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Review

Is Variation in Conspecific Negative Density Dependence Driving Tree Diversity Patterns at Large Scales?

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Half a century ago, Janzen and Connell hypothesized that the high tree species diversity in tropical forests is maintained by specialized natural enemies. Along with other mechanisms, these can cause conspecific negative density dependence (CNDD) and thus maintain species diversity. Numerous studies have measured proxies of CNDD worldwide, but doubt about its relative importance remains. We find ample evidence for CNDD in local populations, but methodological limitations make it difficult to assess if CNDD scales up to control community diversity and thereby local and global biodiversity patterns. A combination of more robust statistical methods, new study designs, and eco-evolutionary models are needed to provide a more definite evaluation of the importance of CNDD for geographic variation in plant species diversity.

Highlights

Stabilizing conspecific negative density dependence (CNDD) is a classical explanation for diversity maintenance in species-rich ecosystems, particularly in tropical forests.

Fifty years after Janzen and Connell popularized this idea, a plethora of empirical evidence suggests that CNDD can be found at all latitudes and for many tree species.

On closer inspection, however, it is still unclear if locally measured density effects are indeed stabilizing community dynamics and, moreover, if they have a causal effect on large-scale diversity and abundance patterns, such as the latitudinal diversity gradient.

More robust and comparable CNDD estimates are needed, coupled with a theoretical research program that aims at understanding the role of CNDD for coexistence in stochastic multispecies communities as well as macroecological and macroevolutionary diversity patterns.

CNDD: A Potential Driver of Diversity Patterns

Fifty years ago, two seminal papers by Janzen [1] and Connell [2] proposed that specialized enemies maintain the exceptionally high tree diversity in tropical forests. Their hypothesis was motivated by the assumption that more productive and stable environments favor specialization and effectiveness of enemy control in tropical interaction networks, relative to seasonal environments in temperate latitudes [2–4]. The idea that specialized enemies prevent any one species from becoming too abundant in tropical forests, thus maintaining greater diversity compared with temperate forests, became known as the **Janzen–Connell hypothesis** (see Glossary) (Figure 1A). It remains one of the most prominent conjectures in ecology to this day [5–7].

The Janzen–Connell hypothesis is tightly connected to the broader concept of **conspecific negative density dependence (CNDD)** [8]. For a single species, density dependence means that its population growth rate, or more broadly, its **demographic rates**, vary with population density. Most species react negatively to density and eventually all populations must show some kind of negative density dependence, simply because of physical and biological limits to how large a population can grow [9]. Negative density dependence becomes important for coexistence and diversity maintenance when it is stronger for conspecifics (CNDD, typically interpreted as **intraspecific competition**) than for heterospecifics [**heterospecific negative density dependence (HNDD)**, typically interpreted as **interspecific competition**] [10]. If CNDD > HNDD, a species' **fitness** decreases when it becomes dominant. If such negative **frequency dependence** (Figure 1C) is strong enough to overcome intrinsic fitness differences among species, it will lead to **stable coexistence** [11]. Janzen [1] and Connell [2] made this argument implicitly and it was later formalized in the framework of **modern coexistence theory** [12–14].

Stabilizing CNDD (i.e., CNDD > HNDD) can be created by a wide range of mechanisms. In forests, the idea that specialized enemies cause density dependent mortality [6], notably at early life

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stages [15], is particularly prominent. However, species-specific resource requirements, autotoxicity, and other mechanisms could also dampen population growth at high abundance via negative effects on dispersal, growth, mortality, and reproduction [16–18] and we consider all these possible mechanisms (Box 1) in this review.

Directly demonstrating the existence of stabilizing CNDD, however, is extremely challenging, especially for long-lived organisms such as trees (see discussion later). Most empirical studies have therefore evaluated either local density effects on plant performance (e.g., [5,19]) (Figure 1B) or patterns of community structure indicative of density dependence, for example, decreasing spatial clustering with age [20]. Unfortunately, this has led to the confusing situation where Janzen–Connell effects (Figure 1A), empirically measured CNDD effects on tree performance (Figure 1B), and stabilization via CNDD (Figure 1C) are effectively used synonymously in large parts of the literature. The concepts are intimately related, but they are not equivalent.

The idea that CNDD could be an important driver of plant community dynamics has fundamental implications from macroevolution to community ecology to applied conservation management [21,22], for example, regarding the relative importance of neutral and niche processes [23] or our understanding of regional and global variation in abundance patterns [24]. A particularly far-reaching implication is that variation in CNDD may drive or at least contribute to regional and global diversity patterns such as the **latitudinal diversity gradient**, particularly in forest tree communities [25,26].

Fifty Years of CNDD Research in Forests

In the five decades following Janzen [1] and Connell [2], research on CNDD has addressed four aspects of their hypothesis: (i) the existence of local CNDD; (ii) whether CNDD is stronger than HNDD; (iii) the relevance of CNDD for community diversity and coexistence; and (iv) whether regional and global patterns of CNDD, in particular a latitudinal gradient therein, are relevant for geographic diversity patterns. In the following, we review the evidence for these aspects focusing on trees, although we frequently refer to other communities where CNDD and its effects on diversity have been studied, including annual plants.

