NATURAL ENEMIES AND THE MAINTENANCE OF TROPICAL TREE DIVERSITY: RECENT INSIGHTS AND IMPLICATIONS FOR THE FUTURE OF BIODIVERSITY IN A CHANGING WORLD[1]

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Abstract

Over the past five decades, many studies have examined the Janzen-Connell hypothesis, which posits that host-specific natural enemies, such as insect herbivores and fungal pathogens, promote plant species coexistence by providing a recruitment advantage to rare plant species. Recently, researchers have been exploring new and exciting angles on plant-enemy interactions that have yielded novel insights into this long-standing hypothesis. Here, we highlight some empirical advances in our understanding of plant-enemy interactions in tropical forests, including improved understanding of variation in plant species' susceptibility to enemy effects, as well as insect and pathogen host ranges. We then review recent advances in related ecological theory. These theoretical studies have confirmed that specialist natural enemies can promote tree diversity. However, they have also shown that the impact of natural enemies may be weakened, or that natural enemies could even cause species exclusion, depending on enemy host range, the spatial extent of enemy effects, and variation among plant species in seed dispersal or enemy susceptibility. Finally, we end by discussing how human impacts on tropical forests, such as fragmentation, hunting, and climate change, may alter the plant-enemy interactions that contribute to tropical forest diversity.

Key words: Conspecific negative density dependence, insect herbivores, Janzen-Connell hypothesis, modern coexistence theory, plant pathogens, species coexistence, tropical forest.

Explaining plant species coexistence in diverse communities has long posed a challenge to ecologists. Nowhere is this more evident than in highly diverse tropical forests, where hundreds of tree species often coexist in areas of just a few hectares (Wright, 2002). While some of this diversity may be maintained by differences among tree species in resource use (Harms et al., 2001; Silvertown, 2004), resource niche partitioning alone is unlikely to explain the remarkable diversity of tropical tree communities (Wright, 2002). This fact has led many ecologists to focus on another mechanism that might explain coexistence of tropical tree species, namely host-specific natural enemies—such as insect herbivores, seed predators, and microbial pathogens—that may prevent competitive exclusion by attacking individuals of a plant species more frequently as the species becomes increasingly common in the community. The potential contribution of natural enemies to plant diversity was originally recognized by Gillett (1962), who argued that pest outbreaks would prevent any species from becoming too dominant. This idea was expanded upon in the Janzen-Connell hypothesis (Janzen, 1970; Connell, 1971), which added two important observations. First, natural enemies have a larger impact on seeds and seedlings than they do on adults. Second, seeds and seedlings are more likely to be attacked by host-specific enemies if they are close to their parent trees, a phenomenon sometimes called a Janzen-Connell effect. Janzen (1970) proposed that these high-mortality zones could be caused by distance-responsive enemies—which are harbored by an adult tree and do not disperse far—or by density-responsive enemies—which spread rapidly due to high densities of conspecific (same species) seeds and seedlings that occur near adult trees. In either case, seeds that disperse away from parent plants can escape these species-specific natural enemies, provided that they do not land close to a conspecific adult. This leads to negative frequency dependence: the more common a plant

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species is in the community, the less enemy-free space it will have. Under this scenario, tree species would have a recruitment advantage when rare and face an increasing disadvantage as they become more common in the community. This rare species advantage can act as a stabilizing mechanism (sensu Chesson, 2000; see below "Theoretical Developments: Recasting the Janzen-Connell hypothesis into modern coexistence theory"), promoting species coexistence and thereby contributing to the maintenance of tropical tree diversity.

Over the past half century, numerous studies have tested aspects of the Janzen-Connell hypothesis, the results of which have previously been summarized in multiple review papers (see Clark & Clark, 1984; Hyatt et al., 2003; Freckleton & Lewis, 2006; Carson et al., 2008; Terborgh, 2012; Comita et al., 2014; Garcia-Guzman & Heil, 2014; Liu & He, 2019; Basset et al., 2019). Rather than provide another broad review of such studies, our goal here is to highlight some recent advances in our understanding of plant-enemy interactions in tropical forests and discuss their implications for the maintenance of tree diversity. We feature not only empirical studies but also theoretical developments that have yielded new insights into this long-standing hypothesis. Finally, we discuss how anthropogenic impacts on tropical forests (e.g., fragmentation, climate change) may alter the plant-enemy interactions that contribute to tropical tree diversity.

Empirical Studies of Tropical Plant-Enemy Interactions

IDENTIFYING MECHANISMS UNDERLYING JANZEN-CONNELL EFFECTS

Many studies of the Janzen-Connell hypothesis have focused on testing the predictions of distance- and density-dependent survival at early life stages. Many observational studies from tropical forests have reported patterns consistent with the Janzen-Connell hypothesis, i.e., decreasing seedling and sapling growth or survival with increasing densities of conspecific neighbors (e.g., Webb & Peart, 1999; Uriarte et al., 2004; Comita & Hubbell, 2009; Metz et al., 2010). Similarly, experimental studies that have manipulated the density of conspecific seeds/seedlings or the distance to conspecific adult trees having largely supported the predictions of the Janzen-Connell hypothesis (see meta-analysis by Comita et al., 2014). While such evidence of conspecific negative density dependence (CNDD) is consistent with the Janzen-Connell hypothesis, similar patterns could be generated by other factors, such as within-species competition for resources. Therefore, studies of plant performance alone cannot reveal whether natural enemies are the causal mechanism underlying negative correlations between conspecific neighbor density and juvenile survival (or recruitment or growth) (Comita, 2017).

A growing number of studies have employed approaches that provide direct or indirect evidence for the role of insect herbivores and microbial pathogens as drivers of CNDD. These approaches include measurement of detectable herbivore or pathogen damage on plants (e.g., Gilbert et al., 1994; Norghauer et al., 2006), plant-soil feedback experiments (e.g., Mangan et al., 2010), use of genetic methods to identify soil pathogens (e.g., Chen et al., 2019), quantifying neighborhood similarity in plant defenses (e.g., Forrister et al., 2019), and in situ manipulation of enemies using mesh exclosures, fungicides, and/or insecticides (e.g., Bell et al., 2006; Swamy & Terborgh, 2010; Bagchi et al., 2014). Studies using these approaches have demonstrated that natural enemies play an important role in driving tropical tree recruitment and potentially contributing to tropical tree diversity. However, the combined results from these studies also suggest that the overall importance, as well as the relative importance of different enemies (e.g., insects vs. pathogens; Bagchi et al., 2014), varies among sites, among species at the same site, and among life stages (e.g., Fricke et al., 2014; Krishnadas & Comita, 2019). We stress that incorporating such approaches into future studies of CNDD will be key for furthering our understanding of the role of natural enemies in structuring plant communities and maintaining diversity.

