



Special Issue: Defaunation's impact in tropical terrestrial ecosystems

Ecological and evolutionary consequences of living in a defaunated world

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ABSTRACT

Defaunation, the loss or population decline of medium and large native vertebrates represents a significant threat to the biodiversity of tropical ecosystems. Here we review the anthropogenic drivers of defaunation, provide a brief historical account of the development of this field, and analyze the types of biological consequences of this impact on the structure and functioning of tropical ecosystems. We identify how defaunation, operating at a variety of scales, from the plot to the global level, affects biological systems along a gradient of processes ranging from plant physiology (vegetative and reproductive performance) and animal behavior (movement, foraging and dietary patterns) in the immediate term; to plant population and community dynamics and structure leading to disruptions of ecosystem functioning (and thus degrading environmental services) in the short to medium term; to evolutionary changes (phenotypic changes and population genetic structure) in the long-term. We present such a synthesis as a preamble to a series of papers that provide a compilation of our current understanding of the impact and consequences of tropical defaunation. We close by identifying some of the most urgent needs and perspectives that warrant further study to improve our understanding of this field, as we confront the challenges of living in a defaunated world.

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1. Defaunation: a cryptic anthropogenic impact

For many decades, naturalists have noted the pervasive impact of humans on nature, and how it affects the well being of humans themselves (Carson, 2013; Wilson, 2002). More recently, ecologists and conservation scientists have documented how anthropogenic impacts, such as overexploitation of plant and animal resources, pollution, and invasion by exotic taxa, impact biodiversity and its services to human beings (Barnosky et al., 2012; Cardinale et al., 2012). Similar accounts have begun to emerge in relation to the realized or potential impacts of climatic change on biodiversity (Barnosky, 2008; Sekercioglu et al., 2012). But, more frequently, scientists have focused their attention on the effects of land-use change – habitat loss, degradation and fragmentation – as one of the main drivers of biodiversity loss (Bierregaard et al., 1997; Fahrig, 2003; Pardini et al., 2010). The latter is expected as it is visible on many scales, either from direct observation of landscape changes on the ground, or via documentation of land cover change over extensive areas with satellite imagery and associated calculations (Ribeiro et al., 2009). However, such views of human insults

to nature do not allow us to see the magnitude of another critical, yet largely cryptic threat, the decline or outright loss of animals from natural ecosystems (“an invisible threat,” Phillips, 1996). In fact, it has been suggested that defaunation, *i.e.*, the human-driven extinction of medium- and large-sized vertebrates (Dirzo and Miranda, 1991), may represent another global environmental change (Dirzo, 2001). Indeed, evidence from seemingly undisturbed areas (including natural protected areas) sometimes show that medium- and large-bodied vertebrates are disappearing, even in some of the most remote areas of the world (Corlett, 2007; Peres and Palacios, 2007). For instance, we now know, from global data compilations, that nearly one-quarter (22%) of the world's mammal species, most of them medium and large animals, are considered to be globally threatened or extinct (www.iucnredlist.org), and the situation is no better for birds, for which 15% of the species are already extinct or threatened with extinction (www.iucnredlist.org). Such global assessments (Ceballos and Ehrlich, 2002), as well as many local studies (Galetti et al., 2009; Peres, 2001), agree in showing the differential vulnerability of species, depending on body size, whereby large bodied species and/or taxonomic groups of large bodied species (Dirzo, 2001) seem to be singularly vulnerable to extinction. Such differential extinction risk is related to both: (i) intrinsic traits of animals (since, in general, large body size is characterized by long generation times, low fecundity, low intrinsic growth rate,

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large home ranges and consequently requirements for large natural areas as well as natural low population densities (Cardillo et al., 2005)); and (ii) extrinsic factors, particularly preference by hunters and poachers (who selectively persecute these animals for meat, pelts, horns or other (“medicinal”) products (Redford and Robinson, 1987).