Does Local CNDD Exist?

Early tests of the Janzen–Connell hypothesis used either observational data to search for patterns indicative of CNDD, such as spatial repulsion and negative effects of conspecifics on plant performance [27–31], or experiments that exposed seeds or seedlings to different conspecific densities [32–34]. Almost all these early studies reported signs of CNDD: seed and seedling survival was reduced close to conspecific adults and at high conspecific seed and seedling densities and conspecific individuals exhibited spatial repulsion.

Over time, more sophisticated approaches were introduced, for instance, **spatial point pattern** analysis [35] and new experimental designs directed towards identifying the mechanism mediating CNDD (Box 1). An impressive number of observational (e.g., [36–39]) and experimental (e.g., [40–43]) studies consistently reported evidence for CNDD in many, but not all, tree species; particularly during early life stages, but less consistently among seeds [44,45]. The bulk of this research focused on the tropics, but CNDD was reported for temperate forests as well (e.g., [46–50]). Several reviews and meta-analyses summarize this picture, especially those by Hille Ris Lambers *et al*. [26], Hyatt *et al*. [44], Carson *et al*. [51], and Comita *et al*. [45], who concluded more generally that CNDD is ubiquitous in forests worldwide.

Glossary

Conspecific negative density dependence (CNDD): an ecological process (e.g., the population growth rate or a demographic rate) of a species is said to show CNDD when it is negatively influenced by the species' own (local) population density.

Demographic rates: (or vital rates) the parameters that determine the demography of a population, including the rates of reproduction, mortality, and growth.

Fitness: the expected life-time reproductive success or *per capita* growth rate of an individual, phenotype, or species.

Frequency dependence: the phenomenon that fitness depends on the relative abundances (frequencies) of species in a community.

Heterospecific negative density dependence (HNDD): the negative influence of (local) heterospecific population density (i.e., density of species other than the focal species) on demographic processes or the population growth rate as a whole.

Interspecific competition: competition between individuals of different species.

Intraspecific competition: competition between individuals of the same species.

Janzen-Connell hypothesis: the hypothesis that specialized enemies maintain plant species diversity by creating higher seed and seedling mortality at higher conspecific densities and closer to conspecific adults; and that this mechanism is more effective in the tropics, thus contributing to the latitudinal gradient in tree species richness.

Latitudinal diversity gradient: the trend of decreasing species diversity from the equator to the poles.

Modern coexistence theory: a mathematical and conceptual framework for the mechanisms of stable coexistence within communities.

Publication bias: a tendency for certain types of results to be published more than others. In practice, this refers to the tendency to publish only statistically significant results in support of a hypothesis and failing to report negative results (the file drawer problem).

Regression dilution: (or regression attenuation) a statistical phenomenon whereby error in an explanatory variable

Is CNDD Stronger Than HNDD and Thus Stabilizing?

It is thus tempting to conclude that the importance of CNDD for tree diversity is confirmed. One caveat of many early studies, however, is that they measured density effects of conspecifics only (e.g., [31,32,52–54]). Yet, for communities to be stabilized, CNDD must be stronger than HNDD [23] (Figure 1B). Absent such a comparison, the presence of CNDD might simply indicate general, nonstabilizing competition (i.e., CNDD ≈ HNDD).

Recent studies addressed this by estimating HNDD as well (e.g., [8,43]). Moreover, some studies investigated whether enemies are indeed host-specific [55,56], a prerequisite for stabilizing CNDD. However, many studies still fail to compare CNDD with HNDD (e.g., [5,47]), or do so without an explicit statistical test (e.g., [8,57]), indicating that the central importance of demonstrating that CNDD is stabilizing is still not fully appreciated. Of the individual studies that compare CNDD and HNDD, many report stabilizing effects (e.g., [38,58]) and a recent meta-analysis by Adler *et al*. [10] from many plant ecosystems, not just forests, finds overall robust evidence for stabilizing CNDD (see also [36,59]).

Is CNDD Stabilizing Community Diversity?

Another limitation of most existing studies to date is that they evaluate (stabilizing) CNDD in one demographic rate during a particular life stage. It is not always clear, however, if performance measures such as survival reliably correlate with overall fitness [60]. For example, certain mechanisms could lead to a negative correlation of survival with another performance indicator, or survival differences in early life stages could be diluted over time [11]. It would therefore be better to directly measure fitness [61], but this is challenging for long-lived organisms such as trees in forest communities (cf. [62]). This problem is less pronounced in herbaceous systems and a stronger connection between studies of CNDD in the two systems might be fruitful (e.g., [63,64]).

In the absence of holistic measures of fitness, several prominent studies have used fitness surrogates (such as seedling survival) to calculate CNDD and correlated these estimates to community diversity or species abundances. Those have reported stronger CNDD in more diverse communities [25,65–67] and for the seed-to-seedling transition during which diversity increased, both using observational data [52], as well as experiments [68] (but see [5]). LaManna *et al*. [65], Johnson *et al*. [25], and others [8,70] also reported stronger CNDD (or negative effects of conspecific soil pathogens) for rare species, as would be expected if CNDD controlled species abundances [24] and as shown for other taxonomic groups [69]. Other studies, however, found no correlation between species abundance and local CNDD [71–73] and in some cases the correlation is in the opposite direction (i.e., stronger CNDD for common species) [39].