Isolating the effects of natural enemies is critical as ecologists increasingly seek to understand not only whether Janzen-Connell effects occur but also how the strength of such effects varies among sites, or over time, due to differing environmental conditions (Comita, 2017). Janzen (1970) hypothesized that the effectiveness of natural enemies in maintaining plant diversity is greater in wet tropical forests compared to temperate forests or drier tropical forests, since natural enemy activity would be curtailed in harsher and less predictable environments. While several studies of CNDD are consistent with this prediction (e.g., Comita et al., 2014; LaManna et al., 2017; but see Hülsmann & Hartig, 2018, and Chisholm & Fung, 2018), these studies did not examine natural enemy impacts and thus the reported patterns of CNDD could be driven by other mechanisms (Comita, 2017). Indeed, differences among sites in the strength of conspecific density effects on plant performance could result from *at least* five different ecological mechanisms: differences in the strength of (1) host-specific natural enemy impacts, (2) intraspecific competition for resources, (3) chemical effects, (4) benefits from host-specific mutualists (e.g., mycorrhizal fungi), and (5) plant species' habitat preferences. The first two mechanisms would result in a negative correlation between conspecific neighbor density and plant performance. As discussed above, observational studies of plant performance alone cannot differentiate between these two mechanisms. In contrast to the first two mechanisms, the final two mechanisms are likely to result in a positive correlation between conspecific neighbor density and plant performance because plants that are far from conspecifics may be less likely to encounter their mutualists (in the case of #4) or more likely to be located outside of the species' optimal habitat (in the case of #5). Chemical effects may underlie negative impacts of conspecifics on plant performance (e.g., McCarthy-Neumann & Kobe, 2010) or could indirectly benefit conspecifics by having allelopathic effects on heterospecifics (e.g., Hane et al., 2003). The mechanisms listed above may be acting simultaneously (e.g., Liang et al., 2015), meaning that experimental tests are critical to disentangle the underlying drivers of variation in the strength of CNDD (Comita, 2017). As discussed in more detail below, a mechanistic understanding of the drivers of CNDD under different environmental conditions is increasingly important for understanding how forest composition and diversity will be altered by anthropogenic disturbances (e.g., climate change and fragmentation).

AMONG-SPECIES VARIATION IN SUSCEPTIBILITY TO NATURAL ENEMIES

It has long been recognized that tropical tree species vary in their susceptibility to natural enemies (e.g., Coley, 1983). In the past decade, a number of studies have examined the consequences of this variation for tropical tree communities in the context of the Janzen-Connell hypothesis. For example, in an experiment in Panama, Mangan et al. (2010) found that tree species varied in the degree to which conspecific seedling growth was reduced (relative to heterospecific seedling growth) when exposed to soil pathogens associated with conspecific adult trees. Furthermore, they found that species that were less common in the local community tended to have seedlings that were more negatively affected by conspecific soil pathogens compared to species that were more abundant in the local community. This finding is consistent with a previously reported relationship between plant species relative abundance and sensitivity to specialist pathogens in a temperate meadow community (Klironomos, 2002), suggesting that pathogens play a role in driving patterns of rarity and commonness within many plant communities. Mangan et al.'s (2010) results were bolstered by an independent observational study at the same site that found that rarer species tended to have seedlings whose survival was strongly reduced by conspecific neighbors, while seedlings of locally common species were less sensitive to conspecific neighbor density (Comita et al., 2010). Together, these studies suggest that tree species that are more susceptible to host-specific soil pathogens are prevented from becoming common in the community because they suffer more when surrounded by conspecifics.

However, rarity itself may influence a species' sensitivity to pathogens and negative conspecific effects. Marden et al. (2017) hypothesized that species that are locally rare in the community are more likely to have a lower diversity of pathogen resistance (R) genes due to genetic bottlenecks, founder effects, and drift. This lower diversity of R-genes at the population level would mean that conspecific seedlings would be susceptible to the same suite of pathogens, promoting the spread of disease and leading to more negative effects of conspecific density on seedling survival. Marden et al. (2017) tested this hypothesis using a transcriptome approach with six tropical tree species (a subset of those included in Comita et al., 2010 and Mangan et al., 2010). They found that R-gene diversity was positively correlated with species local abundance, and negatively correlated with species' susceptibility to soil pathogens and conspecific neighbor effects. This suggests an eco-evolutionary feedback loop in which the small population size of locally rare species results in lower R-gene diversity, which in turn facilitates the spread of host-specific pathogens among seedlings of these species, resulting in strong pathogen-mediated CNDD that prevents the species from increasing in abundance (Marden et al., 2017).

Research suggests that tropical tree species also vary in susceptibility to natural enemy impacts due to differences in life history strategy (and related plant functional traits). In particular, tree species vary widely in their shade tolerance, reflecting a trade-off between fast growth in high light conditions and high survival under low light conditions (Kitajima, 1994; Kobe, 1999; Wright et al., 2010). In order to survive under low light conditions, species must not only be tolerant of shade but also be well defended against natural enemies, as it is costly to replace lost tissue under low resource conditions (Coley & Barone, 1996). In lowland Neotropical forests, more shade-tolerant tropical tree species have been found to be less susceptible to soil pathogens (Augspurger & Kelly, 1984; McCarthy-Neumann & Kobe, 2008; but see Pringle et al., 2007) and suffer less from conspecific neighbor effects (Kobe & Vriesendorp, 2011; Zhu et al., 2018) compared to more light-demanding species. These relationships with shade tolerance suggest that natural enemies may contribute to the maintenance of tropical tree diversity by reinforcing existing abiotic niche differences (McCarthy-Neumann & Kobe, 2008). In addition to shade tolerance, recent studies from temperate and subtropical forests suggest that susceptibility to natural enemies is linked to plant species' mycorrhizal symbionts, particularly whether a tree species is associated with arbuscular mycorrhizal (AM) or ectomycorrhizal (EM) fungi (Bennett et al., 2017; Chen et al., 2019).

HERBIVORE AND PATHOGEN HOST RANGES

Enemy host range is a key component of the Janzen-Connell hypothesis, with some degree of host specificity assumed for enemies to contribute to the maintenance of plant diversity. Since the hypothesis was first proposed, there have been a number of noteworthy advances in our understanding of enemy host range in tropical forests. Many studies have shown that most natural enemies are not species-specific specialists (Thomas, 1990; Barone, 1998; Novotny & Basset, 2005; Forister et al., 2015). Rather, specialization lies on a spectrum, with different enemies having different host ranges (e.g., Augspurger & Wilkinson, 2007). At the same time, it is important to note that while a pathogen or herbivore may be capable of attacking multiple plant species, the impact of that attack of plant performance may differ among species resulting in host-specific effects (e.g., Sarmiento et al., 2017). Such "effective specialization" of natural enemies can allow multihost enemies to contribute to the maintenance of plant diversity (as reviewed by Benítez et al., 2013).