2. Brief historical account

The far-reaching significance of the effects of the on-going pulse of “contemporary defaunation” in tropical ecosystems was first hinted at 25 years ago in a Symposium of Plant-Animal Interactions at Universidade Estadual de Campinas, Brazil, in 1988, which we both attended. One of us (M. Galetti), was then a biology student in the audience, while the other one (R. Dirzo), the speaker, was a young researcher reporting on efforts to understand the consequences of the local extinction of mammals on plant recruitment and understory plant diversity in tropical forests of Mexico (Dirzo and Miranda, 1991). At that time, many plant community ecologists typically focused on documenting the vegetation types and the pattern of species abundance and richness, mostly in relation to parameters of the physical environment, such as soil type, nutrients, climate and responses to disturbance. With the exception of plant population biology, which underwent an exciting “Darwinian” eco-evolutionary approach (triggered and developed by John L. Harper and associates – see Harper, 1977), the “abiotic” vision has traditionally dominated plant ecology and has been in place for decades – and is still shared by many researchers, particularly vegetation analysts (Amorim and Batalha, 2007; De Castro and Kauffman, 1998; Gentry, 1982), while the “biotic vision” had undergone a slower progress. However, a landmark contribution by two independent researchers Janzen (1970) and Connell (1971), brought to our attention the significance of the biotic element (the “natural enemies”) in determining not only plant recruitment and population establishment dynamics, but plant community diversity in tropical ecosystems (Terborgh, 2013). The so called Janzen–Connell hypothesis has spurred countless studies and remains a crucial framework to understand the role

of natural enemies in structuring plant communities, and is indeed tied to defaunation ecology, as discussed by Terborgh (2013).

The role of predation and other top-down forces (e.g. herbivory, parasitism) in shaping species diversity and community structure in terrestrial and aquatic communities has been supported by plethora evidence arising from natural and controlled experiments where top-down forces were suppressed and the consequences assessed on lower levels of the food webs (Estes et al., 2011). Most of this evidence, however, comes from microcosm experiments and naturally simple or artificial ecosystems (Estes et al., 2011). Therefore, studies are badly needed to assess if such documented relationships in artificial or simplified natural settings could also translate into similar responses in complex ecosystems such as tropical ecosystems (Terborgh et al., 2001) where, at least theoretically, given their degree of mega diversity, species redundancy may attenuate the effects of species extinction via compensatory redundancy (Lawton and Brown, 1993; Naeem, 1998). Nevertheless, significant progress has been made to the point that we can now predict some consequences of defaunation at several ecological scales and processes in tropical ecosystems (Fig. 1). We are also now in a position of being able to identify crucial gaps in our understanding of defaunation ecology and point out to some of the needs, and promising directions for future work in this field; as we will discuss below.

3. Drivers and consequences of defaunation

Defaunation can be driven directly by hunting, poaching and illegal trading of animals or animal parts (Box 1a – Fig. 1). The impact of such activities alone can be of considerable magnitude, for example, of the order of 23 million vertebrates (mammals and birds) killed annually in the Brazilian Amazon (Peres, 2000). Many more are captured for illegal trade (Silva Regueira and Bernard, 2012). Another documented direct driver is invasive (usually exotic) plant or animal taxa, which can displace native animals from a given ecosystem (e.g., Young et al., 2010). Defaunation can also be driven indirectly by land use change (Box 1b), whereby the reduction of area and isolation of natural habitats prevents species from maintaining genetically and demographically viable populations