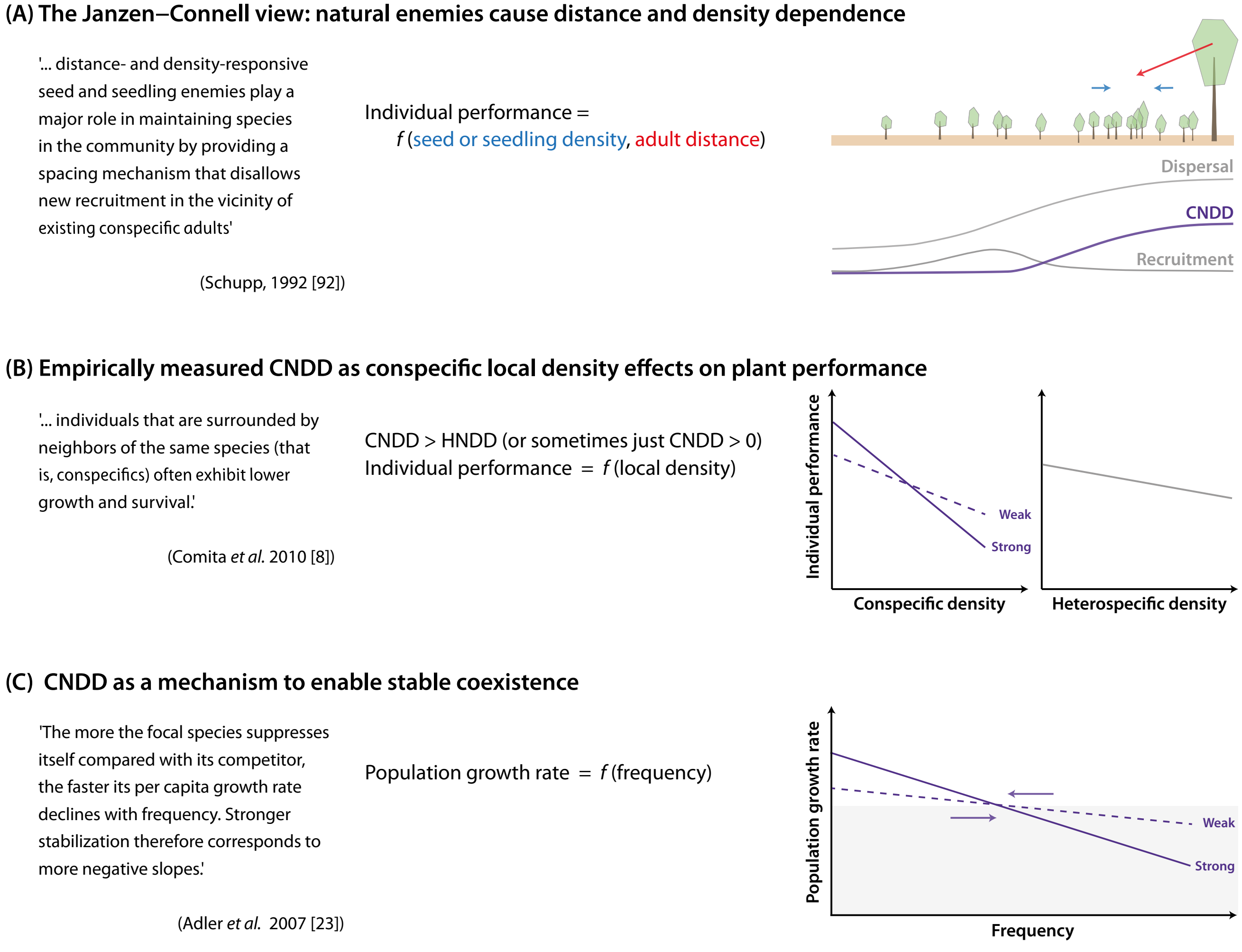
A second indirect line of evidence examines the spatial variation in demographic structure. This approach assumes that, in the absence of CNDD, the local density of recruits should be proportional to the local density of conspecific adults. This proportionality assumption can be tested by spatial discretization (e.g., [25,65]), or by spatial point pattern analysis (e.g., [74]). Studies using this approach have also reported signals of CNDD. These results, however, must be interpreted with caution. While the design integrates over several demographic rates and life stages (and may thus better approximate fitness [75]), it is also prone to confounding with environmental conditions or dispersal [76,77] and suffers from a **regression dilution** bias (Box 2) [78]. These biases are likely to cause a systematic overestimation of CNDD, particularly for rare species, which also casts doubt on reported correlations of CNDD with abundance.

creates a bias in the regression slope (typically towards zero).

Spatial point pattern: a class of statistical data in which single observations are recorded with their exact location. Spatial point pattern analysis explores statistical properties of these patterns (e.g., deviations from randomness).

Stabilization: the phenomenon that species can recover from perturbation to low density, preventing them from going extinct when rare.