Many studies have demonstrated a phylogenetic signal in host range for both insect herbivores (Barone, 1998; Novotny et al., 2002; Odegaard et al., 2005) and fungal pathogens (Gilbert & Webb, 2007), with enemies often specializing on groups of closely related host species (e.g., plant species within the same genus or family). This can result in a "phylogenetic Janzen-Connell effect" (Liu et al., 2012), in which a plant's likelihood of survival is effected by the density and/or proximity not only of conspecific neighbors but also of phylogenetically similar neighbors of other species (e.g., Webb et al., 2006; Bagchi et al., 2010; Metz et al., 2010; Comita et al., 2018). A phylogenetic signal in enemy host range presumably results from phylogenetically conserved defense traits in host plants (Agrawal, 2007). However, even closely related plant species can differ substantially in defenses (Sedio et al., 2017). Sedio et al. (2018) found an absence of phylogenetic signal in leaf metabolomes at a tropical forest site (in contrast to a temperate forest site), with particularly low chemical similarly among congeners. Indeed, within hyperdiverse tropical tree genera (e.g., *Inga* Mill.), there is little evidence for a phylogenetic signal in defenses (Kursar et al., 2009). Instead, shared insect herbivore communities and chemical similarity of tree species within the same genus underlie negative density-dependent growth and survival (Forrister et al., 2019).

While the above studies indicate that many enemies specialize above the species level, there is increasing evidence for specialization at the within-species level in tropical forests, particularly for soil pathogens. The impacts of genotype-specific pathogens are well known from agricultural systems (Croll & McDonald, 2017), and Gillett (1962) suggested that such highly specialized pathogens may contribute to genetic diversity in natural plant communities. Several recent studies support the idea that soil pathogens that specialize within species have a significant influence on seedling growth and survival in tropical and subtropical forests. Specifically, in shade house experiments conducted on two tree species in south China (Liu et al., 2015) and one tree species in Panama (Eck et al., 2019), seedlings grown in soil collected beneath their own parent had lower performance compared to seedlings grown in soil collected beneath another adult tree of the same species. Liu et al. (2015) further showed that this difference in survival was influenced by genetic distance (between seed and soil source) and disappeared when soils were sterilized, strongly suggesting that the observed differences in seedling survival were driven by genotype-specific microbial pathogens. Consistent with these findings, in a forest in Ecuador, Browne and Karubian (2016, 2018) found a survival advantage for seedlings with rare genotypes over seedlings of the same species with common genotypes (but did not explicitly examine the underlying mechanism). Further empirical studies are needed to determine the degree to which these findings hold for additional species and sites. More generally, an increased understanding of pathogen and herbivore host-specificity is critical because, as discussed below, theoretical models show that levels of host-specificity influence the degree to which natural enemies maintain plant diversity. Furthermore, information on host specificity is critical for understanding not only the maintenance of plant diversity, but also how tropical diversity is generated through coevolution of plants and their enemies (Marquis et al., 2016).

THEORETICAL DEVELOPMENTS

The Janzen-Connell hypothesis describes a community-level phenomenon, and it has many parts, which makes testing difficult (Carson et al., 2008). A true test would involve removing all of the natural enemies from a forest over the spatial and temporal scales needed to determine whether tree diversity declines in their absence, a task that is logistically challenging. Instead, most empirical studies have tested the assumptions of the hypothesis—Are enemies distance-responsive? Are enemies specialists? etc.—and assumed these effects would scale to allow coexistence. A few empirical studies have shown that natural enemies maintain plant community diversity from the seed to the seedling stage over a few square meters in tropical forests (e.g., Bagchi et al., 2014; Krishnadas et al., 2018), but it is not certain from these studies whether this local-scale phenomenon scales to allow forest-wide coexistence. Theoretical models of forest dynamics are therefore needed to test whether empirical observations actually scale in the way we expect. Though the Janzen-Connell hypothesis has had a long history of empirical testing, theoretical work has lagged behind. Over the past few decades, several theoretical models have suggested that Janzen-Connell effects can allow many species to coexist. For example, a recent study (Levi et al., 2019) showed that distance-responsive natural enemies can maintain the high levels of diversity observed in tropical forests by acting as a stabilizing mechanism that favors rare species (as previously shown by Leigh, 1982; Armstrong, 1989; and Volkov et al., 2005). While this result is consistent with the Janzen-Connell hypothesis, other recent theoretical studies (discussed below) have challenged several elements of the hypothesis.

RECASTING THE JANZEN-CONNELL HYPOTHESIS INTO MODERN COEXISTENCE THEORY

The Janzen-Connell hypothesis predates most currently held concepts of species coexistence, and, as such, parts of the hypothesis have changed as our understanding of coexistence has changed. Connell (1971) originally argued that natural enemies promote diversity by reducing the amount that trees compete with one another. This idea has been debunked, since under conditions of high mortality, species can be excluded with less competition (Chesson & Huntly, 1997; Fox, 2013). Instead, species coexist when intraspecific density dependence (i.e., density dependence from conspecifics) outweighs interspecific density dependence (i.e., density dependence from heterospecifics) (Lotka, 1932). When this occurs, every species will have a rare-species advantage (sometimes called negative frequency dependence), which can prevent competitive exclusion under most circumstances (but see Schreiber et al., 2011). In 1971, “density dependence” generally meant resource competition or interference competition, though it is now defined as any mechanism where two individuals have a negative effect on one another (Chesson, 2000). In particular, density dependence via natural enemies is called apparent competition and occurs if a prey species’ density alters the density or behavior of its natural enemies (Holt, 1977). Apparent competition is thus a top-down mirror of resource competition (Holt et al., 1994). Janzen-Connell effects are a form of intraspecific apparent competition, and enemy spillover is a form of interspecific apparent competition (Mordecai, 2011).

Additionally, the Janzen-Connell hypothesis was originally proposed as the main explanation for how tropical trees coexist (Janzen, 1970; Connell, 1971); however, it is now generally believed that many mechanisms are acting in most systems, and their net impact determines if species coexist (Wright, 2002). Factors that increase intraspecific density dependence relative to interspecific density dependence—such as Janzen-Connell effects—produce stabilizing mechanisms (Chesson, 2000; Adler et al., 2007). Stabilizing mechanisms give species a frequency-dependent advantage when rare and are a necessary but not sufficient condition for coexistence. Factors that give one species an advantage or disadvantage over its competitors—such as differences in density-independent seedling survival—produce competitive differences or mean fitness-differences (Chesson, 2000; Adler et al., 2007; Barabás et al., 2018). Together, species coexist if the stabilizing mechanisms outweigh any competitive differences (Chesson, 2000; Adler et al., 2007). Thus, stabilizing mechanisms set the bandwidth for coexistence between species: the stronger the stabilizing mechanisms, the more different coexisting species can be in their fitness (though see Barabás et al., 2018; Song et al., 2019). Many factors produce both effects (Song et al., 2019). In particular, Janzen-Connell effects produce a stabilizing mechanism; however, they can also produce competitive differences if species are differently susceptible to their natural enemies (Stump & Comita, 2018; Ke & Wan, 2019; Kandlikar et al., 2019), or if enemy spillover is occurring (Stump, 2017). Thus, a more modern view of the Janzen-Connell hypothesis is that Janzen-Connell effects are a factor producing stabilizing mechanisms—likely one of many—and that they can allow coexistence if they are stronger than any competitive differences in the community. The mortality caused by Janzen-Connell effects are lower-level processes that create higher-level processes at the community level (e.g., negative frequency-dependent selection and spatially variable selection as categorized by Vellend, 2016: 150; or variation-independent mechanisms and fitness-density covariances as categorized by Chesson, 2000; Barabás et al., 2018).

