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Special Issue: Defaunation's impact in tropical terrestrial ecosystems

Using Janzen–Connell to predict the consequences of defaunation and other disturbances of tropical forests

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ABSTRACT

The Janzen–Connell (J–C) model of tropical tree recruitment and diversity has come of age and can now be applied to predict the consequences of defaunation and other disturbances. J–C describes a process of recruitment at a distance that results from spatially varying rates of seed dispersal and subsequent survival. The per-capita success of seeds is low under reproductive conspecifics where propagules are killed by host restricted enemies (seed predators, herbivores and pathogens). Undispersed seeds consequently experience negligible success, whereas dispersed seeds benefit from escape from enemies. At our site in Amazonian Perú, a scant rain of dispersed seeds ($<1/m^2$-yr for common species) gives rise to a low density of seedlings (ca. 5 m^2), suggesting that intracohort interactions (density dependence, competition) are weak. Defaunation and other disturbances distort or curtail the vital processes of dispersal and propagule survival. Seed dispersal is most vulnerable to hunting and other disturbances because it is disproportionately carried out by large-bodied birds and mammals that are selectively harvested by hunters or that disappear from fragments. Reduced dispersal leads more or less directly to reduced recruitment. In contrast, compensatory adjustments to missing seed predators appear to be common. Thus the escape process of J–C is more resilient to distortions in the large vertebrate community than is seed dispersal. These principles appear to be robust and can be employed to predict the consequences of defaunation and other kinds of disturbances to tropical forests.

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1. Introduction

In 1989 I attended a conference on the management of tropical forests where I presented a paper emphasizing that animals were crucial to the successful reproduction of many tropical forest trees, primarily via the services they provide as seed dispersers (Terborgh, 1995). The resulting volume of conference proceedings contained 17 chapters, of which mine was the only one to offer anything more than passing mention of animals (Lugo and Lowe, 1995). Although the landmark papers of Janzen (1970) and Connell (1971) had been published nearly 20 years earlier, the profession of tropical forestry was essentially blind to animals in 1989. Unfortunately, little has changed in the ensuing 24 years.

While foresters and proponents of neutral theory continue to ignore the roles animals play in determining the species composition of tropical forests, the field of plant–animal interactions has bloomed. Stimulated by Janzen's pioneering work on seed predation (Janzen, 1971a), a host of investigators took up the related topics of pollination (Bawa, 1974), seed dispersal (Howe, 1977; Howe and Smallwood, 1982; Gautier-Hion et al., 1985), and herbivory (McKey et al., 1978; Coley et al., 1985). The contributions

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of these and other authors greatly enriched the scope of plant–animal interactions and led to a profuse flowering of studies through the 1980s and 1990s. Research on plant–animal interactions was central in transforming tropical ecology from a largely observational science to an experimental one.

The rapid expansion of scientific knowledge during this period was nevertheless fragmented, as if one were building the components of a complex machine in a suite of separate factories, none of which possessed the blueprint for the final product. We were learning a lot, mostly from single-species studies, about how different classes of interactions worked, but integration of the pieces into a coherent overview of how forests worked remained a distant goal. Indeed, the very diversity of interactions and their often surprising complexity, sometimes involving multiple trophic levels (Letourneau and Dyer, 1998), made that goal seem distant indeed.

Progress toward a more integrated approach required an intellectual jolt, and that jolt was provided by Redford's (1992) signal paper on the "empty forest." Redford's prescient vision, published before the appearance of major empirical studies, with the notable exception of Dirzo and Miranda (1991), refocused attention on the whole rather than on the individual parts. All of us who are participating in this volume owe gratitude to these early visionaries. Now, 20 years later, it is time to ask: how far have we come since the early 1990s, and how far do we have to go?

The empty forest problem, though fundamentally important, is inherently messy, not the kind of science preferred by experimentalists. Reduction of animal populations alters a multitude of processes along a scale of possible states between the intact community and complete functional absence. Where animals are depleted by overhunting, large-bodied species typically suffer the greatest declines (Corlett, 2007; Peres and Palacios, 2007). But in most tropical forests around the world, large-bodied species represent multiple trophic guilds: herbivores (tapir, deer, duikers), seed predators (peccaries, suids), frugivore-dispersers (primates, large birds) and also the major predators of all of these. Some species participate in two or all three of these guilds, such as the duikers, pigs, peccaries and deer. The duikers of the African forest, for example, constitute a diverse collection of species, all of which browse seedlings in addition to consuming large amounts of fruit, in some cases crushing and digesting the seeds and in others, dispersing them (Feer, 1995; Dubost, 1984). Amazonian ungulates display a similar diversity of behaviors (Bodmer, 1991).