Stable coexistence: the long-term persistence of several competing species in a closed system, without any one species being excluded.



(A) The Janzen–Connell view: natural enemies cause distance and density dependence

'... distance- and density-responsive seed and seedling enemies play a major role in maintaining species in the community by providing a spacing mechanism that disallows new recruitment in the vicinity of existing conspecific adults'

(Schupp, 1992 [92])

Individual performance = *f* (seed or seedling density, adult distance)

(B) Empirically measured CNDD as conspecific local density effects on plant performance

'... individuals that are surrounded by neighbors of the same species (that is, conspecifics) often exhibit lower growth and survival.'

(Comita *et al.* 2010 [8])

CNDD > HNDD (or sometimes just CNDD > 0)
Individual performance = *f* (local density)

(C) CNDD as a mechanism to enable stable coexistence

'The more the focal species suppresses itself compared with its competitor, the faster its per capita growth rate declines with frequency. Stronger stabilization therefore corresponds to more negative slopes.'

(Adler *et al.* 2007 [23])

Population growth rate = *f* (frequency)

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Figure 1. Different Viewpoints on Conspecific Negative Density Dependence (CNDD). (A) The classic formulation of the Janzen–Connell hypothesis depicts how specialized enemies can create CNDD in a spatially explicit context [85], here visualized following the graphical model of Janzen [1]: pathogen loads are higher close to conspecific adults (distance dependence, red); and where the density of conspecific seeds, seedlings, or recruits is high (density dependence, blue). As a result, recruitment happens preferentially for individuals that have dispersed further away [132], thereby increasing the spacing of adults, the spatial intermingling of species, and ultimately the number of species per unit area [157]. (B) The main empirical approach to CNDD has been to measure aspects of plant performance (e.g., mortality [5] or the transition probability between life stages [19]) as a function of local conspecific and sometimes heterospecific density [8]. (C) Coexistence theory is interested in CNDD as a stabilizing mechanism that decreases population growth when a species becomes relatively more abundant (frequency dependence [69]). In both (B) and (C), the slopes of the lines correspond to the strength of density or frequency dependence, indicating strong and weak stabilization for the unbroken and broken purple lines, respectively. Arrows in (C) point towards equilibrium frequency. See [8,23,92].

Does CNDD Exhibit Regional or Global Patterns?

The final assertion of the Janzen–Connell hypothesis is that CNDD explains geographic variation in species diversity, including the latitudinal diversity gradient. The first large-scale test of this idea was a meta-analysis of field studies by Hille Ris Lambers *et al*. [26] in the early 2000s, who found no latitudinal gradient in the proportion of tree species that experience CNDD. The study was limited in that it used vote-counting [79], but later meta-analyses using more robust methods found no latitudinal trend in CNDD from experiments on seed and seedling survival either [44,45].

Box 1. Mechanisms Causing Conspecific Negative Density Dependence (CNDD) to Be Stronger Than Heterospecific Negative Density Dependence (HNDD)

A prominent explanation for stabilizing CNDD is that specialized enemies accumulate where a host tree species is abundant [132], thereby suppressing its population growth, in particular via elevated mortality of seeds, seedlings, and saplings (Figure IA). Organisms that could exert such effects in trees include fungi, bacteria, arthropods, and small mammals [72,133–135].

A second explanation for stabilizing CNDD is interspecific variation in resource requirements, including nutrients, moisture, and light [117]. Stabilization occurs because the resource that a species specializes on gets locally depleted when the species is at high abundance (Figure IB) and the species therefore limits itself more than others. For trees, although there is certainly some resource specialization, the number of essential resources seems too small to allow coexistence of a large number of species (see also the 'paradox of the plankton' [136]). Ecologists have explored various mechanisms that could expand the number of niches, such as the temporal storage effect [137], but even so, there has been no convincing explanation for how resource niches alone could stabilize hundreds of species. This is part of the motivation for focusing on natural enemies and empirical evidence seems to support the importance of such Janzen–Connell effects [6,138,139] (but see [7]).

Additional mechanisms have been suggested, though less frequently. For example, root secretion or decomposition could lead to accumulation of toxic substances around a plant that disproportionately damage conspecifics [56,140] (Figure IC). Such autotoxicity has been observed for some tree species [56,141,142], but it has questionable adaptive value [143] making it rather unlikely as a broad mechanism. Another mechanism is specialized plant–pollinator interactions, which create a disadvantage when a tree species becomes more common and its pollinators are limited [18]. A third example is interspecific facilitation, for instance through hydraulic lift [144], which could weaken HNDD, thus contributing to a situation where CNDD > HNDD.

Each species most likely has its own combination of mechanisms, which may even be of varying importance over space and time [120,121,145]. For example, mycorrhizal fungi and higher-order predators can interact with CNDD-inducing enemies [146–148]. Despite these challenges, experiments, notably plant–soil feedback studies, pesticide treatments, enemy exclosures or inoculations [16,68,135,149], and observational studies that correlate CNDD with species' traits such as defense strategy, resource acquisition, and mycorrhizal type [6,72,146] have helped to identify, or at least narrow down, the CNDD-inducing mechanisms for individual tree species (e.g., black cherry *Prunus serotina* Ehrh. [16,145]). Correlations between CNDD and species traits [5,15,71] may be helpful to identify CNDD mechanisms also for less well-studied species.