Finally, we should note that local-scale negative effects of conspecific neighbor density on plant performance reported by empirical ecologists (e.g., Webb & Peart, 1999; Comita et al., 2010), commonly referred to as CNDD, differs slightly from the classic term “density dependence.” Specifically, density dependence typically refers to a property at the population-level—the more common a species is, the lower survival or fecundity is for individuals (at least on average). They are of course linked: CNDD at the local scale generally causes population-level density dependence (Stump & Chesson, 2015). However, there are subtle differences. For example, density dependence in the population need not be a localized phenomenon. Also, species coexistence is not guaranteed even when CNDD outweighs heterospecific NDD for all species since competitive exclusion can still occur due to fitness differences (Murrell, 2010; Miranda et al., 2015; Stump & Comita, 2018). However, interspecific density dependence outweighing intraspecific density dependence should always lead to exclusion (Chesson, 2000). Throughout this paper, we use CNDD to refer to the localized negative effects of conspecifics.

DISPERSAL AND SPACE

A defining element of the original Janzen-Connell hypothesis was the population recruitment curve (PRC), which describes how seedling recruitment varies as a function of distance from the parent (Fig. 1). Janzen (1970) originally predicted that distance- and density-responsive enemies would produce a unimodal PRC, as survival would be low near the parent and seed dispersal would be low far away (Fig. 1A). He claimed that a unimodal PRC would force dominant species to be spaced out, allowing space for weaker competitors to recruit (Janzen, 1970). Models have shown problems with this claim. First, distance- and density-responsive predators can produce PRCs that are not unimodal (Hubbell, 1980; McCanny, 1985; Nathan & Casagrandi, 2004; Mari et al., 2008; Beckman et al., 2012; Vincenot et al., 2017; Marchand et al., 2019). For example, if few seeds disperse far away, then recruitment may be highest near the parent, even if survival is lowest there (Hubbell, 1980). Second, the "allowing space for recruitment" mechanism is weak; for example, if conspecifics could not recruit within five crowns of one another (an effect much stronger than what has been observed empirically; Clark & Clark, 1984; Comita et al., 2010), then this would only allow 27 species to coexist (Hubbell, 1980). Finally, Janzen-Connell effects can promote coexistence even if the PRC is not unimodal (Stump & Chesson, 2015). Rather, Janzen-Connell effects promote diversity by causing species to have higher seedling survival when they become rare (Grover, 1994; Stump & Chesson, 2015). As such, if enemies are spread throughout the forest, rare seeds would have higher seed survival everywhere (due to having few enemies) but would have high recruitment near conspecific adults (due to limited seed dispersal) (Fig. 1B). Thus, we feel that tests for a unimodal PRC should not be used as a test of the Janzen-Connell hypothesis.

Natural enemies can promote coexistence even if they do not generate high mortality zones. Specialist natural enemies create a stabilizing mechanism because a species that becomes rare has fewer specialist enemies, allowing it to recover; this can take the form of that species having more enemy-free sites, or of its enemies being uniformly rare across the landscape (Bever, 2003). However, the spatial arrangement of specialist natural enemies will alter the strength of the mechanism. Theoretical studies have shown that if natural enemies are distance- or density-responsive, then the stabilizing mechanism they produce is weakened, making enemies less able to promote diversity (Muller-Landau & Adler, 2007; Mack & Bever, 2014; Stump & Chesson, 2015; Stump & Comita, 2020). The stabilizing mechanism is weakened because if specialist natural enemies stay near their host, and most seeds do not disperse far from their parent, then the benefits of rarity are reduced: a seedling could be rare on the landscape, but still be at a high risk of mortality due to CNDD from its parent (Stump & Chesson, 2015; Stump & Comita, 2020) (Fig. 2). An influential early study suggested that CNDD is more able to maintain diversity if it is localized (Adler & Muller-Landau, 2005); however, later work showed that this model contained an additional diversity-promoting factor, and when that factor was accounted for, localized CNDD was less able to maintain diversity (Stump & Chesson, 2015). Thus, natural enemies do not need to create localized CNDD in order to promote diversity, and when they do, they are actually less able to promote diversity (particularly when seed dispersal is low).

Models have also shown that if competing tree species differ in seed dispersal, this could alter the impact of Janzen-Connell effects. If species have different seed dispersal distances, then species with low dispersal are at a competitive disadvantage, as their seeds are less likely to escape from natural enemies (Fig. 3) (Stump & Comita, 2020). However, if species with lower dispersal are less susceptible to natural enemies, then the disadvantage of low dispersal could be offset, thereby promoting coexistence by reducing competitive differences (Stump & Comita, 2020). Such a scenario is not unlikely—escape from natural enemies is one explanation for the evolution of seed dispersal (Howe & Smallwood, 1982)—and this selective pressure would presumably be stronger for plant species that are more susceptible to their natural enemies. Additionally, there is evidence that rare species may have a dispersal advantage: birds may selectively disperse the seeds of rarer species farther (Carlo & Morales, 2016). If this occurs, it will produce a stabilizing mechanism by making rarer species more likely to escape from their natural enemies (Morán-López et al., 2018).

STRENGTH OF SUSCEPTIBILITY

Janzen-Connell effects produce a rare-species advantage because rare species have more enemy-free sites in which to recruit, and therefore higher seedling survival. The stabilizing effect thus depends on how harmful CNDD is to seedling survival: if it is very harmful, then tree species gain a huge benefit when

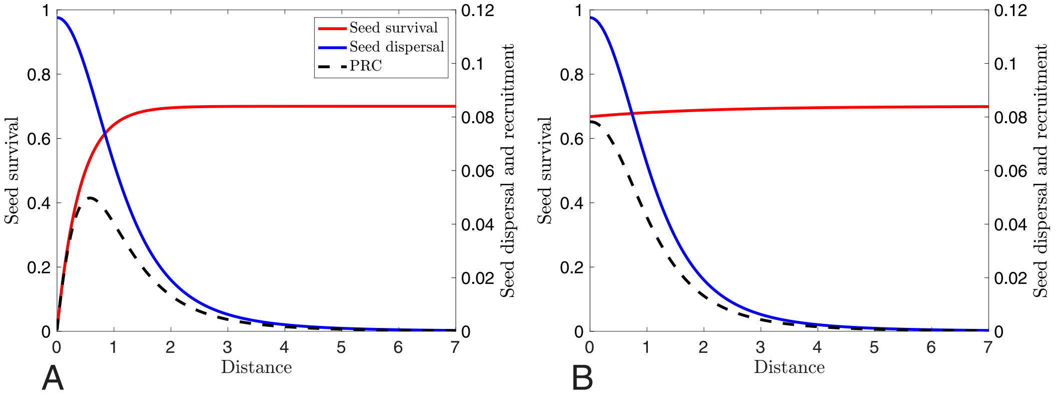

Figure 1. Unimodal population recruitment curves (PRCs) are not necessary for the Janzen-Connell hypothesis to operate. —A. Here, the impact of conspecific negative density dependence (CNDD) is concentrated near adult trees. As such, seed survival is low there, producing a unimodal PRC. —B. Here, the impact of CNDD is spread throughout the landscape (it has the same mean impact as in Fig. 1A). As such, recruitment peaks near an adult tree. However, both scenarios would produce a stabilizing effect, and, in fact, the stabilizing effect here is slightly stronger than the stabilizing effect in Figure 1A because the impact of CNDD is more spread out (Stump & Chesson, 2015; Stump & Comita, 2020).

