct and indirect contributions of ecosystems to human well-being (TEEB, 2010). First, the Atlantic Forest provides water for > 125 million Brazilians, representing three-quarters of the country's population. Sap flow measurements were used to demonstrate that certain large emergent tree species inhabiting the lowland Atlantic Forest, such as *Hyeronima alchorneoides* Allemão (Phyllanthaceae), may transpire > 350 l d⁻¹ during the dry season and 525 l d⁻¹ in the wet season (Rosado, 2011). Smaller understory plants, such as *Rustia formosa* Klotzch (Rubiaceae), transpire 65 l d⁻¹ in the winter and 79 l d⁻¹ in the summer (Rosado, 2011).

Water provided by the Atlantic Forest is important not only for drinking but also for producing electricity, mainly in the Parana River watershed. The complex of reservoirs and dams within the Atlantic Forest produces *c.* 130 GWh (62% of Brazil's production) and includes the second-largest hydroelectric power station in the world, Itaipu (<http://www.itaipu.gov.br/en>). Additionally, the Atlantic Forest provides food. The fruits of the Myrtaceae species, as well as those of palms, legumes and passion flowers (*Passiflora* spp.), are an important component of the diet of traditional and local people, while other species provide important raw materials such as fibres (Satyanarayanaa *et al.*, 2007) and oils (Apel *et al.*, 2006). The most widely recognized Atlantic Forest fruit is that of the monkey puzzle tree/Brazilian pine (*Araucaria angustifolia*). Hunting of native species is not permitted in Brazilian territory, although many traditional populations still rely on vertebrates of the Atlantic Forest as a complementary source of protein (Hanazaki *et al.*, 2009). Although proof is scarce, the Atlantic Forest cover probably affects the productivity of adjacent estuarine areas and coral reefs, which historically support subsistence and commercial fisheries along the Brazilian Atlantic coast (Hanazaki *et al.*, 2009).

Undoubtedly, the Atlantic Forest has an important role in climate regulation. Although published data remain sparse, the forest plays an important role in rainfall distribution throughout the year. The stability of this system controls soil stability on the steep slopes of the Serra do Mar as well as the levels of rivers and reservoirs. The consequences of disrupting this stability include

landslides and floods, which have occurred every summer, from December to March, in the heavily populated areas of Santa Catarina, Sao Paulo and Rio de Janeiro (Manfré *et al.*, 2012). In terms of agriculture-related services, for example, the Atlantic Forest hosts *c.* 60 species (Peruquetti *et al.*, 1999) of Euglossini bees, known to be long-distance pollinators as a consequence of their exceptional flight performance and characterized by large populations with high gene diversity and gene flow (Rocha Filho *et al.*, 2013). However, the performance of these species as pollinators of local crops is at risk because of habitat loss, invasion by exotic species and climate change (Giannini *et al.*, 2012; Imperatriz-Fonseca *et al.*, 2012).

Finally, the cultural value of the Atlantic Forest dates back > 8000 yr. Paleo-Indian records of the so-called 'Sambaqui Culture' indicate that coastal and riverine shell mounds were used for sacred and secular activities (Gaspar *et al.*, 2011; Villagran *et al.*, 2011; Figuti *et al.*, 2013). Currently, Atlantic Forest remnants are important for recreational purposes in urban areas, where they serve as parks or urban forests. Perhaps the most striking example is the Tijuca National Park in Rio de Janeiro, which began in 1861 as a restoration project to protect springs that supply water to the city. Over a period of 13 yr, > 100 000 seedlings of native species were planted in the area (Drummond, 1996), and it is now considered one of the largest urban forests in the world. The forest also ensures soil stability and protects the slopes surrounding Rio de Janeiro City. All those services provided by the Atlantic Forest are nowadays threatened by human degradation. As in most tropical biotas, we have just begun to study and understand the spectrum of goods and services provided by the Atlantic Forest, which has supported the development of Brazilian society (Dean, 1997).

3. Disturbance history

Since the European colonizers disembarked on the Brazilian coast 500 yr ago, the Brazilian Atlantic Forest has been exposed to high levels of deforestation and fragmentation, which have affected its highly diverse biota. Its history of deforestation started on 22 April 1500, the day of discovery, marked by the cutting of a tree to build a cross at the landing site (Dean, 1997). Discovery was followed by a long period of exploitation that started in the 16th Century with the logging of the Pau-Brasil tree (*Caesalpinia echinata*), which is now an endangered species. This activity was followed by the economic exploitation of different commodities, such as sugar cane in the northeast during the 17th Century, coffee in the southeast during the 18th and 19th Centuries and cocoa in Bahia throughout the 19th and 20th Centuries (Tabarelli *et al.*, 2005). Soil degradation under coffee plantations eventually led to the expansion of cattle ranching in Sao Paulo and Minas Gerais. More recently, *Eucalyptus* plantations for cellulose and paper production have replaced cattle ranching in southeastern states.

The forest was also replaced by cities, which are now home to *c.* 125 million Brazilians, as all of the state capitals from the south, southeast and northeast regions, including Porto Alegre, Curitiba, São Paulo, Rio de Janeiro, Belo Horizonte, Salvador and Recife, are within the Atlantic Forest domain. Although decoupled from agricultural expansion (Lapola *et al.*, 2013), new areas of forest are

still lost every year, mainly as a result of urban growth or the expansion of infrastructure, such as roads, gas and oil pipelines and water reservoirs. The expansion of urban areas, as either slums or luxurious condos, is also an important pressure further reducing the area of the Atlantic Forest (Torres *et al.*, 2007).

When considering stands larger than 100 ha, only 7.6% of the original Atlantic Forest remains today (Fig. 1a and detailed map at <http://www.sosma.org.br/projeto/atlas-da-mata-atlantica>). Regarding intermediate secondary forest stands and fragments smaller than 100 ha, which make up *c.* 32–40% of the standing forest, the remaining Atlantic Forest coverage ranges from 11.4% to 16% (Ribeiro *et al.*, 2009); protected areas represent only 9% of the remaining forest and 1% of the original forest cover. As overarching protection, all Atlantic Forest remnants were incorporated within the Atlantic Forest Biosphere Reserve by UNESCO (<http://www.rbma.org.br>).