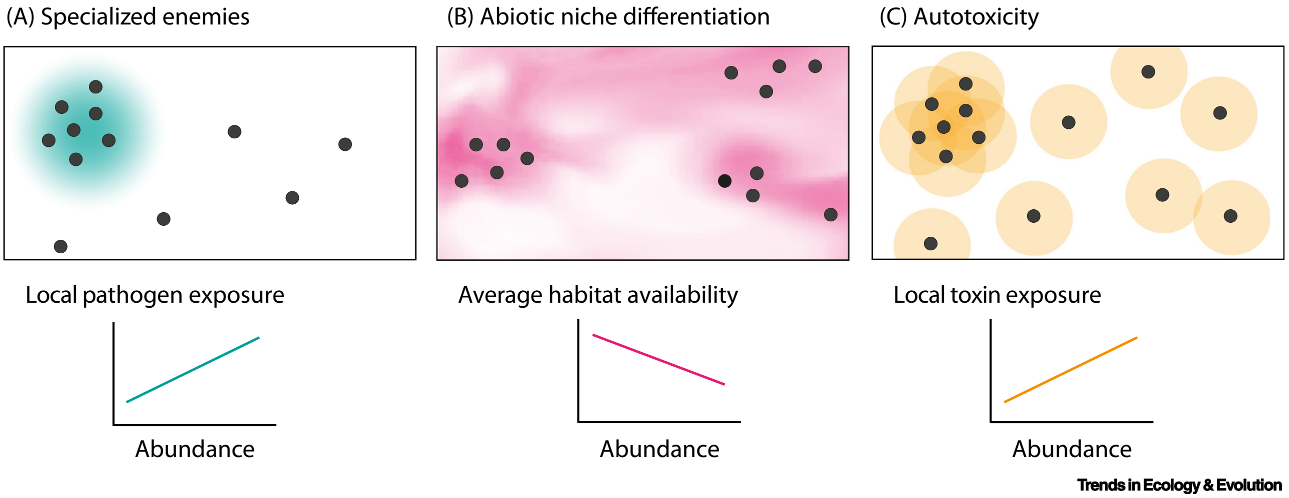

Figure I. Functioning of the Mechanisms That Create Conspecific Negative Density Dependence (CNDD). The upper panels show the spatial association of each mechanism (colored area) and the focal species (black dots), while the lower panels indicate how the mechanisms depend on a species' abundance.

By contrast, two studies that used the local tree demographic structure to quantify CNDD however found striking regional and global variation in CNDD consistent with predictions of the Janzen–Connell hypothesis [25,65]. Both studies, however, have been criticized for the earlier-mentioned methodological problems and simulations demonstrate that these biases are strong enough to produce the reported patterns, even when CNDD is completely absent [76,80,81].

Evidence for variability in CNDD along other gradients is similarly limited [82]. While a global meta-analysis revealed slightly stronger CNDD in wetter climates [45], variability in CNDD along edaphic gradients is typically studied only locally. For instance, Huang *et al*. [83] identified stronger CNDD where nitrogen availability is locally higher.

Box 2. Regression Dilution and Apparent Conspecific Negative Density Dependence (CNDD) in Recruitment Studies

Regression dilution, also known as regression attenuation, is a well-known cause of statistical bias [150]. It occurs when a regression model assumes that the explanatory variable is quantified without error, but this assumption is violated [151]. In this case, the regression slope (i.e., effect size) is usually biased towards zero (Figure I).

Although regression dilution is likely present in most ecological analyses, it is regularly ignored. This may be justifiable in studies where the null hypothesis is the absence of a relationship between predictor and response, because then the bias induced by regression dilution is conservative. The problem becomes more insidious when the null hypothesis specifies a specific relationship between predictor and response, as in studies that test for CNDD in recruitment. For example, if the null hypothesis is a proportional relationship between recruitment and adults, with negative deviations from proportionality at high conspecific abundance being interpreted as CNDD [152], then regression dilution can create the appearance of CNDD even where there is none [68], both for linear and nonlinear models of density dependence. This bias is doubly pernicious because its strength can be affected by species' abundances, leading to spurious correlations between CNDD and abundance [78].

Despite warnings by Freckleton *et al*. [153], several analyses have used a design based on proportionality to test for CNDD in trees over the last decades, both for spatial associations of adults and recruits (e.g., [25,65]) and transition rates between different life stages (e.g., [52,154]). While errors in study designs that analyze CNDD in transition rates are random and can be corrected via repeated measurements, for example, using multiple seed traps (e.g., [68,78]), errors in studies that rely on spatial associations of recruits and adults have a different nature.