they become rare; if it has little effect, then species gain little benefit from rarity (Turnbull et al., 2010; Chisholm & Muller-Landau, 2011; Stump & Chesson, 2015; Eppinga et al., 2018). Also, like all stabilizing mechanisms (Chesson, 2000; Stump, 2017), this mechanism becomes weak in high-diversity systems: if every species has a low density at equilibrium, then most sites will be enemy-free already; in this case there is little benefit to further rarity (Turnbull et al., 2010; Stump & Chesson, 2015; Levi et al., 2019).

However, while specialist natural enemies can help coexistence if they have a uniformly strong effect, they can undermine coexistence if host species differ in their susceptibility (Fig. 4). As discussed above, empirical studies have found wide variation in susceptibility among co-occurring tropical tree species. Theoretical models have demonstrated that species that are more susceptible to their predators tend to have lower equilibrium abundances (Mangan et al., 2010; Chisholm & Muller-Landau, 2011; Mack & Bever, 2014; Bauer et al., 2015), consistent with empirical findings (Klironomos, 2002; Mangan et al., 2010). Simply, the more self-limiting a species is, the less abundant it can become. Additionally, differential susceptibility may weaken the stabilizing mechanism: if the most abundant species can tolerate their natural enemies, then rare species have relatively less of an advantage (Stump & Comita, 2018) (Fig. 4). Differential susceptibility also produces competitive differences (Stump & Comita, 2018; Ke & Wan, 2019; Kandlikar et al., 2019): if a species is highly susceptible to its natural enemies, and most seeds of that species are unable to disperse away from those enemies, then that species will be at a disadvantage compared to species that can tolerate their natural enemies (Stump & Comita, 2018) (Fig. 4). This can create situations where every species experiences CNDD, but they do not coexist because those that are more susceptible to CNDD are at too much of a competitive disadvantage (Murrell, 2010; Miranda et al., 2015; Stump & Comita, 2018). However, differences in susceptibility to natural enemies may promote coexistence if it trades off with other factors, such as differences in seed dispersal or density-independent survival (Stump & Comita, 2020).

The result that differential sensitivity to CNDD could lead to exclusion was surprising, as recent work suggested that coexistence should be stronger if rare species suffer higher density dependence (Yenni et al., 2012). We think that both studies were correct, but used a different basis for comparison, and a different focus on density dependence. In a stochastic world, species are more likely to persist if they have a high equilibrium density and/or a high growth rate when they are extremely rare (Nisbet & Gurney, 1982). Yenni et al. (2012) focused on density dependence at the population level. They showed that a less common species will persist longer if it has stronger self-limitation, as this leads it to have a higher growth rate when rare. In particular, this work was meant to focus on species with a rare but unique niche, such that when they became rare, their niche became empty (Peter Adler, pers. comm.). Other work focused on CNDD at the individual-level (Murrell, 2010; Miranda et al., 2015; Stump & Comita, 2018). These studies showed that high susceptibility to CNDD lowered both a species' abundance and its growth rate when rare, making that species more likely to go extinct (Stump & Comita, 2018). We feel these latter studies are more appropriate for tropical trees, because when a tree

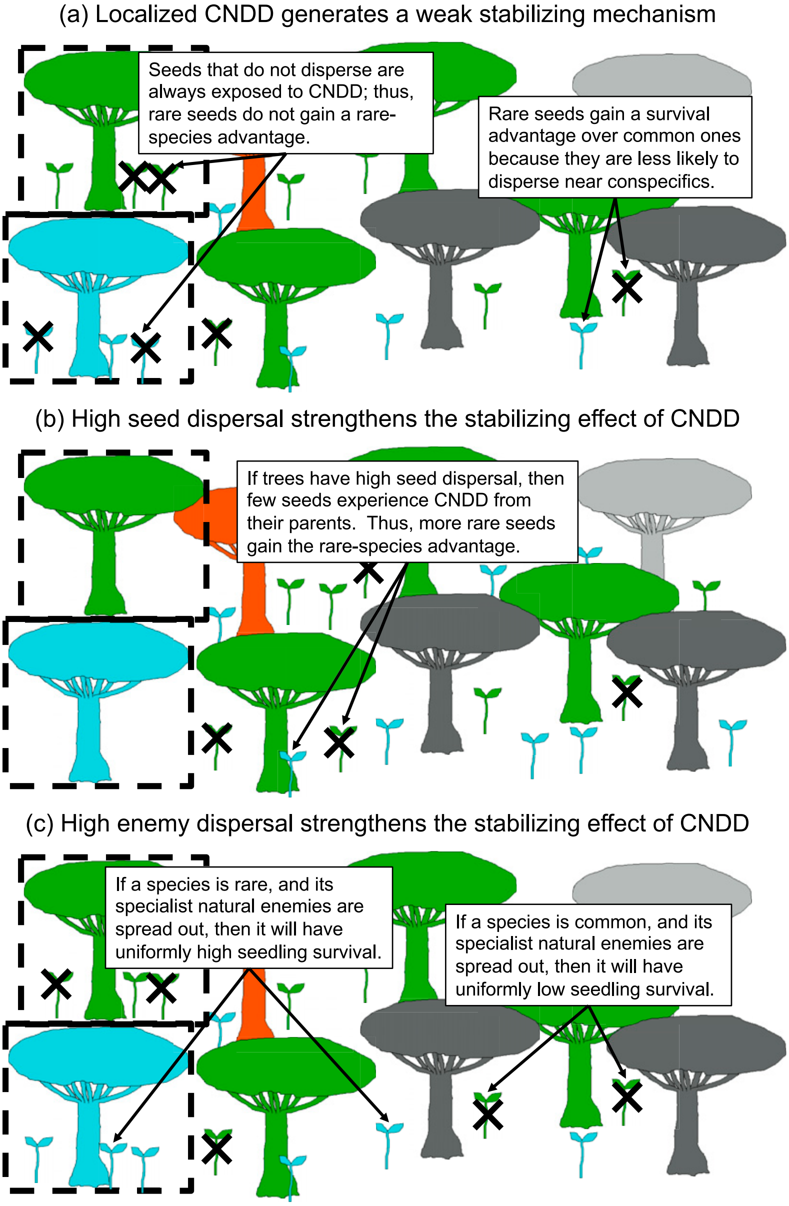

Figure 2. Low seed dispersal and low enemy dispersal weakens the stabilizing effect of Janzen-Connell effects. (a) Janzen-Connell effects produce a stabilizing mechanism because the rarer a species is, the less likely a seed is to disperse near a conspecific adult, and therefore the higher seed survival will be. However, if a seed does not disperse, then it will still experience conspecific negative density dependence (CNDD) from its parent; such seeds therefore gain less benefit from rarity. (b) If the trees have high seed dispersal, this will strengthen the stabilizing impact of CNDD: the more that seeds disperse, the higher fraction of rare seeds will experience the rare-species advantage. (c) Also, the stabilizing mechanism will be stronger if natural enemies are spread more uniformly throughout the landscape (instead of producing such localized CNDD). Here, seeds of rare species will have uniformly high survival because their natural enemies are uniformly rare, and seeds of common species will have uniformly low survival because their natural enemies are uniformly common.

species becomes rare, it still experiences strong competition for light and space in forest ecosystems.

