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SYNTHESIS

Consequences of Local Conspecific Density Effects for Plant Diversity and Community Dynamics

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ABSTRACT

Conspecific density dependence (CDD) in plant populations is widespread, most likely caused by local-scale biotic interactions, and has potentially important implications for biodiversity, community composition, and ecosystem processes. However, progress in this important area of ecology has been hindered by differing viewpoints on CDD across subfields in ecology, lack of synthesis across CDD-related frameworks, and misunderstandings about how empirical measurements of local CDD fit within the context of broader ecological theories on community assembly and diversity maintenance. Here, we propose a conceptual synthesis of local-scale CDD and its causes, including species-specific antagonistic and mutualistic interactions. First, we compare and clarify different uses of CDD and related concepts across subfields within ecology. We suggest the use of local stabilizing/destabilizing CDD to refer to the scenario where local conspecific density effects are more negative/positive than heterospecific effects. Second, we discuss different mechanisms for local stabilizing and destabilizing CDD, how those mechanisms are interrelated, and how they cut across several fields of study within ecology. Third, we place local stabilizing/destabilizing CDD within the context of broader ecological theories and discuss implications and challenges related to scaling up the effects of local CDD on populations, communities, and metacommunities. The ultimate goal of this synthesis is to provide a conceptual roadmap for researchers studying local CDD and its implications for population and community dynamics.

1 | Introduction

For over a century, ecologists have sought insights into the maintenance of species diversity and relative abundances by studying intra- and interspecific biotic interactions (Bever, Mangan, and Alexander 2015; Gause and Witt 1935; Lotka 1925; MacArthur 1972; Volterra 1927; Wright 2002). A prominent idea in this context is conspecific density dependence (CDD), which is integrated into multiple ecological theories, including the Janzen–Connell hypothesis, resource-competition theory, and coexistence theory (e.g., Chesson 2000; Thompson et al. 2020; Tilman 1982). The phenomenon of reduced demographic performance at higher conspecific densities is known as negative conspecific density dependence ("negative CDD" or CNDD). If conspecific densities reduce plant demographic performance more than heterospecific densities (termed "stabilizing CDD" in Hülsmann et al. 2024), then these effects should decrease spatial aggregation of conspecific individuals on the landscape (Kalyuzhny et al. 2023), open space for other species, and maintain species diversity over time all else being equal (Hülsmann, Chisholm, and Hartig 2021; Levi et al. 2019). For example, the concept of CDD often overlaps with the Janzen–Connell hypothesis, which posits that relatively host-specific density- or distance-dependent interactions between plants and their natural enemies (e.g., pathogens, herbivores, and predators) reduce plant survival and/or recruitment near conspecifics. As a result, plants should experience reduced performance with increasing conspecific relative to increasing heterospecific densities, favoring more diverse local species assemblages (Connell 1971; Janzen 1970). Recent reviews and meta-analyses have found broad support for reduced per-capita survival in younger age classes under elevated local conspecific densities (Comita et al. 2014; Hülsmann, Chisholm, and Hartig 2021; Song et al. 2021). These findings are often interpreted to be caused by biotic interactions, which is a plausible mechanism supported by an accumulating number of small-scale manipulative experiments (Bagchi et al. 2014; Krishnadas et al. 2018; Luskin et al. 2021; Mangan et al. 2010; McCarthy-Neumann and Kobe 2010; Petermann et al. 2008).

Despite such empirical support for CDD, several key challenges have hindered our ability to better understand the causal mechanisms that generate local CDD as well as their influence on broader scale ecological processes and patterns. These challenges stem from different definitions and approaches to studying CDD across subfields. Another major barrier has been the widespread misconception about how local measurements of CDD fit within the context of broader ecological theories such as community-assembly and coexistence theories. These challenges have resulted in recent debates in the literature that focused on how to robustly measure local CDD as well as its implications for species diversity and coexistence (e.g., Detto et al. 2019; Hülsmann and Hartig 2018; LaManna, Mangan, and Myers 2021). We have been actively involved in those debates and offer this conceptual synthesis as a set of consensus recommendations on these important challenges and how to move forward as a field. A companion second paper is in preparation that will offer detailed technical and methodological recommendations and worked examples for how to robustly measure local CDD (Krishnadas et al. in prep).