On the plant side, things are equally complex. Although a few species are dispersed by abiotic means and fewer still are pollinated abiotically, the great majority of species depend on animals for carrying out the indispensable reproductive services of fertilization and seed dispersal. Although pollinators and dispersers can be shared across species, each tree species is likely to attract a distinctive suite of pollinators, dispersers and seed predators, rendering community-level generalizations problematic (Gautier-Hion et al., 1985).

One might be tempted at this point to abandon any further effort toward seeking a conceptual framework for predicting the consequences of decimating large vertebrates in hyperdiverse tropical forests. Fortunately, however, there is a now thoroughly validated conceptual framework for making predictions at the community level, and that is the Janzen–Connell model (Terborgh, 2012). The Janzen–Connell Hypothesis (J–C), now 42 years old, has only recently come to be recognized as essentially correct (Terborgh et al., 2002; Carson et al., 2008; Terborgh, 2012). Long-delayed acceptance of the ideas contained in the J–C model can be attributed to a variety of misunderstandings and inconclusive experiments, as discussed in Terborgh (2012). We do not need to cover this ground again here.

2. Consequences of defaunation as predicted by Janzen–Connell

Most readers of this volume will be familiar with the Janzen–Connell model. In brief, the model balances two opposing processes, both of which operate in a spatially explicit fashion: dispersal of potentially viable seeds vs. propagule mortality driven by "enemies" (herbivores, pests and pathogens). Both processes vary radially around seed-bearing adult trees, such that the seed rain is assumed to decrease with distance, whereas the potential for escape from enemies is assumed to increase. The seed rain decreases with radial distance from a source largely because undispersed as well as dispersed seeds are tallied, a point to which I shall return (Clark et al., 2005; Muller-Landau et al., 2008).

In contrast, the escape curve rises from zero or near-zero to positive values along the same radial axis because density- and distance-responsive enemies are assumed to concentrate their searching for seeds or seedlings close to reproductive trees. The recruitment of offspring thus depends on the product of the seed shadow and escape curves (number of seeds falling per m^2 times the probability that a given seed will survive). For a given species, the spatial distribution of offspring will depend on the quantitative particulars of both the seed shadow and escape curves, for there is great variability in both (Swamy and Terborgh, 2011). Some common species recruit within 5–10 m of reproductive conspecifics, whereas most species in the forest at Cocha Cashu, Perú recruit at distances >50 m (mean distance to nearest conspecific adult; Terborgh et al., 2002).

Under J–C, most or all propagule mortality is caused by the actions of enemies and is thus bitrophic in nature. Within-cohort density effects (both intra- and interspecific) are assumed to be weak or absent (Terborgh, 2012). Indeed, it is the lack of strong interspecific competition that lies at the heart of J–C and its prediction of high species diversity. When intracohort interactions do occur, they are mostly limited to certain stages of ontogeny, especially the post-germination stage, when crowded seedlings may germinate from clumped seed deposits (Howe, 1989; Harms et al., 2000). Otherwise, seedling densities in most mature tropical forests are low, in the range of 5–25 per m^2, or well below 100 m^2, the density at which intracohort interactions become intense (Terborgh and Wright, 1994; Wiener, 1995; Terborgh et al., 2002; Harms et al., 2004; Paine et al., 2008).

Crucial to distinguishing J–C from other models (e.g., negative density dependence) is knowing what kills propagules and how propagule mortality relates to distance from reproductive conspecifics. There is now a huge amount of empirical data, both observational and experimental, that implicates biotic agents in the death of both seeds and seedlings (Janzen, 1971a; Carson et al., 2008; Pringle et al.,2007, Swamy and Terborgh, 2012; Alvarez-Loayza and Terborgh, 2011) and a conspicuous dearth of data implicating intra-cohort effects of crowding or interspecific competition (Moles and Westoby, 2004; Paine et al., 2008). Thus, for the purpose of the remainder of this discussion, I shall focus on bitrophic interactions as described by the J–C model and variants thereof, and largely ignore intra-cohort effects as being weak and of relatively little consequence.

Of great relevance to predicting the consequences of defaunation on tree recruitment in empty forests is strong evidence indicating that nearly all saplings arise from dispersed seeds (Howe and Miriti, 2000; Cordeiro and Howe, 2003, Terborgh and Nuñez-Ituri, 2006). The essential observation is that saplings arise at varying distances from reproductive conspecifics but seldom near or underneath their crowns, even though large fractions of the seed crop may fall in this zone (Terborgh et al., 2002, 2011). Using a subset of the seed rain that excluded seeds falling near conspecific adults, Terborgh et al. (2011) showed that the spatial pattern of