Here, problems arise in particular from the assumption that the parent trees of saplings observed within a given quadrat are all still alive and within the same quadrat. LaManna *et al*. [155,156] responded to critiques of their sapling–adult analyses [76,80] by presenting an alternative distance-weighted approach to estimating conspecific adult density, along with null-model simulations using species-specific estimates of dispersal. Although this improves upon the original quadrat-based approach, the resulting CNDD metric is still prone to regression dilution, because of dispersal distances not being accurately known for most of the species and other possible sources of error in the adult counts, arising, for example, from adult trees being dead or outside the plot boundaries. These errors are extremely difficult to eliminate [76,78].

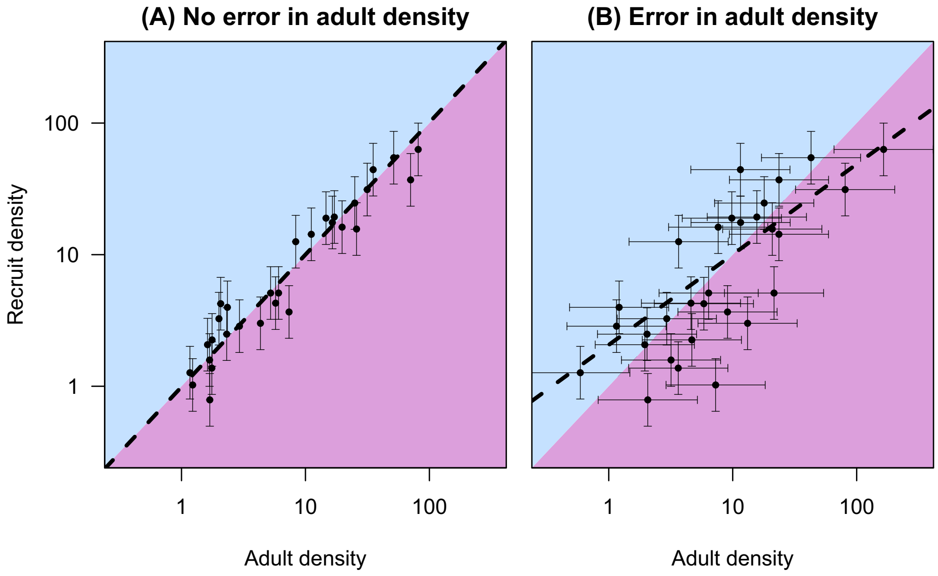

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Figure I. Regression Dilution and the Effect of Measurement Errors on Conspecific Negative Density Dependence (CNDD) Estimates in Recruitment Studies. Analyses of associations between adults and recruits can be biased by regression dilution. Here we apply a linear model on log–log transformed densities, such that the null hypothesis is a slope of one indicating proportionality, and a slope smaller than one is interpreted as CNDD. We simulated data for which recruits are proportional to adults (i.e., there is no CNDD). When there is no error in measured adult density, the estimated slope on log–log axes is unbiased and centered around one (A). However, with errors in the measurement of adult density (error bars), the regression slope is biased towards zero (B), creating apparent disproportionality that could be mistakenly interpreted as CNDD. This problem is general and not limited to the particular linear model fitted here. Each broken line is averaged over independent linear fits to 1000 simulated datasets; the black dots on each panel show one simulated dataset for illustration purposes. Adapted from Detto *et al*. [78].

A Synopsis of Current Knowledge

In summary, there are four subhypotheses to the overall hypothesis that CNDD drives large-scale diversity patterns: (i) CNDD exists; (ii) CNDD > HNDD; (iii) CNDD stabilization scales up to the community; and (iv) this effect varies along ecological gradients and drives diversity patterns.

For tree communities, there is ample evidence for claim (i), and somewhat weaker, but still convincing evidence for claim (ii) in the published literature. We have highlighted some technical problems in this research and it can be expected that, just as in other fields, **publication bias** may have favored dissemination of those studies that found support for CNDD [84]. Nevertheless, we believe that the multiple lines of evidence outweigh such uncertainties and conclude that seedlings and saplings of many tree species likely experience stabilizing CNDD, although the phenomenon may be not as strong or pervasive as sometimes claimed (e.g., [52,65,85]).

The empirical evidence for claims (iii) and (iv) is much weaker, both because of the large spatial and temporal scales involved and the technical problems when evaluating CNDD indirectly via static patterns. Although models show that local CNDD can scale up to the community and beyond ([86,87] but see [88,89]), no compelling empirical evidence for a significant causal effect of CNDD on larger-scale patterns of tree diversity has been presented to date.

Obstacles to Assessing CNDD and Its Implications in Forests

The validity of the Janzen–Connell hypothesis in its entirety is thus still surprisingly unresolved. In this section, we provide a more detailed account of current challenges.

Conspecific Exposure Is Difficult to Quantify

Analyses of CNDD in forests and other communities inherently rely on a definition of local conspecific exposure. This poses several questions that likely require species-specific answers: how does the conspecific effect attenuate with distance [90,91]? Should we measure conspecific exposure by distance or density [44]? Is density better approximated by stem number, basal area, or biomass, and what classifies as an adult versus a juvenile tree? Is the functional response to density linear or does it accelerate or saturate above certain density thresholds [78]? These considerations are crucial because using imperfect proxies of true conspecific exposure can create regression dilution that biases analyses (Box 2).