The first key challenge addressed here is reconciling differing viewpoints on CDD across ecology. CDD and related concepts are studied across several different subfields of ecology, including plant–soil feedback, Janzen–Connell effects, population ecology, and resource competition. Different definitions for overlapping and interrelated terms across subfields have resulted in confusion about the implications of CDD for population and community dynamics. We compare these different overlapping uses of CDD and offer recommendations for clearer terminology.

The second key challenge is that the study of CDD across different subfields often focuses on different types of mechanisms. This can result in progress in one area not being recognized in another not only because of different terminology but different conceptual frameworks or focal mechanisms. This challenge is particularly evident when researchers fail to consider mechanisms generating positive CDD (increased demographic performance at higher conspecific densities). Although local-scale plant CDD research has been shaped by the frequent observation that CDD is generally negative (Bever, Westover, and Antonovics 1997; Bever, Mangan, and Alexander 2015; Song et al. 2021), mechanisms that generate positive CDD still influence net CDD (Jiang et al. 2020; Liang et al. 2021). Moreover, such processes interface with other mechanisms that affect conspecific aggregation (e.g., dispersal limitation, habitat heterogeneity) and organisms' ability to escape areas of high conspecific density, including dispersal, intraspecific competition, abiotic niche partitioning, and allelopathy (Chase and Leibold 2003; Kalyuzhny et al. 2023). A better understanding of the interplay among different CDD-related mechanisms is necessary to synthesize CDD research across ecological subfields.

The third key challenge is that implications of local-scale CDD for community and metacommunity diversity and dynamics remain unclear, largely due to uncertainty about how local CDD fits within the context of broader ecological theories such as metacommunity and scale-transition theories (Chesson 2012; Thompson et al. 2020). For example, empirical measurements of negative CDD in individual demographic performance at local spatial scales do not necessarily translate to negative CDD or frequency dependence in population growth, and thus how local CDD influences community and metacommunity properties remains largely unclear (Cannon et al. 2020; Chisholm and Fung 2020; Hülsmann, Chisholm, and Hartig 2021; May et al. 2020; Smith 2022). One reason this challenge persists is that while broader ecological theories incorporate density- and frequency-dependent effects at the population level, there has been relatively less work upscaling individual plant-level density effects to population scales where ecological theories operate (but see Amarasekare et al. 2004; Chesson et al. 2005; Ellner et al. 2022; Shoemaker and Melbourne 2016). We address this third challenge by placing local-scale CDD within the context of broader ecological theories and discussing issues involved in scaling the effects of local CDD on population, community, and metacommunity dynamics.

In the remainder of this paper, we expand on these three key challenges and suggest possible solutions. We first discuss the different ways in which CDD has been used in ecological literature and clarify key terms (Section 2). Second, we synthesize across biological mechanisms that are expected to generate local CDD (Section 3). Third, we discuss challenges and approaches to upscaling local CDD to broader-scale patterns of biodiversity and metacommunity dynamics, including a synthesis of CDD-related predictions at different spatial and organizational scales (Section 4). We conclude by highlighting future avenues for research within the field.

2 | How Do Ecologists Define and Measure CDD?

In its broadest context, CDD represents an increase or decrease in demographic performance with increasing conspecific density. This CDD definition does not invoke an underlying mechanism, nor does it explicitly define the spatial or temporal scale at which CDD occurs.