It is sometimes claimed that a prediction of the Janzen-Connell hypothesis is that seedlings of common species should have lower survival (or growth or recruitment) than those of rare species, a phenomenon referred to as a community compensatory trend (CCT) (Connell et al., 1984). However, the above models show

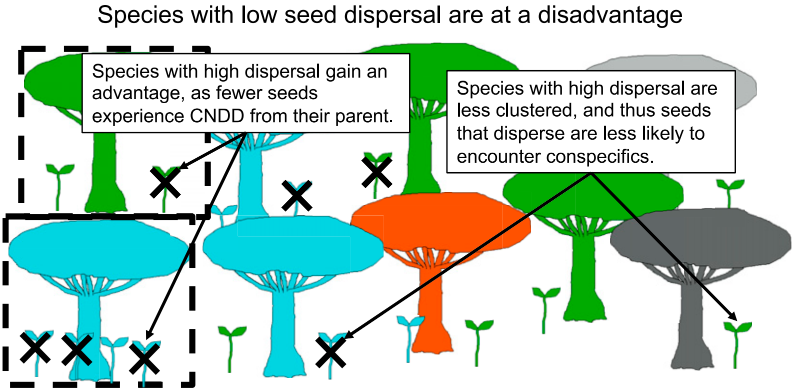

Figure 3. Low seed dispersal puts species at a competitive disadvantage. Species with low seed dispersal are at a competitive disadvantage compared to those with high seed dispersal. First, their seeds are more likely to not disperse, and thus experience conspecific negative density dependence (CNDD) from their parent (Stump & Comita, 2020). Second, such species tend to be more clustered around the landscape; as such, seeds that disperse a few crown lengths away from their parent are also likely to experience CNDD (Stump & Comita, 2020). If these effects are strong enough, species with low seed dispersal may be outcompeted by species with high seed dispersal. However, if seed dispersal and susceptibility to CNDD trade-off, then this may promote coexistence by canceling different competitive differences.

that this is not the case. Not every rare species is recovering from rarity; some could just have a low equilibrium abundance due to low competitive ability. This low competitive ability could be caused by high susceptibility to pathogens or by other factors that make it poorly suited to a site (Fig. 5A) (Chisholm & Muller-Landau, 2011; Mack & Bever, 2014; Stump & Comita, 2018). As a result, CNDD can promote coexistence without generating a correlation between species' mean seedling survival rates and species abundance (Fig. 5B); and indeed, there is no reason to expect such a correlation in real systems. In fact, differences among tropical tree species in mean seedling survival rates typically are driven by differences in life history strategy (i.e., shade tolerance; Comita & Hubbell, 2009). Therefore, empirically testing how CNDD scales to the community level requires testing how seedling survival changes as a species' density changes, not how seedling survival differs between species with different observed abundances.

HOST RANGE

The Janzen-Connell hypothesis is often described in terms of natural enemies that are species-specific specialists, i.e., those that consume only one host species. Indeed, models have shown that the mechanism does not work with purely generalist natural enemies, i.e., those who harm all host species in the community equally (Murrell & Law, 2003; Sedio & Ostling, 2013). However, models have also shown that specialization per se is not critical, but rather that the natural enemies must harm their main host more than other species (Bever et al., 1997; Turnbull et al., 2010; Chisholm & Muller-Landau, 2011; Stump & Chesson, 2015). Thus, an adult's natural enemies could greatly reduce the survival of heterospecific seedlings, as long as they reduce survival of conspecific seedlings even more. However, for a given impact, the more specialized the natural enemies, the more strongly they will promote diversity. Because of this, enemies who specialize at the genus or family level can promote coexistence, just not as effectively as species-specific specialists (Sedio & Ostling, 2013; Stump, 2017). Seed and enemy dispersal patterns do not alter this result (Sedio & Ostling, 2013). Additionally, natural enemies that are not species-specific specialists may create competitive differences due to enemy spillover (Stump, 2017). For example, as discussed above, numerous empirical studies have found that related species are more likely to share natural enemies; as such, a species with many close relatives in the community may experience high seedling mortality even when rare, which could lead to its exclusion (Stump, 2017).

As described above, some natural enemies, particularly pathogens, appear to specialize on host genotypes within tropical tree species (e.g., Eck et al., 2019). Like genus- or family-specific specialists, sub-species specialists are capable of promoting species diversity but are less effective than species-specific specialists. This is because genetically diverse species could become common without a large increase in seedling mortality, thus reducing the benefit to rarity (Eck et al., 2019) (Fig. 6). If species differ in their genetic diversity, this could lead to species being differently susceptible to their pathogens (Marden et al., 2017; Stump et al., 2020); as described above (Fig. 4), such differential susceptibility

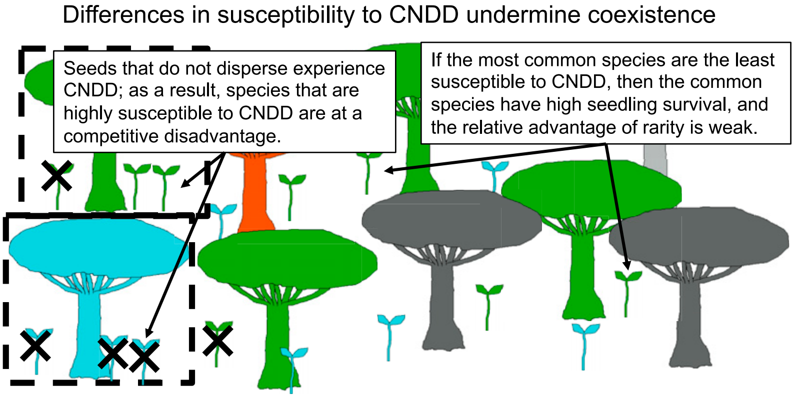

Figure 4. Differences in susceptibility to conspecific negative density dependence (CNDD) undermine coexistence. CNDD generally promotes coexistence; however, between-species differences in susceptibility generate two effects which likely undermine coexistence. First, if the most common species are the least susceptible to CNDD (as shown empirically, Mangan et al., 2010; Comita et al., 2010), this weakens the stabilizing mechanism: rare seeds have high survival by having few conspecifics, though common seeds have high survival by not being susceptible to CNDD, and thus the relative advantage to rarity is small (Stump & Comita, 2018). Second, a seed that does not disperse far from its parent always experiences some CNDD. Thus, species who are not susceptible to CNDD gain an advantage, because seedlings are more able to recruit near their parent (Stump & Comita, 2018). If interspecific differences in susceptibility are strong enough, and seed dispersal is low enough, then Janzen-Connell effects can actually drive species extinct (Murrell, 2010; Miranda et al., 2015; Stump & Comita, 2018).