As a result of this long history of disturbance, most of the remaining Atlantic Forest is immersed in human-modified landscapes, with a dynamic combination of the following main habitat components (Tabarelli *et al.*, 2010b): a few large patches of old-growth forest; many small, edge-affected forest remnants with varying degrees of disturbance (Ribeiro *et al.*, 2009); early- to late-secondary forest patches recovering from cropland or pasture abandonment; small patches of assisted regenerating forests (*sensu* Chazdon, 2008); agroforestry patches; and managed plantations of exotic trees, such as *Pinus* and *Eucalyptus* (Fonseca *et al.*, 2009). Agro-mosaics are spatially arranged as variegated or relictual landscapes and experience cycles of land abandonment resulting from agricultural fallow periods, the suppression of secondary forest patches for crop or pasture lands and shifting economic activities (Cartes, 2003; Metzger *et al.*, 2009; Teixeira *et al.*, 2009). In addition to reduced forest coverage, many landscapes have experienced a process of severe defaunation with the complete extirpation of large-bodied vertebrates (Canale *et al.*, 2012). Finally, the majority of land set aside for conservation purposes is recognized as marginal agricultural land resulting in highly modified landscapes across lowland areas, including those considered as centres of species endemism (Tabarelli *et al.*, 2010b). Thus, the Atlantic Forest has been converted into an anthrome *sensu* Ellis *et al.* (2010).

III. Biotic homogenization and forest secundarization

Overall, human disturbances, ranging from selective logging and poaching to the fragmentation of native forests to agriculture, produce rapid shifts in the frequency and abundance of species in particular ecological groups. These changes impact the structure of biological communities and ecosystem functions at multiple spatial scales, which we will discuss below in this section, based on studies on trees.

In the Atlantic Forest, tree species (≥ 10 cm diameter at breast height (DBH)) surveys in some aging, human-modified landscapes have documented the emergence of impoverished tree assemblages across edge-affected habitats (*i.e.* forest edges and small forest fragments). Specifically, we refer to assemblages experiencing a reduction in species richness (*i.e.* up to a 50% reduction) and

increased levels of species dominance. Briefly, tree species bearing large seeds or large fleshy fruits, those pollinated by specialized biotic vectors, those with supra-annual reproduction and those with large adults (i.e. emergent tree species) become rare in edge-affected habitats, whereas a limited number of successional or pioneer taxa tend to proliferate (Girão *et al.*, 2007; Oliveira *et al.*, 2008; Tabarelli *et al.*, 2010a,b; Farah *et al.*, 2014). Epiphytes, particularly those endemic to the Atlantic Forest and inhabiting the emergent forest layer, are sensitive to the human disturbances imposed on this biota (Siqueira-Filho & Tabarelli, 2006; Leão *et al.*, 2014).

Shifts in the ecological profiles of plant assemblages are thought to cause (1) reduced functional diversity (Lopes *et al.*, 2009), particularly in terms of reproductive strategies; and (2) a loss of phylogenetic information (Santos *et al.*, 2010; Arroyo-Rodríguez *et al.*, 2012). Habitat desiccation and seed dispersal limitation have been reported as the main forces driving the reorganization of plant assemblages at multiple spatial scales (Silva & Tabarelli, 2000; Melo *et al.*, 2007; Santos *et al.*, 2008; Costa *et al.*, 2012). These drastic shifts in the nature of adult tree assemblages are consistent with patterns documented in seedling assemblages across edge-affected habitats of the Atlantic Forest, including impoverished assemblages dominated by small-seeded species that are mostly classified as early-successional species (Melo *et al.*, 2007; Santo-Silva *et al.*, 2013). These findings suggest that tropical forests may experience biotic homogenization or floristic or functional convergence at the regional level as natural landscapes are converted to human-modified landscapes. For example, comparisons of flora in the Atlantic Forest of northeastern Brazil based on plant records before and after 1980 revealed an increase of nearly 20% in cross-community species similarity. This increase was partially a result of increased abundance of successional and small-seeded tree species, which were classified as winner species (Lôbo *et al.*, 2011).

At the ecosystem level, impoverished assemblages dominated by a few successional species that support reduced aboveground biomass (Oliveira *et al.*, 2008; Paula *et al.*, 2011) indicate that edge-dominated forest fragments move towards early-successional systems; that is, a type of retrogressive succession or forest degeneration (Santos *et al.*, 2008; Tabarelli *et al.*, 2008). It is true that edge effects tend to favour a small set of biologically homogeneous species (i.e. pioneer or successional species) and edge-affected habitats may support tree assemblages that are almost indistinguishable, in terms of tree species richness and species or functional composition, from patches of early- to mid-successional secondary forests (i.e. < 45 yr old) that remained distinct from tree assemblages in old-growth forest interior areas (Santos *et al.*, 2008). These pioneer-dominated assemblages may approach near-equilibrium conditions, thereby representing a quasi-final successional stage that is more stagnant than transient, that is, an alternative state of equilibrium. Furthermore, these assemblages tend to persist as matrices and remain dominated by open habitats such as grasslands (Tabarelli *et al.*, 2008; Paula *et al.*, 2011).

Given that human-modified landscapes generally favour a small set of biological strategies and thus maintain impoverished assemblages across edge-affected habitats, forest remnants and

secondary forest patches tend to converge in terms of community structure and ecosystem function as both forest degeneration and regeneration proceed. In this context, community- or ecosystem-level key attributes (e.g. species richness, ecological composition and aboveground biomass) are determined by a combination of patch and landscape metrics such as patch size and connectivity, here referred to as landscape integrity (Fig. 2a; Tabarelli *et al.*, 2012b). In this context, cross-biota differences in response to the emergence of human-modified landscapes largely result from the relative importance of old-growth flora or forest-dependent species in the regional pools of species (Banks-Leite *et al.*, 2012; Martensen *et al.*, 2012). In other words, biotas naturally supporting a high proportion of disturbance-adapted species in the baseline flora (e.g. pioneer species) are expected to experience reduced levels of forest degeneration and permit appropriate forest regeneration across human-modified landscapes (Fig. 2b). Conversely, those supporting a high proportion of species requiring undisturbed forest habitat tend to experience intense degeneration of their forest remnants, while secondary forest stands face a form of arrested succession supporting impoverished communities (Fig. 2c) (Arroyo-Rodríguez *et al.*, 2012; Tabarelli *et al.*, 2012b).