2.1 | Different Viewpoints on Conspecific Density Dependence in Ecology

In practical studies, ecologists need to operationalize this broad definition of CDD. Unfortunately, this has led to different outcomes that are all called by the same name. First, CDD is often used to describe the density responses of a single species, without comparing CDD across species in a community or to possible density-dependent effects caused by heterospecifics. This type of CDD study is therefore inadequate to determine whether CDD is stabilizing at the community level. For example, if local CDD is negative but equivalent to the local negative effects of heterospecific density, then the underlying mechanism driving both effects could be crowding (Kenkel, Hendrie, and Bella 1997) which would not necessarily be expected to create a stabilizing effect on species diversity (Broekman et al. 2019).

A second line of research seeks to assess the impacts of species interactions on community dynamics and focuses on local biotic interactions that reduce or enhance demographic performance with increasing conspecific density *relative to* increasing heterospecific density. These studies often use CDD to refer to the outcomes of spatially-explicit neighborhood-scale interactions with relatively host-specific antagonists or mutualists. For example, host-specific natural enemies reduce host performance with increases in conspecific density but not increases in heterospecific density (Connell 1971; Janzen 1970; Song et al. 2021). Such species-specific reductions in performance can also result from stronger intraspecific than interspecific competition (Lotka 1925; Tilman 1982; Volterra 1927). This CDD definition invokes one of several underlying biological mechanisms, is specific to local neighborhood scales, and incorporates a comparison between conspecific and heterospecific density effects across species within a community. While the Janzen–Connell hypothesis addresses neighborhood-scale interactions among species and multi-species extensions of Lotka–Volterra competition models address population-level interactions among species, both models predict that if conspecific density effects are more negative than heterospecific density effects across species within their respective spatial scales, then species diversity should be enhanced at that respective spatial scale all else being equal (Connell 1971; Janzen 1970; Lotka 1925; Volterra 1927).

2.2 | Introducing Stabilizing and Destabilizing CDD

In Box 1, we offer definitions for some of the different ways in which CDD, density dependence, frequency dependence, and related terms have been used. These definitions sometimes overlap, reflecting the array of terminology used for these concepts in the many fields interested in CDD.

To reduce confusion, we suggest the terms “stabilizing CDD” and “destabilizing CDD” for negative and positive density effects of conspecifics, respectively, adjusted for heterospecific density effects. This definition is analogous to the terminology used in Hülsmann et al. (2024), where they used the term “stabilizing CDD” to refer to the difference between predicted annual mortality probability for an individual compared to predicted annual mortality if one additional conspecific at a standardized size and distance was placed within its neighborhood while removing a same-sized heterospecific to keep total density constant. In this framework, stabilizing CDD occurs when increasing conspecific densities reduces species' demographic performance more than increasing heterospecific densities (Hülsmann et al. 2024). In other words, stabilizing CDD is CDD corrected for general (non-species specific) density effects. Stabilizing CDD might result from interactions with relatively host-specific natural enemies or stronger intra- than the interspecific competition for limited resources. Analogously, we define the opposite case as “destabilizing CDD,” which occurs when increasing conspecific densities reduce species' demographic performance less than increasing heterospecific densities. Under this definition, destabilizing CDD might result from interactions with relatively host-specific mutualists (e.g., mycorrhizae, endosymbionts) or stronger inter- than intraspecific competition. Distinct mechanisms generating stabilizing and destabilizing CDD may act jointly, meaning the net effect of these combined mechanisms will be the result of their relative strength.

These definitions of stabilizing and destabilizing CDD correspond to taking the difference between conspecific and heterospecific density effects when measured on the same demographic rate: negative values indicate stabilizing CDD, and positive values indicate destabilizing CDD (Krishnadas et al. in prep). Importantly, we are not proposing to replace the term CDD when referring to analyses that do not explicitly compare conspecific and heterospecific density effects. Stabilizing and destabilizing CDD would refer specifically to the comparison of conspecific to heterospecific (or general) density effects across species, which makes it analogous to negative/positive plant–soil feedback and comparisons of intra- and interspecific competition in Lotka–Volterra and coexistence models (Box 2).