Performance in One Life Stage Does Not Necessarily Translate into Fitness

Ultimately, we are interested in how conspecific density regulates population growth [92]. When measuring CNDD in plant performance, particularly in early life, we have to understand if those effects propagate through the entire life cycle, rather than being canceled out or diluted at later life stages [11,39,93].

Indirect Measures Calculated from Static Data Are Prone to Confounding Factors

Looking for indirect evidence of CNDD via emergent patterns in forest structure (e.g., [20,65,94]) seems appealing, but comes with additional caveats, in particular the need to control for confounders. For example, repulsion between conspecifics is often interpreted as evidence for community stabilization via CNDD (e.g., [95,96]), but other processes, including environmental variability, dispersal, and nonspecialized biotic interactions, also affect this pattern and it is difficult to correct for them [77,97].

Furthermore, many studies that examine such emerging patterns essentially perform an ontogeny-for-time substitution (recruits versus adults) to assess the influence of conspecific density on population dynamics (e.g., [25]). This approach is associated with additional uncertainties:

By what criteria are adults and recruits separated? Are recruits far away from adults because of broad dispersal or because they suffer from strong CNDD? What happens if adults and recruits have different habitat preferences?

Measuring Multispecies Coexistence Is an Open Problem

Another, more subtle point, is how to define stable coexistence. As Broekman *et al*. [11] point out, CNDD > HNDD or frequency dependence in population growth rates is a sufficient (though not necessary) condition for stabilization, but not a sufficient condition for stable coexistence at the community level. For the latter, the comparison of all pairwise density effects from a focal species to itself and to and from all other species would be needed [10,11]. But even if those values could all be estimated (an unlikely prospect in a diverse tree community), it is still unclear how to translate them into a meaningful metric for coexistence in stochastic multispecies communities with a much richer set of dynamics than a two-species system [98–100]. Possibly, it would be more productive to discard the concept of stable coexistence in favor of broader stability concepts such as average residence time of species in the community (e.g., [101]).

Statistical Methods Are Often Biased or Misinterpreted

Finally, the statistical methods for evaluating CNDD have a history of bias and misinterpretation. In particular, regression dilution distorts CNDD estimates that rely on a null hypothesis of proportionality between two variables of interest (e.g., recruit and adult abundance) and typically results in an overestimation of both the frequency and strength of CNDD (Box 2). Another, less appreciated issue is that many CNDD analyses (mortality studies in particular) rely on generalized linear models with a nonlinear link function. The resulting estimates of regression slopes cannot be directly compared across models, species and sites, because, depending on the intercept of the model, their effect on the predicted mortality probability changes [102,103].

How to Move Forward: A Roadmap for CNDD Research

Despite the challenges, we are optimistic about research on CNDD and plant diversity. Here, we delineate what we think are suitable methods for this research program.

Generating Robust and Comparable Estimates of Local CNDD

The first component of a successful CNDD research program in forest tree communities is to quantify the strength of CNDD more reliably and comparably. Long-term observational studies on large forest plots can in principle yield estimates of CNDD within entire communities under natural conditions [104]. We strongly advocate that such plots be continuously measured and expanded in the coming decades, with more consistent efforts directed towards collecting associated data on confounders of CNDD (cf. [39,47,91]), alternative metrics of conspecific exposure (cf. [78]), and information on seeds and seedlings [47,78]. This will facilitate estimation of CNDD over large parts of species' life cycles and ultimately its effect on population growth rates (e.g., [105]). Remote sensing may become an additional source of observational data that could, for example, help to estimate the strength of repulsion between conspecifics at unprecedented scales [106,107].

Observational studies nevertheless have inherent limitations in identifying causality and underlying mechanisms [78,108]. We therefore recommend accompanying experiments to validate the findings from observational data and to identify CNDD mechanisms and the conditions under which they are effective. We recognize that practical limitations may confine experiments to early life stages of a relatively small number of species [45] and thus recommend that focal species be stratified across functional groups, relative abundance, and expected strength of CNDD. Experimental designs should also consider advice formulated for herbaceous systems (e.g., [63]).

In both observational and experimental studies, there is a need for CNDD metrics that are unbiased, comparable between species and ecosystems, and relevant for stabilization and coexistence. Until better metrics of multispecies coexistence are developed, studies should continue to evaluate the strength of CNDD relative to HNDD [23], with explicit statistical tests against a null hypothesis of CNDD = HNDD (not CNDD = 0). Studies should focus on estimating CNDD in dynamic responses (i.e., growth, mortality, and transitions between life stages; cf. Box 2). When comparing the strength of CNDD between species, species groups, or sites using models with a nonlinear link function, effect sizes should be expressed as a change in the response (e.g., in mortality probability; marginal effects, see [109]). Regression models where the null hypothesis is a zero effect size should be preferred to reduce the risk that regression dilution creates apparent CNDD if there is none (Box 2) [78].