Such 'secdarization' experienced by edge-affected habitats via the permutation of the old-growth flora by successional plant species is likely to involve at least two waves of species loss across hyper-fragmented landscapes dominated by open-habitat matrices (Tabarelli *et al.*, 2012a). The first wave results from the replacement of highly diversified old-growth flora by a small set of ecologically redundant but phylogenetically unrelated native r-strategist species. The second wave of extinctions includes the extirpation of fauna associated with old-growth flora, such as large frugivorous vertebrates and specialized pollinators and herbivores, as the collapse of the old-growth flora reduces the spectrum of resources for species using these plants (see Lopes *et al.*, 2009; Tabarelli *et al.*, 2010a). Therefore, trophic interactions in human-modified landscapes are expected to be preferentially composed of generalist-generalist mutualisms, as proposed by Tabarelli *et al.* (2012a). This bottom-up reorganization of the Atlantic Forest operates in parallel to the potential effects caused by the defaunation of human-modified landscapes and the consequent collapse of the dispersal services provided by these vertebrates (Canale *et al.*, 2012; Galetti & Dirzo, 2013). The proliferation of leaf-cutting ants across edge-affected habitats in both Atlantic Forest and Amazonian landscapes (Urbas *et al.*, 2007; Dohm *et al.*, 2011) represents a didactic example of the trophic cascade triggered by habitat fragmentation and the consolidation of human-modified landscapes because these organisms benefit from the proliferation of disturbance-adapted, palatable plant species across forest edges; that is, the relaxation of bottom-up population control (Leal *et al.*, 2014). Finally, human-dominated landscapes, where edge-affected habitats are prevalent, tend to exhibit a limited capacity for providing ecosystem services, such as carbon storage and flood control, because these habitats experience a collapse of the aboveground biomass (Oliveira *et al.*, 2008; Paula *et al.*, 2011).

Some of the patterns documented in the Atlantic Forest have been found elsewhere, particularly in the Amazon Forest (see Laurance *et al.*, 2006; Michalski *et al.*, 2007; Santos *et al.*, 2012).

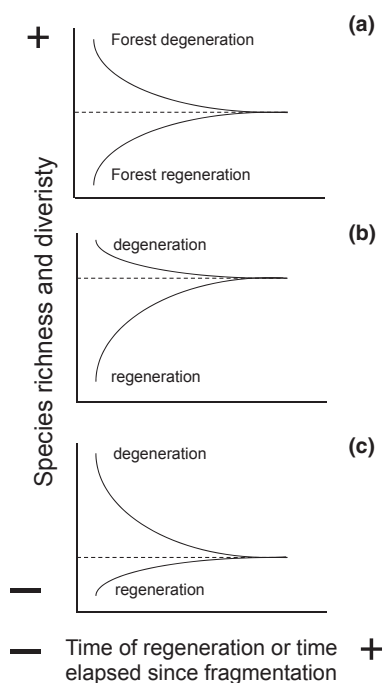


Fig. 2 Degeneration of forest remnants and regeneration across secondary-forest stands in human-modified landscapes dominated by edge-affected habitats. (a) Both processes are time dependent (x -axis) and tend to reach a potential climax community (dotted line), which is conditioned by 'landscape integrity' and exhibits corresponding attributes at the community or ecosystem level (y -axis), such as species richness and diversity; (b) considering the same level of landscape integrity, biotas supporting a diverse flora of disturbance-adapted species are less susceptible to degeneration and exhibit higher levels of resilience; (c) compared with biotas supporting a higher proportion of disturbance-sensitive species. Adapted from Tabarelli *et al.* (2012b).

Overall, the patterns suggest the 'secondarization' of tropical forest remnants as occupants of human-modified landscapes, but the magnitude and generality of this trend remain obscure, as do its implications for the persistence of biodiversity and the maintenance of ecosystem services (see Arroyo-Rodríguez *et al.*, 2012, 2013). Despite this uncertainty, forest secondarization and biotic convergence/homogenization at multiple spatial scales represent a form of biological reorganization. This process is congruent with other potential responses to the emergence and consolidation of human-modified landscapes exhibited by the tropical forest ecosystem, such as forest die-back via receding forest edges (Gascon *et al.*, 2000) caused by a combination of climate change and fire (Nepstad *et al.*, 1999) or frequent fires (Barlow & Peres, 2008). Additionally, findings from the Atlantic Forest reinforce the following key notions: (1) forest response, at least in terms of intensity, is context- or landscape-dependent as it is largely affected by the historical use of natural resources, landscape spatial configuration and matrix use among a myriad of driving forces (Gardner *et al.*, 2009; Arroyo-Rodríguez *et al.*, 2013); (2) species loss and biodiversity decline are highly deterministic and associated with biological strategies that are sensitive to human-induced disturbances (Oliveira *et al.*, 2004; Siqueira-Filho & Tabarelli, 2006; Rigueira *et al.*, 2013; Leão *et al.*, 2014); (3) some native plant

species are able to proliferate at multiple spatial scales (i.e. 'winner species'), largely contributing to biotic homogenization (Tabarelli *et al.*, 2012a); (4) large patches of old-growth forest represent irreplaceable habitat for biodiversity conservation (Santos *et al.*, 2008); (5) it is unlikely that we will achieve biodiversity-friendly landscapes without effective management and regulation of land use (Tabarelli, 2010; Melo *et al.*, 2013a); and (6) cross-forest comparisons and long-term ecological research are required to better understand the final or transient nature of tropical forests immersed in human-modified landscapes.