BOX 1 | Commonly used CDD and related terms.

Literature on conspecific density dependence (CDD) uses different terms that may be used interchangeably although they refer to different but related concepts. We define them here for clarity.

Density dependence: The covariation of population density and population growth rate or demographic performance (Herrando-Pérez et al. 2012), including survival, growth, dispersal, and fecundity. Density dependence can be species-specific (i.e., conspecific density dependence), general, or specific at higher or lower taxonomic levels (e.g., genus-specific, genotype-specific).

Conspecific density dependence (CDD): "An ecological process (e.g., demographic rate, including population growth) of a species is said to show conspecific DD when it is negatively (or positively) influenced by the species' own (local) population density" (Hülsmann, Chisholm, and Hartig 2021).

Heterospecific density dependence (HDD): When demographic performance of a species varies with the densities of non-focal species or heterospecifics.

Stabilizing/destabilizing CDD: All else equal, CDD may maintain species diversity when more negative than HDD. We refer to this as stabilizing CDD (i.e., CDD < HDD). Conversely, destabilizing CDD (i.e., CDD > HDD) should erode species diversity. Stabilizing CDD has been referred to as negative CDD, CNDD, or Janzen–Connell effects (the latter assuming a specific mechanism). Destabilizing CDD has been referred to as reverse Janzen–Connell effects (Zahra, Novotny, and Fayle 2021) and has been associated with priority and Allee effects (Fukami 2015; Vellend 2016). While we suggest the terms stabilizing/destabilizing CDD, this does not mean that these local processes will ultimately cause community stabilization or destabilization (Hülsmann et al. 2024). Net stabilizing CDD (outcome of mechanisms that generate stabilizing and destabilizing CDD) must scale up to the community level to maintain diversity, although these criteria are not necessarily sufficient for species coexistence because fitness differences may still drive species exclusion.

General density dependence: Density dependence that is general with respect to species identity, also known as general competition, crowding, or self-thinning in silviculture (Kenkel, Hendrie, and Bella 1997).

Conspecific distance dependence: When performance depends on distance from a conspecific. In many classic Janzen–Connell studies, vital rates of seedlings are measured near to and far from adult conspecifics (Hyatt et al. 2003).

Frequency dependence: The phenomenon that performance depends on the relative abundances (frequencies) of species in a community (Hülsmann, Chisholm, and Hartig 2021).

Fitness difference: Differences in demographic performance among species at comparable local densities of all individuals and conspecifics. For stabilizing CDD to maintain species diversity, it must be large enough to overcome fitness differences among species (Chesson 2000). Fitness differences can be measured at different scales of biological organization (e.g., individual organism vs. population).

Niche difference: In coexistence theory, niche differences between two species are conceptually like stabilizing CDD. Theory suggests that stabilizing CDD should occur because of niche differences, implying that a species has a greater negative impact on its own population than its impact on another species' population.

Coexistence theory: General theory for the coexistence of two species given their fitness and niche differences (Chesson 2000). If two species differ in fitness, then the species with higher fitness is expected to exclude the other unless fitness differences are overcome by niche differences. Neutral theory is a special case with no fitness or niche differences (Adler, HilleRisLambers, and Levine 2007). In coexistence theory, equalizing forces are processes that minimize fitness differences while stabilizing forces are those that give species at low abundances an advantage (i.e., niche differences).

Janzen–Connell hypothesis: "The hypothesis that [relatively] 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" (Hülsmann, Chisholm, and Hartig 2021). Janzen-Connell mechanisms are expected to generate local stabilizing CDD.

Plant–soil feedback: When a plant alters biotic and/or abiotic properties of the soil environment in a way that influences its own fitness or that of conspecifics (Bever, Westover, and Antonovics 1997). Plant–soil feedback can result in both stabilizing and destabilizing CDD. The plant–soil feedback concept can be extended to include plant-phyllosphere feedback (Whitaker et al. 2017).