would weaken stabilizing mechanisms and create fitness-differences (Fig. 6). Such pathogens could also create a rare-species disadvantage: if a species that becomes rare experiences a genetic bottleneck, they may lose R-gene diversity and become more susceptible to their pathogens (Marden et al., 2017; Stump et al., 2020). However, genotype-specific pathogens may have two positive effects on plant diversity. First, if R-genes are costly to maintain, then plant species that become rare benefit by not maintaining costly resistance (Stump et al., 2020). Second, theoretical studies have shown that genotype-specific pathogens select for seed dispersal more strongly than species-specific pathogens (Eck et al., 2019), and as described above (Fig. 2), Janzen-Connell effects promote diversity more strongly when seeds have high dispersal (Muller-Landau & Adler, 2007; Mack & Bever, 2014; Stump & Chesson, 2015; Stump & Comita, 2020).

Finally, most multispecies models assumed simple forms of host range, typically either that all natural enemies are species-specific specialists (e.g., Adler & Muller-Landau, 2005; Stump & Comita, 2018; Levi et al., 2019) or that they affect all heterospecifics equally (e.g., Chisholm & Muller-Landau, 2011; Stump & Chesson, 2015). However, empirical studies have suggested that host range can differ between natural enemies, and that this variation can lead to between-species interactions that are quite complex. For example, empirical studies have shown that natural enemies sometimes create intransitive competitive effects (Mack et al., 2019), e.g., that species A outcompetes species B, species B outcompetes species C, and species C outcompetes species A. Theoretical studies have shown that such complex dynamics may strongly allow species to coexist (Grilli et al., 2017; Mack et al., 2019).

PLANT-ENEMY INTERACTIONS AND THE MAINTENANCE OF DIVERSITY IN A CHANGING WORLD

Tropical forests continue to face numerous threats from human activities (Malhi et al., 2014; Lewis et al., 2015). Deforestation clearly causes large biodiversity losses in the tropics; however, large declines in diversity have also been linked to degradation of remaining tropical forests via human impacts such as ground fires, hunting, and fragmentation (Barlow et al., 2016). Even remote forests that appear to be untouched are likely to be affected by climate change, specifically through increasing temperatures, shifting precipitation patterns, and more frequent extreme natural disturbances (e.g., hurricanes, droughts) (Malhi et al., 2014). Human disturbances undoubtedly alter ecological interactions that structure tropical communities (Morris, 2010), including plant-enemy interactions that help maintain diversity. Exactly how these interactions will be altered and the resulting consequences for biodiversity are not yet clear. However, empirical ecologists are increasingly focusing on this topic, and the theoretical studies discussed above offer several insights into the potential consequences of altered plant-enemy interactions for tropical tree diversity.

Many studies have examined how the loss of vertebrate seed dispersers impacts seedling recruitment and survival (e.g., Terborgh et al., 2008; Harrison et al.,

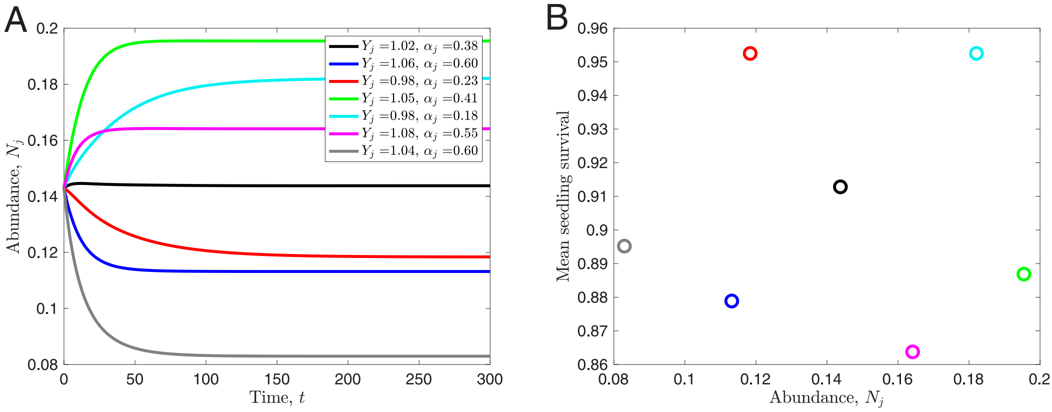

Figure 5. Janzen-Connell effects can promote coexistence without a community-compensatory trend (CCT). The CCT hypothesis predicts that rare species should have higher survival than common ones. However, we argue that this is an unlikely expectation to observe, but also that Janzen-Connell effects can promote coexistence without producing a CCT. —A. We simulated community dynamics using the model in Stump and Comita (2018), previously used to study Janzen-Connell effects. Janzen-Connell effects are the only stabilizing mechanism in this system. Each species is differently susceptible to CNDD (α_j is the probability of mortality of a seed falling near a conspecific adult), and differently adapted to the environment (Y_j is a relative measure of seed production and density-independent seed survival). —B. We show how species abundance covaries with mean seedling survival when the community is at equilibrium. This model does not produce a CCT, as there is a miniscule and positive relationship between abundance and seedling survival ($\rho = 0.028$). Yet, this community is strongly stabilized by the Janzen-Connell effects.

2013; Caughlin et al., 2015). As discussed above (see "Theoretical Developments: Dispersal and space"), if seed dispersal is low, such that nearly all seeds fall close to their parent plant, then rare species will fail to gain an advantage since they will not benefit from the large amount of enemy-free space away from parent plants (Fig. 2). This rare species advantage is key for natural enemies to maintain diversity, and thus reduced seed dispersal is likely to lead to a decline in tree diversity (e.g., Harrison et al., 2013). At the same time, the loss of dispersers will disproportionately affect plant species that are more susceptible to their natural enemies (Fig. 4), as they rely on dispersal to escape those enemies. Vertebrate-dispersed tree species will also be disadvantaged relative to abiotically dispersed species (e.g., Effiom et al., 2014), with tree species that rely on large bird and mammal species (the organisms most frequently targeted by hunters) particularly hard hit (Terborgh et al., 2008) (Fig. 6).