IV. Species persistence at larger scales

Despite the clear and strong effects of biotic homogenization and secondarization leading to plant species extirpation at local and landscape scales, almost all of the Atlantic Forest species recorded in the last 200 yr since Martius & Spix (1981) began to describe and record them in the early 19th Century are still present in some forest remnants, although population sizes are critically low in several cases. Therefore, there are few records of species extinctions in the Atlantic Forest for either plants or animals (Brooks & Balmford, 1996; Brooks *et al.*, 1999). These low extinction rates are not consistent with rates expected by the well-documented species–area relationship (Dengle, 2009), which predicts the loss of almost half of the endemic species when 90% of the original cover is lost. Considering the presence of *c.* 3200 endemic tree species in the Atlantic Forest (Mittermeier *et al.*, 2004), we would expect 1000–1500 species to be extinct by now. However, only seven tree species are presumed to be extinct: Aspleniaceae: *Asplenium beckeri* Brade; Acanthaceae: *Ruellia chamaedrys* (Nees) Angely; Isoetaceae: *Isoetes bradei* Herter; Rubiaceae: *Hindsia violacea* Benth.; Solanaceae: *Solanum spissifolium* Sendtn.; Symplocaceae: *Symplocos altissima* Brand and *Symplocos neglecta* Brand. Three Bromeliaceae (*Cryptanthus fosterianus* L.B.Sm., *Neoregelia binotti* (Antoine) L.B.Sm and *Nidularium utriculosum* Ule) are considered extinct in the wild. An additional 275 species from the Atlantic Forest, including trees (Apocynaceae, Araucariaceae, Burseraceae, Combretaceae, Fabaceae, Lauraceae, Lecythidaceae, Monimiaceae, Myrtaceae, Rubiaceae and Sapotaceae), palms (*Euterpe* and *Bacrtis*), ferns (Aspleniaceae, Blechnaceae and Dicksoniaceae) herbaceous plants (Acanthaceae, Amaranthaceae, Heliconiaceae and Solanaceae) and epiphytes (Araceae, Bromeliaceae, Cactaceae, Gesneriaceae, Orchidaceae and Passifloraceae), are listed as endangered (Brasil, 2008).

This discrepancy or paradox between local biological homogenization and the lack of massive large-scale species extinctions may be because intense biotic homogenization and forest secondarization are not a general response across all Atlantic Forest types (from evergreen to deciduous forests). However, at least the following three additional landscape processes, explored in research projects developed in the Atlantic Forest, can help explain this paradox: landscape supplementation and complementation, nonlinear extinction processes and time-lagged responses to deforestation. These processes suggest that the Atlantic Forest biota is more resilient to extinction than inferred from particular landscapes or local-scale data.

1. Landscape supplementation and complementation

The landscape context can be as important as local conditions for understanding species persistence in fragmented landscapes. This context has been well documented in the Atlantic Forest, where even small fragments can support a large number of tree species (Metzger, 1997, 2000) if the forest is not highly degraded or invaded by exotics. Tree species richness is not commonly related to the size of the fragment but, rather, to forest connectivity surrounding the focal fragment. In other words, small forest fragments linked structurally or functionally (e.g. through seed dispersal) to neighbouring fragments by corridors and stepping-stones can be as rich as larger fragments. This pattern suggests that the effective habitat area is not limited by the size of the fragments; in fact, this area may be composed of the sum of several neighbouring fragments if the matrix and spatial arrangement of the fragments allow for biological flux among them (Martensen *et al.*, 2008). Organisms or populations can thus supplement their resource needs using habitat patches scattered across the landscape according to a process known as 'landscape supplementation' (Dunning *et al.*, 1992).

Additionally, there is strong evidence that several forest-dependent species can use, and even live in, certain types of inter-habitat matrices acting as a lower quality habitat or highly permeable region. This evidence is especially clear for matrices that are structurally similar to the forest, such as agroforestry patches (Cullen *et al.*, 2001; Faria *et al.*, 2006; Schroth *et al.*, 2011) or *Eucalyptus* plantations with an understory composed of regenerated natural forest (Fonseca *et al.*, 2009). Organisms or populations that are able to use resources from different types of habitat are able to complement their resource needs ('landscape complementation', sensu Dunning *et al.*, 1992). When the matrix is highly permeable, fragment size and fragmentation effects can be completely masked by landscape supplementation and complementation processes, and as a consequence, species persistence can only be understood considering the entire landscape composition and arrangement (Pardini *et al.*, 2009).

In this context, the concepts of landscape supplementation and complementation, and of habitat reachability or availability (the amount of habitat that a species can reach or use not only in a focal patch but also in the entire landscape given its dispersal capacity; Pascual-Hortal & Saura, 2006; Saura & Rubio, 2010) are more useful concepts for understanding species richness distribution than species–area relationships or even island biogeography theory. All of those theories overemphasize the importance of fragment areas, disregarding the importance of the matrix and oversimplifying the effect of isolation. Isolation is usually measured only as the distance to the nearest fragment or to a large neighbouring fragment. However, isolation should be considered comprehensively by taking into account the distance to and size of all fragments within a neighbouring region and weighting the distance by the quality of the matrix. Better measures of isolation are provided by graph theory (Urban & Keitt, 2001) and habitat availability or reachability indices. Furthermore, habitat availabilities at different spatial scales may interact. Consequently, the species–area relationship can be

modulated by habitat cover at a larger scale (Banks-Leite *et al.*, 2012). This modulation means that a large fragment, in the context of a paucity of available habitat in the landscape, can be just as rich as a small fragment with abundant available habitat in the surrounding region (Banks-Leite *et al.*, 2012; Martensen *et al.*, 2012).

In summary, species richness cannot be explained by a simple species–area relationship, disregarding matrix and other landscape effects; in particular, local species loss can be avoided or postponed, depending on the landscape context, through landscape complementation and supplementation effects.

2. Extinction and fragmentation thresholds

Landscape context matters mainly because recolonization from surrounding fragments may compensate for local species extinction (Pardini *et al.*, 2010), as long as extinction does not occur simultaneously in all fragments in a landscape. This process is similar to metapopulation dynamics but does not require that all species comply with the strict assumptions of metapopulation theory. Species respond to habitat availability at larger scales, which are often composed of several proximal fragments; this finding has led some authors to argue that the most important explanatory factor affecting species occurrence and abundance is the amount of habitat that occurs at an appropriate scale for the focal species (Fahrig, 2003, 2013).