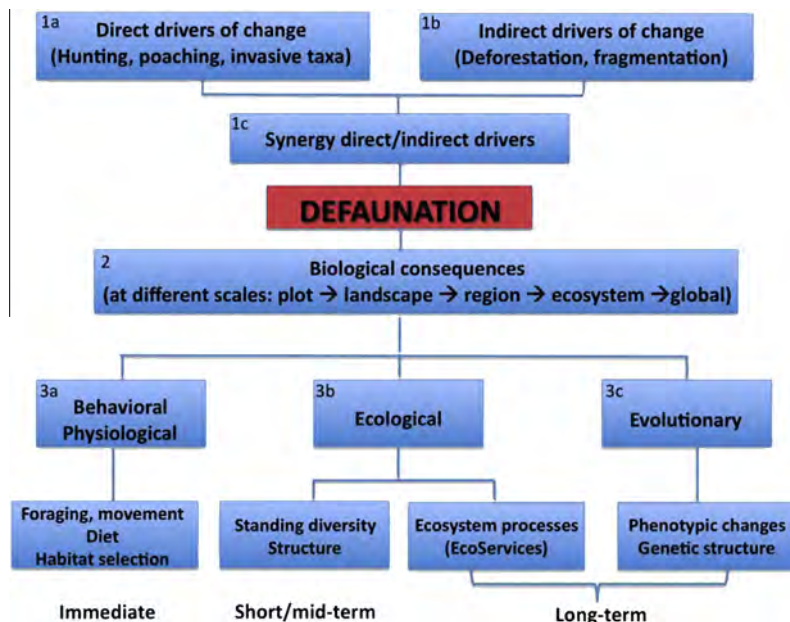


Fig. 1. A path diagram depicting the drivers of defaunation, and the immediate, short- and long-term consequences of defaunation on behavioral, ecological and evolutionary processes, which may occur at different spatial scales.

(Dixo et al., 2009; Gilpin and Soulé, 1986). Finally, it can also be driven as a by-product of synergy among several drivers (Box 1c). For instance, current spatial configuration of fragmented landscapes in many tropical regions not only reduces the chance of holding viable, genetically diverse populations of some species (particularly the large-bodied ones, as they require larger areas), but it also facilitates the access of hunters to what formerly were remote, less accessible areas located towards the interior of large, continuous forests (Michalski and Peres, 2007). Under this current scenario of human impact occurring in numerous locations the world over, we are confronted with a planetary pulse of contemporary defaunation that can be reflected in estimates as worrisome as those suggesting that 50% of all mammal species can be placed under serious risk of extinction in as short a period as 200 years (Smith et al., 1993; Dirzo, 2001).

The biological implications of defaunation (Box 2 – Fig. 1) are multiple and can occur at a variety of spatial scales and, indeed, detailed studies document that the effects of losing large bodied vertebrates can be detected at the plot level (a few m²) (Beck et al., 2013; Brocardo et al., 2013; Dirzo and Miranda, 1991), can scale up to the local level (Harrison et al., 2013; Wright et al., 2007; Wright et al., 2000), up to a regional level (Steinmetz et al., 2013), and to an entire ecosystem (Jorge et al., 2013). It has been argued that the impacts of defaunation can be even felt at the global level (Brodie and Gibbs, 2009; Poulsen, 2013). Changes in the vegetation dynamics, at the scale of small plots in tropical forests throughout the world, can be translated into global-scale impacts, because the majority of trees from tropical forests, where a very large amount of the carbon on Earth is stored (Ashton et al., 2012), depend of the dispersal services of frugivorous vertebrates (Almeida-Neto et al., 2008; Jordano, 1992). Therefore, the differential local defaunation can collectively have a domino effect scaling up to the entire globe (Poulsen et al., 2013).

The phenomena via which these multi-scale effects (in space and time) occur, range across a variety of levels of biological organization, from behavioral and physiological changes of individual organisms, to changes in ecosystem process within biomes and have the potential for driving evolutionary changes over longer time-scales (Boxes 3a–c – Fig. 1). To illustrate many of the behavioral and ecological elements of this gradient of consequences, we use a case study, manifested in a tropical insular system undergoing a particular type of defaunation: the loss/decline of the large birds of the Palmyra atoll in the Central Pacific (McCauley et al., 2012). For the potential evolutionary consequences (Box 3c) we use information derived from independent studies or from reasoned speculations derived from our knowledge in other tropical systems.

At the Palmyra atoll, the human-facilitated proliferation of the invasive coconut palm (*Cocos nucifera*) on some islets (but not other) creates a patchwork mosaic of palm-dominated islets intermingled with native forest-dominated islets, within the same general ecological setting. Palm-dominated habitats affect the movement, behavior and habitat selection of marine birds to the point that they consistently avoid the simple and unstable canopy of palm-dominated islets (Box 3a and Box below it), in favor of the more complex and stable canopy of native forests. Compared to native forest islets, palm dominated islets become dramatically defaunated, with an almost 5-fold decline in bird abundance and these behavioral impacts have profound ecological consequences (cf. Box 3b). This lead to the suppression of nutrient input brought by the birds onto those islets, which consequently reduces nutrient subsidies (causing, for example, a 5-fold decline in soil nitrogen), which decreases foliar nitrogen in the remaining native plants present in the palm forest (Box 3b and Boxes below it, Fig. 1). From a human perspective this translates into a dramatic loss of soil fertility (an important ecosystem service), should these tropical islets be used for productive activities. Nitrogen reduction in the soil