In addition to loss of dispersers, there is evidence that fragmentation—particularly through changes occurring at fragment edges (i.e., edge effects)—alters plant-enemy interactions in tropical forests (Benítez-Malvido & Lemus-Albor, 2005). Fragmentation-related changes in these biotic interactions may have negative consequences for the maintenance of tree diversity. For example, Krishnadas et al. (2018) found that the diversity of seedling recruits was higher at sites > 90 m from the forest edge compared to sites < 60 m from the forest edge in a fragmented landscape in southern India, despite similar diversity of seeds arriving at all distances. Treating seedling plots with fungicide and/or insecticide reduced seedling diversity at sites > 90 m from the edge but had no effect on seedling recruit diversity at sites < 60 m from the forest (Krishnadas et al., 2018). This shows that natural enemies had a diversifying effect on seedling recruitment in the forest interior, but their diversifying effect was lost close to forest edges. Such effects were likely the result of changes in environmental conditions near forest edges, namely reduced humidity, reduced soil moisture, increased light, and increased temperatures (Murcia, 1995), which could alter the density, composition, or virulence of natural enemies and/or the susceptibility of plants. For example, classic studies by Augspurger (1984) and Augspurger and Kelly (1984) found reduced pathogen-mediated seedling mortality of tropical tree species in Panama under high light conditions compared to in the shade. More recently, Álvarez-Loayza et al. (2011) found that an endosymbiotic fungus associated with an Amazonian palm species became pathogenic in high light, restricting the recruitment of endophyte-harboring seedlings to the shade.

There is also evidence that forest loss and fragmentation may favor generalist enemies over specialists (Mueller et al., 2016; Rossetti et al., 2017; Bagchi et al., 2018). As discussed above (see "Theoretical Developments: Host range"), host specialization is a critical component of the Janzen-Connell hypothesis, and a shift from specialized to generalist enemies should

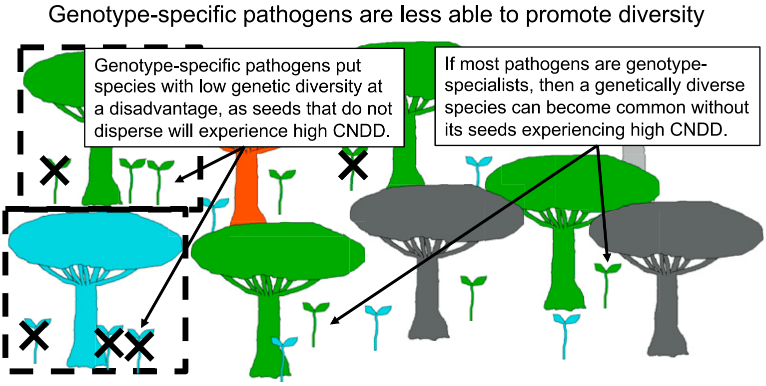

Figure 6. Genotype-specific pathogens are less able to promote diversity than species-specific pathogens. Species-specific specialist pathogens create a rare-species advantage because the more common a species is, the more likely a seed is to disperse a conspecific adult and be killed. If pathogens are mostly genotype-specific specialists, however, then the rare-species advantage is likely weakened: the seed of a common species will only die if it disperses near a conspecific adult of the same genotype, and if the species is genetically diverse, this may be less likely to happen (Eck et al., 2019). Additionally, seeds that do not disperse will be exposed to pathogens from their parent; this puts species with low genetic diversity at a disadvantage because seeds are likely to share more genotype-specific pathogens with their parent (Stump et al., 2020). If there are fixed genetic differences between species, then genotype-specific pathogens will create competitive differences; if species who become rare suffer from genetic bottlenecks, then genotype-specific pathogens will create a rare species disadvantage.

result in decreased plant diversity. Shifts in plant species composition in fragments will also likely alter plant-enemy interactions. Specifically, fragmentation typically results in an increase in light-demanding plant species, which, as discussed above, tend to be less well defended against insect herbivores and pathogens compared to more shade-tolerant species (Augspurger & Kelly, 1984; Coley & Barone, 1996; García-Guzmán & Heil, 2014). This could actually promote diversity, as the species that are most susceptible to CNDD would also be the most common (a situation that is the opposite of what is shown in Fig. 4). At the same time, top-down control of insect herbivores by predators (e.g., birds) may be weakened in fragmented forests, indicating the importance of considering changes to both top-down and bottom-up control of enemies in human-impacted forests (Guimarães et al., 2014). This could promote tree diversity if it increased CNDD uniformly for all species, but could also undermine tree diversity if it increased CNDD disproportionately for some species (Fig. 4).

As in the case of fragmentation, shifts in abiotic conditions resulting from climate change will undoubtedly influence plant-enemy interactions. Indeed, it has long been recognized that plant-pathogen interactions, in particular, are influenced by environmental conditions, a concept in plant pathology known as the "disease triangle" (Agrios, 2005). Liu and He (2019) recently reviewed how awareness of the disease triangle helps us understand the impact natural enemies have on tree species coexistence, including in the context of climate change. Briefly, increases in temperature under climate change may promote pathogen growth and infection, leading to increased severity of plant disease, but only up to some (species- and/or system-specific) optimal temperature, beyond which pathogen activity would likely decline (Liu & He, 2019). Soil moisture and humidity are also well known to influence pathogens, with higher pathogen activity generally associated with wetter conditions (e.g., Brenes-Arguedas et al., 2009). Changing precipitation regimes in tropical forests will likely alter plant-pathogen interactions, although the implications for tropical tree diversity are unclear (see review by Milici et al., 2020). Experimental watering resulted in higher pathogen-caused seedling mortality in a study on one tropical tree species (Swinfield et al., 2012). However, interactive effects of drought stress and pathogen and herbivore damage on trees can vary depending on multiple factors (Jactel et al., 2011). Clearly, more research is needed to understand how plant-enemy interactions will respond to climate change and to predict the implications for tropical tree diversity.

Similarly, we are still largely in the dark about how plant-enemy interactions are impacted by human disturbances, such as fire and selective logging. Furthermore, we do not know whether such interactions fully recover following deforestation in tropical forests. Secondary and degraded forests now make up more than half of the forest cover in the tropics (Chazdon, 2014) and yet we know relatively little about plant-enemy interactions in these forests. Interestingly, plant-enemy interactions may not only be responding to changing conditions in forests undergoing succession, they may actually play a role in driving tropical forest succession.

Studies from temperate herbaceous communities suggest that a buildup of species-specific soil pathogens over time, combined with differences in plant species' susceptibility to pathogens, plays a role in successional dynamics (van der Putten et al., 1993; Bauer et al., 2015). In forest ecosystems, studies of succession have largely focused on how abiotic variables, namely light, drive shifts in composition from early to later successional plant species. However, a recent study by Szefer et al. (2020) reported that natural enemies (specifically insect herbivores) played a role in shaping initial stages of succession in lowland tropical forest in Papua New Guinea. Thus, a key area of future research is to assess how plant-enemy interactions contribute to the speed and trajectory of tropical forest succession following human disturbance.

In summary, evidence increasingly suggests that plant-enemy interactions play an important role in shaping the composition and diversity of tropical forests. As tropical forests continue to be subjected to multiple forms of human disturbance, it is increasingly critical to understand the mechanisms that maintain tropical diversity in intact forests and assess the degree to which those mechanisms are being negatively impacted in disturbed forests. While the loss of large animals from tropical forests has generated a massive amount of concern from both scientists and the general public, the consequences of losing some of the smallest organisms—microbial pathogens and insect herbivores—may be just as dire for the future of tropical forest diversity.

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