Consequently, the risk of species extinction should not be measured at the fragment scale but, rather, at the landscape scale. This risk increases as the amount of forest decreases, but this relationship is not linear. There is a clear extinction threshold (ET), that is, a minimum amount of habitat that allows species to persist (Fahrig, 1997; Fig. 3a). Recent data from the Atlantic Forest support the existence of these thresholds and, interestingly, suggest that several groups of plants and animals share the same threshold, in which local extinction is triggered when remaining habitat is < 30% of the original landscape cover.

This threshold was found for Sapotaceae (Lima & Mariano-Neto, 2014) and Myrtaceae (Rigueira *et al.*, 2013) species in the northeastern Atlantic Forest and for birds (Martensen *et al.*, 2012), small mammals (Pardini *et al.*, 2010) and amphibians (M. Dixo *et al.*, unpublished) in the southeast. An explanation for this common extinction threshold that occurs for such diverse taxonomic groups in different regions of the Atlantic Forest is the occurrence of several drastic changes in landscape structure when 30–50% of the habitat cover remains, when spatial variability is higher (Fig. 3b) and landscape connectivity tends to decrease rapidly (Fig. 3c). At this intermediate habitat cover, there is a rapid reduction in the mean fragment size and a sharp increase in the number of fragments and isolation among fragments, which may accelerate the effects of fragmentation on species persistence (Fahrig, 1997, 2003). Habitat configuration (i.e. the spatial arrangement of habitat at a given time) can also be relevant for species persistence, particularly if the configuration affects a species' movement throughout the landscape. For some authors, those effects occur when the amount of habitat is low, for example, below 20–30%, a level known as the 'fragmentation threshold'

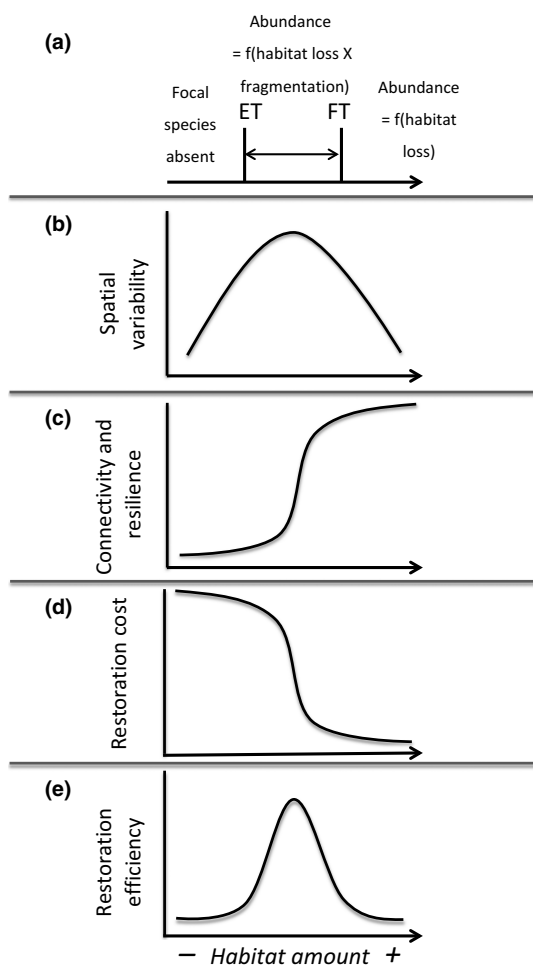


Fig. 3 According to the conceptual model proposed by Villard & Metzger (2014), (a) habitat loss and fragmentation are expected to interact, affecting species abundance at an intermediate range of habitat amount, between the fragmentation threshold (FT) and the extinction threshold (ET), and (b) when variability in the spatial arrangement of habitat patches (i.e. their spatial configuration) is higher. (c) Landscape connectivity typically presents a nonlinear modification with habitat amount, with a sharp decrease at an intermediate cover level (Metzger & Décamps, 1997). Landscape resilience, as defined by Tambosi *et al.* (2014), is closely related to habitat amount and connectivity and thus follows the same shape of landscape connectivity. (d) Restoration cost is inversely related to landscape resilience if we consider the same level of local degradation. (e) Consequently, restoration efficiency (the balance between cost and benefit) should be maximized at an intermediate level of habitat amount, when the cost is not so high, and the benefit is not too low (in other words, when resilience is not too low or too high).

(FT; Fig. 3a). However, a more recent theoretical model suggests that the habitat amount and configuration interact at an intermediate range of habitat cover, between the ET and FT (Fig. 3a), when the habitat configuration is more variable (Villard & Metzger, 2014; Fig. 3b).

The finding that landscapes with intermediate habitat coverage (i.e. *c.* 20–50%) are those in which the risk of extinction increases rapidly calls attention to the urgent need to develop consistent conservation and restoration actions for these landscapes (Fig. 3d,e; see Section VI).

3. Time-lagged response to deforestation

If extinction is accelerated when *c.* 20–50% of the forest remains, why have so few extinction events been documented for the Atlantic Forest despite most of the region presenting a forest cover below this limit? The most consistent answer is the existence of a time-lagged response of species to landscape changes. Changes in landscape structure affect population and metapopulation processes, generally leading to a progressive reduction in species abundance over time, thus postponing extinction events until after a specific delay (also known as 'relaxation time'; Diamond, 1972), which can be particularly lengthy for long-lived species.