then cascades up to changes in palatability and herbivory by native crabs, which are also significantly reduced in these palm-patches (Young et al., 2010). Associated to this, the diversity of the plant community is also reduced significantly, not only in terms of the canopy, but at the understory level as well (cf. Box 3b and Boxes below it in Fig. 1). The effects of this peculiar defaunation transcend the terrestrial part of the ecosystem, as rain water running off native forests carries ca. 27-times more nitrogenous compounds to adjacent shores than in shores of palm forests. This leads to dramatic changes in chlorophyll and in phytoplankton growth and zooplankton biomass. A further cascading consequence, is that the foraging behavior and abundance of manta rays become significantly less abundant in palm forest shores; indeed, although there is no impediment for mantas to forage across the entire atoll system, they essentially concentrate their feeding on native forest coastlines (McCauley et al., 2012). Now let us suppose these insular systems were the object of eco-tourism activities: obviously, such ecosystem services would be negatively impacted as well.

The situation illustrated by this unusually fortunate example is not difficult to imagine happening, when tropical defaunation eliminates large frugivorous animals (Chapman and Onderdonk, 1998; Farwig and Berens, 2012; Jordano et al., 2002), leading to changes in pre-dispersal predation of seeds, in seed rain shadows, in turn leading to tweaked post-dispersal predation patterns, which co-vary with seed size and differential recruitment (Dirzo et al., 2007; Kurten, 2013). Potentially, such altered recruitment patterns (Dirzo and Miranda, 1991), in the absence of compensatory effects, could lead to changes in the structure and diversity of the forest as a whole. The extent to which the remaining (resilient) species can fill the ecological gap left by large-bodied frugivorous species is still largely unknown (Donatti et al., 2009).

Over the longer-term, usually beyond the scope of funded ecological studies, it is conceivable that evolutionary consequences may also take place, but this long-term escalation is poorly documented (Carroll and Fox, 2008). Selective extinction or phenotypic changes in body mass and reproductive conditions of large vertebrates due to overexploitation and its consequences for the food web have been well studied in aquatic systems (Horn et al., 2011; Scheffer et al., 2005), but remains poorly investigated in terrestrial ecosystems. Since most large bodied vertebrates interact with several plant species, we can envision that their absence leads to changes in selective pressure in important traits, such as seed size, hardness, and leaf toughness. In fact, a recent study documented rapid change in a key phenotypic trait (seed size) in a keystone palm due to bird functional extinction, demonstrating that defaunation can have long term evolutionary consequences (Galetti et al., 2013).

What is becoming clear from the available evidence is that the loss of medium and large vertebrates cannot and should not be seen only as an unfortunate catastrophic effect on standing biodiversity, but that it can also have enormous implications for ecosystem functioning, ecosystem services and human well-being.

4. Perspective for future studies

Since the pioneer papers that envisioned the consequences of defaunation on ecosystem processes were published (Dirzo and Miranda, 1991; Redford, 1992), there has been a significant increment of studies on this topic. In a review published 10 years ago, Wright (2003) argued that defaunation studies should include more comparative studies to evaluate the first-order indirect effects of partial vertebrate defaunation. In addition, he suggested more experimental manipulations designed to probe causal relationships between partial vertebrate defaunation and the associated indirect effects and he even suggested that researchers should target the myriad higher order indirect effects that may fol-

low after partial vertebrate defaunation. Stoner and collaborators (Stoner et al., 2007) also added into this list, a series of recommendations, such as increasing the number of studies, and incorporating long term genetic and demographic studies on the species affected. Although there is still much to do to be able to implement Wright's and Stoner and collaborators' recommendations, we believe that future studies that attempt to understand the consequences of defaunation should also pursue the following avenues:

- (1) To describe and quantitatively measure vertebrate communities (and the functional groups) in the studied sites. There has been a great amount of work done by ecologists to census vertebrate fauna in many localities and more sophisticated tools are now available (e.g. camera traps), but few of them are geared to defaunation studies. As pointed out by Kurten (2013), "hunted", "defaunated", "empty" do not reflect real wildlife abundance, nor their contribution to the ecological processes studied (McConkey and Drake, 2006). The adoption of a common defaunation index may be useful in this regard (Giacomini and Galetti, 2013).
- (2) To understand the complementarities and redundancy among the species' functional roles (Buono et al., 2013; Poulsen et al., 2002). For instance, Donatti et al. (2009) found that squirrels and spiny rats do not cache and effectively disperse seeds of *Astrocarium* in the Atlantic rainforest, compared to the larger frugivorous dispersal agents of this plant.
- (3) To better understand the behavioral and ecological role of the species involved in the trophic cascades studied (e.g. "ecology of fear", Brown et al., 1999). To this effect, we now have several new tools that are available that could be used, such as isotopic analysis. For heuristic purposes, defaunation ecologists tend to simplify the trophic relationships among species, but basic natural history of the species involved in trophic cascades is badly needed (Moreno et al., 2006).
- (4) To tease apart the effects of animal loss as compared to the other ecological effects. Since many studies have been conducted in fragmented regions, scientists should be aware of confounding factors, such as edge effects, and isolation.
- (5) To use comparative experiments with similar sampling protocols in different regions and biomes because they will be essential to establish generalities and particularities regarding the nascent field of defaunation ecology.
- (6) Finally, to understand the role of re/faunation (i.e. reintroduction of extinct species or functional similar species) in resurrecting ecological processes (Brodie and Aslan, 2012). There have been few studies on how we can revert the consequences of defaunation (Griffiths et al., 2010) and this will be certainly a most-needed new field of research.

5. About this special issue

Our inspiration to edit and compile this special issue resulted from having organized a Symposium on "Trophic downgrading in tropical ecosystems" as part of the Association for Tropical Biology and Conservation's Annual Meeting held in Bonito, Brazil, in 2011. This symposium was highly attended and motivated us to organize a Special Issue in *Biological Conservation* to share our current understanding of the impact of defaunation in tropical ecosystems.

Here we bring together 15 papers that approach the impact of defaunation in different scales and have a broad geographical distribution. The issue starts with two synthesis papers of broad scope. Corlett (2013) assesses the likely impacts of prehistoric megafaunal extinctions in the lowland tropics and discusses the implications for contemporary conservation management, while Terborgh (2013) discusses the force of the Janzen–Connell frame-

work in helping our understanding of plant recruitment and changes of forest biodiversity in light of contemporary defaunation. These overviews of the field are followed by a review paper in which Kurten (2013) presents a detailed analysis of the literature regarding the effects of defaunation on herbivory, seed predation and dispersal. While we are delighted to see the proliferation in the use of the general concept of defaunation, we recognize the need of a rigorous, operational and quantitative definition of the term; this key point is shared by many field ecologists and conservation scientists. In light of the previous, Giacomini and Galetti (2013) present a simple way to define defaunation by means of a quantitative index that allows comparisons in space and time.

Following the overview, synthesis and conceptual framework papers, a section composed of original papers starts with a theoretical discussion on the implications of defaunation from a network perspective (Vidal et al., 2013), moving to large-scale approaches particularly using occupancy modeling (Brodie and Giordano, 2013; Steinmetz et al., 2013) or species distribution modeling (Jorge et al., 2013). The hope is that this could be a promising avenue for other researchers interested in understanding the effects of defaunation on broader scales. Following that, several contributors present in sequence, a series of study cases on the indirect effects of defaunation on other organisms, such as amphibians and reptiles (Reider et al., 2013), and dung beetles (Culot et al., 2013). Finally, the last four papers deal with the consequences of defaunation on primate seed dispersal (Levi and Peres, 2013), plant diversity and functional groups (Brocardo et al., 2013), seedling density (Beck et al., 2013) and forest structure and carbon storage (Poulsen et al., 2013).

All these studies present one or more of the elements depicted in our conceptual diagram of Fig. 1, and also highlight the variety of aspects we need to work on to improve our understanding of the myriad consequences of defaunation and its impact for human societies. We are sure that many more researchers are working in topics that are directly relevant to defaunation and are not part of this special issue; we hope that this issue will motivate other students and researchers to move ahead in this field by bringing new perspectives and tools on-board, so we can better understand the consequences of defaunation to biodiversity and human well-being, as we confront the challenges of living in a defaunated world.

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