If null hypotheses of proportionality or specific effect sizes must be used, there are a couple of ways to mitigate the regression dilution problem. One is to verify that the null hypothesis holds in a no-CNDD treatment, indicating that the regression dilution problem is minimal. For example, Bagchi *et al*. [110] used a fungicide treatment to show that the relationship of final to initial seedling density was roughly proportional in the absence of CNDD. Another is to collect data such that the strength of the predictor error can be estimated (Box 2), which permits the application of models that account for such random errors (e.g., [69]).

In general, given the challenges of designing a reliable CNDD metric, we recommend an abundance of caution in all CNDD studies. For instance, it may be instructive to check whether different reasonable CNDD metrics lead to consistent conclusions [26]. Also, candidate CNDD metrics should always be validated by showing that they give estimates close to zero without spurious correlations when applied to null models without CNDD [111]. Using null models to correct biased CNDD estimators, however, although theoretically possible, is far less robust than using an unbiased estimator in the first place [76].

Assessing Geographical Variation in CNDD

To assess geographical variation in CNDD, we advocate observational cross-site studies (e.g., [39,45]) with standardized data (e.g., ForestGEO network [112]) over meta-analyses. Even so, a challenge in these studies will be to determine the direction of causality. Structural equation modeling and adjustment for confounding variables can to some extent address the problem of causality [113,114]. More ambitiously, a coordinated global experiment (for an example see NutNet [115]) could be used to estimate CNDD with standardized methods at many sites for a subset of species to corroborate observational analyses and yield a more mechanistic understanding of CNDD [116], albeit at large monetary cost.

Linking CNDD to Community Stabilization and Diversity

An alternative to experimental studies for answering the question of how CNDD affects diversity would be a mechanistic model that accurately predicts community assembly and dynamics. Such mechanistic models have been successfully developed for resource-based CNDD in simple two-species communities [117] and for low-diversity temperate forests [118]. Also, models with a phenomenological representation of CNDD, parameterized with species-specific empirical data, have helped to link CNDD and diversity in herbaceous systems (e.g., [62,119]). But in tropical tree communities, with hundreds of long-lived species, such approaches seem doomed by the curse of dimensionality [11]. A minimal set of processes would include dispersal, demographic stochasticity, CNDD, and species' responses to spatial and temporal variation in resources and environmental conditions, all of which require species-specific parameters. To complicate matters, CNDD itself may vary temporally and spatially in response to resource availability and enemies

[120,121]. The problem may be simplified by modeling functional groups (e.g., [122] but see [123]) or tradeoffs between CNDD and life history strategies or defense traits [5,6,15,124,125], but the feasibility of creating predictive community models via this route is uncertain.

While we wait for breakthroughs in scaling up forest dynamics mechanistically, one possible contribution for theoreticians may be to provide back-of-the-envelope calculations that approximate how important CNDD is at the population level (e.g., [88]). In population genetics, there is a rule of thumb that assesses when selection is stronger than drift for a focal allele ($2Ns \gg 1$, where N is the effective population size and s the selection coefficient). A similar approximation for CNDD may involve parameters such as community size, mean community CNDD, and mean community invasion growth rate. Another important parameter is within-community variability of CNDD, which must be low for coexistence to occur [89,126]. It is conceivable that, via such back-of-the-envelope calculations, we will be able to broadly accept or reject the hypothesis that CNDD is strong enough to have an important effect on diversity.

Examining CNDD in an Eco-Evolutionary Context

If the scientific question of interest is not just about how CNDD affects local diversity, but also whether it scales up to affect regional diversity over longer timescales, mechanistic models will need to go even further and follow a multiscale eco-evolutionary approach [127–129]. Recent theoretical studies have only begun to look at the cross-scale question [86,88,89]. Also, the topic of how CNDD affects speciation, which has been experimentally touched on in other life forms [130], seems an area ripe for theoretical investigation [131].

Concluding Remarks

Our review shows convincing evidence that stabilizing CNDD occurs in forest tree communities at all latitudes. It remains unclear, however, to what extent CNDD maintains local species diversity and contributes to geographical diversity patterns (see Outstanding Questions). As these are two crucial aspects of the Janzen–Connell hypothesis, also fundamental to our general understanding of the role of CNDD for biodiversity, future research should focus on testing these subhypotheses. In our roadmap for CNDD research, we argue that the key to this will be developing more robust and meaningful CNDD metrics, conducting large-scale comparative studies based on dynamic data, and integrating CNDD into both community-ecological and macroevolutionary modeling frameworks. This will pave the way to a more holistic understanding of CNDD and its implications for species diversity.

Outstanding Questions

How prevalent is strongly stabilizing conspecific negative density dependence (CNDD) in tropical and temperate forests and is there a latitudinal gradient in CNDD?

What is the relative importance of the different mechanisms that cause CNDD and are natural enemies as important for CNDD and diversity as the Janzen–Connell hypothesis suggests?

Does locally stabilizing CNDD scale up to regional and global diversity patterns and how does it interact with macroevolutionary processes?

What would be a robust and comparable CNDD metric that is meaningful for stabilization and community diversity and is it possible to develop back-of-the-envelope calculations that approximate whether CNDD is strong enough to outweigh other processes based on a few key parameters?

How can we address the problem that CNDD is not a fixed attribute of a species but an emergent property of spatial and temporal variability, including enemy dynamics?

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