Studies on time-lagged responses of plant species to landscape changes have mostly been limited to temperate regions, especially grasslands (e.g. Lindborg & Eriksson, 2004; Ernout *et al.*, 2006; Koyanagi *et al.*, 2012; Takkis *et al.*, 2013). This process is poorly studied or understood in tropical forest environments. In the Atlantic Forest, the first evidence of a time-lagged response is that certain species respond better to past than present landscape structure, particularly long-lived species, such as most trees (Metzger, 1998; Metzger *et al.*, 2009; Rigueira *et al.*, 2013). The extent of this time lag is related to species traits other than species longevity, such as aging, trophic level, dispersal ability and the degree of habitat specialization (Ewers & Didham, 2006). Studies in the Atlantic Forest have shown that this time lag can be longer than 50 yr for trees and birds (Brooks *et al.*, 1999; Metzger *et al.*, 2009; Lira *et al.*, 2012a), suggesting that these species have not yet responded to the most recent deforestation events. Consequently, the Atlantic Forest probably carries a large *extinction debt*, that is, a large number of species that are predicted to go extinct, even without further landscape modification, because the threshold condition for their persistence is no longer satisfied (Tilman *et al.*, 1994).

Therefore, landscape supplementation and complementation in association with nonlinear extinction and time-lagged extinction responses to deforestation may explain why so few species have gone extinct in the Atlantic Forest (i.e. at the biota spatial scale) despite tangible responses to human disturbances, particularly in terms of the tree assemblage structure at the local scale.

V. Future threats: climate change impacts

In addition to deforestation and fragmentation effects, the highly diverse Atlantic Forest biota is threatened by climate change, which can considerably modify the abiotic conditions for species survival in the future (Colombo & Joly, 2010; Souza *et al.*, 2011).

Using species distribution modelling with nine climatic parameters, Colombo & Joly (2010) determined the present and future geographical distribution of 38 tree species typical of the Brazilian Atlantic Forest. They considered two scenarios: (1) an optimistic scenario based on a 0.5% increase in the concentration of CO₂ in the atmosphere and an increase of up to 2°C in the Earth's average temperature; and (2) a pessimistic scenario based on a 1% increase in the concentration of CO₂ in the atmosphere and a temperature increase of ≤ 4°C. The results showed an alarming reduction of the areas in which the studied species are likely to occur in the future

(Fig. 4) as well as a shift towards southern Brazil. The optimistic scenario predicts a 20–25% reduction, whereas in the pessimistic scenario, reduction reaches 30–50%. The species that showed the largest reduction in their distribution were *Euterpe edulis*, *Mollinedia schottiana*, *Virola bicuhyba*, *Inga sessilis*, *Vochysia magnifica*, *Hyeronima alchorneoides*, *Schefflera angustissima*, *Andira fraximifolia* and all studied Myrtaceae species (Fig. 4). These results reinforce the idea that species with restricted habitat conditions, such as the palm heart tree (*Euterpe edulis*) and *Mollinedia schottiana*, are the most threatened.

Colombo & Joly (2010) also found a strong tendency for the present species distribution to shift towards southern Brazil, northwestern Rio Grande do Sul State, western Santa Catarina State or areas where the topography ensures cooler climates, such as the Serra do Mar, a range of coastal mountains in Parana-Sao Paulo and Rio de Janeiro States. Similar results were found in research on other taxonomic groups, such as *Lutzomyia* species, which are leishmaniasis vectors in South America (Peterson & Shaw, 2003); the nonnative invasive bullfrog, *Lithobates catesbeianus* (Giovanelli *et al.*, 2008); marsupials (Loyola *et al.*, 2012); and major Brazilian crops (Zullo *et al.*, 2006; Assad *et al.*, 2013).

Therefore, climate change may be an additional pressure or may even intensify local biotic homogenization and secondarization processes, accelerating the payment of the present ‘extinction debt’ carried by the Brazilian Atlantic Forest, as already proposed for other biodiversity hotspots (Piqueray *et al.*, 2011). The potential synergism between climate change and shifts in land use poses a major threat to tropical biodiversity, ecosystem services and human well-being (Tabarelli *et al.*, 2004) and has launched a new era of uncertainty regarding tropical forests.

VI. Atlantic Forest conservation: integrating basic and applied research agendas

The Atlantic Forest has suffered from a long and intensive disturbance history that has led to the impoverishment of its biota in several locations, but most of its original species are still present if we consider the entire biome. This situation provides unique opportunities to plan and act for the conservation of this forest.

The findings examined in this review reinforce the need for research agendas to address the following topics: (1) biodiversity description and identification (new species, from plants to primates, are still being described); (2) the forest response to human disturbances across different forest types and socio-economic contexts; (3) the relationship among biodiversity, ecological processes and ecosystem services considering different climate change scenarios; and (4) economic instruments to support sustainability. Because the forest response to human disturbances and climate change operates over many years, we emphasize the utility of long-term, socio-ecological research initiatives able to integrate basic and applied topics, including the socio-economic constraints to implementing highly complementary approaches on the ground, such as biodiversity-friendly landscapes, smart landscapes and biodiversity corridors. Among integrated/comprehensive biodiversity-focused initiatives, perhaps the most ambitious and replicable is the BIOTA/FAPESP Program (Joly *et al.*, 2010; and www.biota.org.br), which is run by a public scientific agency (State of São Paulo Research Foundation, FAPESP). This programme encompasses a conceptually inductive research programme involving the description, conservation, restoration and sustainable use of biodiversity and ecosystem services based in

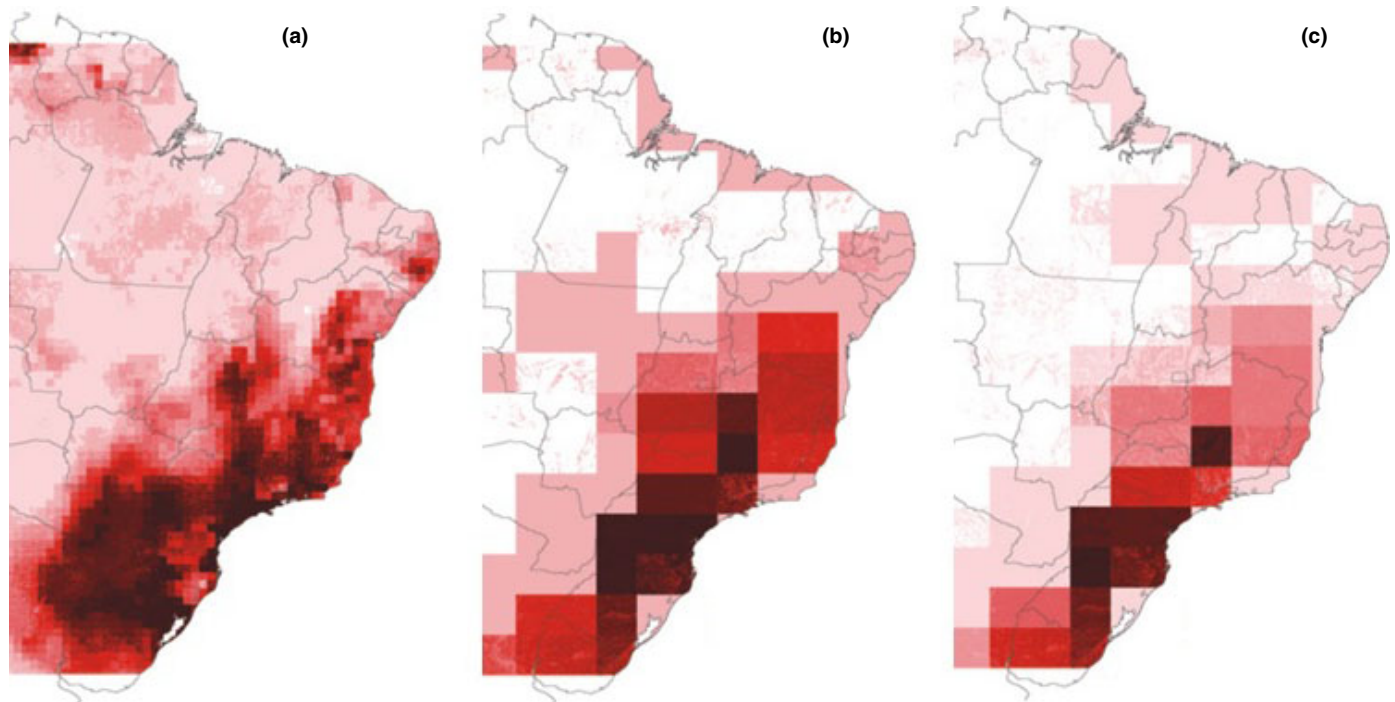


Fig. 4 Sum of the areas of potential occurrence for the 38 species studied in optimistic and pessimistic climate change scenarios. The darker the area, the higher the probability of occurrence. (a) Present occurrence of these species; (b) occurrence of these species in the optimistic scenario; (c) occurrence of these species in the pessimistic scenario. Modified from Colombo & Joly (2010).

the state of São Paulo. In addition to increasing knowledge, this programme has proposed measurable outcomes in terms of (1) capacity building (including a myriad of stakeholders, from elementary school teachers to researchers operating in private companies and academics devoted to biodiversity science); and (2) supporting public policies regarding biodiversity conservation, land use planning, the use of natural resources and biodiversity research.

In terms of biodiversity description and use, we highlight the link with the private sector based on identifying new natural compounds to be used by the pharmaceutical, cosmetic and food industries through bioprospecting. A percentage of the royalties generated by licensing patents obtained by the programme will be invested in biodiversity conservation actions. To date, BIOTA has produced eight patents, two of which are in the licensing process. Exploring the chemodiversity of the Atlantic Forest biota may add value to biodiversity, transforming conservation and sustainable use into highly profitable activities for forest inhabitants (Pavarini *et al.*, 2012).

A practical result of the BIOTA/FAPESP Program is the identification of priority areas for biodiversity conservation, including those in which habitat restoration is a requirement, highlighting the importance of considering landscape parameters to improve the biodiversity conservation value of Atlantic Forest landscapes. These results have been used by the state government to improve the environmental legal framework and to establish agro-ecological zoning for sugar cane expansion. There are now 23 legal instruments based on the results of the BIOTA/FAPESP Program.

These outcomes required 7 yr of data entry into databanks developed by the BIOTA/FAPESP Program (<http://sinbiota.biota.org.br/>), including cross-referencing species information with a detailed cartographic layer, before they could be used to establish priority areas for biodiversity conservation and restoration. This time span highlights the following two fundamental aspects of biodiversity science: (1) the requirement for long-term, consistent funding based on achievements and goals; and (2) the imperative for long-term, well-structured databanks with a friendly interface for multiple users and full interoperability with similar databanks, such as those maintained by the Global Biodiversity Information Facility (GBIF; www.gbif.org). Because they are designed to support the permanent development of new modules, including those addressing global climate change, such databases support a myriad of initiatives and approaches, such as the biodiversity scenarios (Pereira *et al.*, 2010). As a combination of socio-economic scenarios and models of impacts of global change on biodiversity, biodiversity scenarios represent an essential tool for (1) better understanding and synthesizing a broad range of observations; (2) alerting decision makers to undesirable future impacts of global change, such as land use change, invasive exotic species, overexploitation, climate change or pollution; (3) providing decision support for developing adaptive management strategies; and (4) exploring the implications of alternative socio-ecological development pathways and policy options.

BIOTA has also supported habitat restoration projects. Acknowledging the fact that biodiversity persistence in human-modified landscapes in many situations relies on ambitious

initiatives of habitat restoration, the Atlantic Forest stakeholders have long been engaged in this topic by providing restoration technology, legal support, regulation and economic opportunities (Rodrigues *et al.*, 2011). Restoration projects are in fact the only way to avoid paying the Atlantic Forest's extinction debt. Almost 30 yr of experience were recently consolidated in the Atlantic Forest Restoration Pact (ARFP), which aims to restore 15 million hectares over the next 50 yr (Melo *et al.*, 2013b). To achieve this ambitious outcome, it is necessary to develop efficient large-scale restoration programmes that preferentially use a landscape ecology perspective to take advantage of the landscape structure, leading to the reduction of restoration costs and an increase of restoration outputs (Leite *et al.*, 2013; Metzger & Brancalion, 2013). According to a recently proposed restoration framework, restoration investments are optimized when *landscape resilience*, the capacity of the landscape-wide biota to recover from local species losses in individual patches through immigration at the landscape scale, is intermediate (Tambosi *et al.*, 2014; Fig. 3c). When the habitat amount is low, the restoration cost is too high (Fig. 3d), and when the habitat amount is high, the landscape is resilient and therefore does not require management intervention (Fig. 3e). This window of restoration opportunity coincides with the range of habitat cover in which the forest amount and configuration interact more intensively to determine species abundance and occurrence (Fig. 3a,b). There are 15 million hectares, an area equivalent to the present forest cover, of Atlantic Forest in this intermediate landscape resilience condition, which may be the first targets for restoration (Tambosi *et al.*, 2014). Despite such theoretical advances, much remains to be learned in terms of (1) the reintroduction of multiple taxa and functional groups into restored forest patches; (2) restoration monitoring and effectiveness assessment; (3) economic instruments for forest restoration; and (4) the role played by forest restoration as a component of biodiversity conservation in human-modified landscapes and conservation strategies (Rodrigues *et al.*, 2011; Brancalion *et al.*, 2012).

The experience acquired by the BIOTA/FAPESP Program and the ARFP has highlighted that to be effective, research focused on biodiversity conservation, the provision of ecosystem services, habitat restoration and sustainable use requires integrative approaches. Research teams must bring natural science and social science researchers, landowners, policy makers and other relevant stakeholders together from the initial planning stages. This conclusion is in line with changes seen at the international level in initiatives such as Future Earth (<http://www.icsu.org/future-earth>), the decisions made by the Belmont Forum (<https://www.igfagr.org/belmont-forum>) and the recently approved conceptual framework and work programme of the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES; <http://www.ipbes.net/plenary/ipbes-2.html#meetingreport>).

In light of its promising and effective achievements, the BIOTA/FAPESP Program, initially launched as a 10-yr research initiative, was renewed until 2020. Other Brazilian states, such as Bahia, Minas Gerais and Mato Grosso do Sul, have adopted BIOTA as a model for their own biodiversity research programmes. Recently, BIOTA/FAPESP served as the model

for BIOTA Brazil and began supporting research initiatives in the Brazilian Long-Term Ecological Research Program (PELD), an initiative inspired by socio-ecological research to support policymaking that considers both social and environmental factors and operates as a network of research sites across Brazil's main biotas (Tabarelli *et al.*, 2013).

As well as integrating key scientific topics into socio-ecological and basic-applied research agendas, BIOTA offers a conceptual/operational platform and framework to integrate both national and international initiatives in the context of biodiversity science and sustainability, from providing knowledge to capacity building and the development of public policies. Such a comprehensive approach fits well into what Moran (2010) refers to as socio-ecological research. However, such an approach is still incipient in tropical forest regions. More programmes and long-term research initiatives integrating basic and applied topics into socio-ecological contexts are required to document, develop, implement and disseminate successful experiences on the sustainable use of tropical forests immersed in human-modified landscapes.

VII. Concluding remarks

The wide variety of human-modified Atlantic Forest landscapes, in conjunction with the presence of a large academic community, has helped elucidate key evolutionary and ecological aspects of tropical forests and to determine how these irreplaceable biotas respond to human disturbances at multiple levels of biological organization and spatio-temporal scales. Despite all the efforts devoted to biodiversity-related research in the Atlantic Forest, there are still several topics that require attention if we intend to preserve the biological heritage of this irreplaceable biota. First, we must understand the underlying processes that maintain observed tropical forest resilience and species persistence at large spatial scales, despite local species extirpation and homogenization, if we want to use this information for conservation policies.

Biodiversity knowledge, use and conservation in a changing world pose enormous challenges, even to a relatively robust academic community (note that Brazil contributes nearly 1.5% of total global scientific production) and a well-known biota. One of these challenges in the Brazilian Atlantic Forest is to better understand forest transition processes. Some regions of the Atlantic Forest are experiencing forest transition as a result of a higher regeneration than deforestation rate (Baptista & Rudel, 2006; Teixeira *et al.*, 2009; Lira *et al.*, 2012b), whereas others become progressively degraded, probably exceeding their resilience thresholds (see Silva & Tabarelli, 2000). We must better understand the economic, social and biological factors that promote natural regeneration processes and therefore enable an increase in forest cover with minimal economic investment.

Another challenge is related to ecosystem services. If we want to protect and restore the Atlantic Forest outside marginal lands, we must go beyond the understanding of biodiversity patterns and ecological processes and move towards understanding how changes

in native biota also affect *ecosystem services*. There is now strong evidence that biodiversity and ecological processes can affect the regulation of important services, such as pollination (Ricketts *et al.*, 2008; Garibaldi *et al.*, 2013), but we still lack data for other services, such as pest control, disease propagation, water supply, nutrient cycling (Carmo *et al.*, 2012) and carbon stocks (Alves *et al.*, 2010; Vieira *et al.*, 2011). By making these links clearer and by quantifying and pricing these services, we will develop new tools to promote conservation actions in association with economic development, particularly by implementing consistent payment for ecosystem service programmes. There is still a large knowledge gap in this field, not only in the Atlantic Forest, but across the entire tropical region.

In summary, beyond basic biodiversity and ecological studies of tropical forests, we must understand how these forests respond to human disturbances at multiple levels of biological organization and spatial-temporal scales to inform society about the threats posed and the potential opportunities offered by human-modified landscapes in the context of sustainability, including the economic value of remaining habitats and retained biodiversity. Future research is expected to cover a wide range of topics, naturally organized from basic (e.g. biodiversity description) to applied dimensions (e.g. biodiversity as a source of both social and economic development). In other words, biodiversity description, use and protection represent a triad that should be simultaneously addressed in any context in which sustainable development is intended.

The Atlantic Forest is one of the best examined tropical biota. We hope the Atlantic Forest experience (i.e. ecological findings and conservation initiatives) stimulates more effective and ambitious scientific agendas, research programmes and conservation actions in the entire tropical forest region to address the increasing human pressure and demand for agricultural land expected in the coming decades (Laurance *et al.*, 2012).

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