Intraspecific and interspecific competition: Competition for limited resources between individuals of the same (intraspecific competition) or different species (interspecific competition). Resource competition theory holds that two or more species may coexist if they consume their own limiting resource faster than limiting resources for other species (i.e., intraspecific stronger than interspecific competition). Examples include R* (Tilman 1982, 1988) and contemporary niche theory (Chase and Leibold 2003). It also includes indirect competition: when one species affects the resource of another species without direct interactions.

BOX 2 | Formulae for stabilizing CDD and analogs.

We introduce how stabilizing CDD might be measured and discuss analogs in other ecological theories.

Stabilizing CDD in performance: Stabilizing CDD can be measured in individual fitness components, including survival and somatic growth. For trees, recent approaches use the general formula:

$$\phi_i = \beta_0 + \left(\beta_{\mathrm{DBH}} \times \mathrm{DBH}_i\right) + \left(\beta_{\mathrm{sCDD}} \times \mathrm{conden}_i\right) + \left(\beta_{\mathrm{TDen}} \times \mathrm{totalden}_i\right) + \varepsilon_i \qquad \text{(Eq 1)}$$

where ϕ_i is survival or diameter growth rate for focal individual i, β_0 the intercept, β_{DBH} is the effect of increasing DBH on performance, DBH_i is the diameter at breast height (DBH) for individual i, β_{sCDD} is the stabilizing/destabilizing CDD in performance for the given species (stabilizing if <0; destabilizing if >0), conden_i is the neighborhood density of conspecifics around individual i, β_{TDen} is the effect of total neighborhood density on performance, $\mathrm{totalden}_i$ is the total neighborhood density around individual i (conspecific plus heterospecific density), and ε_i is the error term (residual) for individual i (binomially distributed for survival; Gaussian distributed for diameter growth). This parameterization (viz Hülsmann et al. 2024) allows a direct measure of conspecific density effects *relative to total density effects*, as opposed to measuring conspecific and heterospecific effects separately and then comparing them against one another. β_{sCDD} is then a measure of local stabilizing or destabilizing CDD in performance when averaged across species in a community. Increased performance in favorable habitat conditions associated with higher conspecific densities can resemble destabilizing CDD, and habitat affinities should ideally be modeled directly (Krishnadas et al. in prep).

Stabilizing CDD in population growth rates: General density dependence can be measured in population growth rate functions as carrying capacity (typically denoted as K). To measure stabilizing CDD, we would need to compare the effect of conspecific density against total density, which can be done with most population growth rate equations. Here we use the Ricker model:

$$N_{t+1} = N_t \times \mathrm{e}^{\left(r + \left(\beta_{\mathrm{sCDD}} \times N_t\right) + \left(\beta_{\mathrm{TDen}} \times \mathrm{totalden}_t\right) + \varepsilon_t\right)} \qquad \text{(Eq 2)}$$

or equivalently

$$\ln\left(\frac{N_{t+1}}{N_t}\right) = r + \left(\beta_{\mathrm{sCDD}} \times N_t\right) + \left(\beta_{\mathrm{TDen}} \times \mathrm{totalden}_t\right) + \varepsilon_t \qquad \text{(Eq 3)}$$

where N_t is population abundance of a focal species in a focal population at time t, N_{t+1} its population abundance at time $t+1$, r is the population growth rate at low abundance with no competitors, β_{sCDD} is the stabilizing/destabilizing CDD for the given species, conden_t is the population density of conspecifics at time t, β_{TDen} is the effect of total density, $\mathrm{totalden}_t$ is the total density of all species in the same area as the focal population (conspecific plus heterospecific density) at time t, and ε_t is the error term at time t. Such population growth functions assume a closed population, i.e., no immigration or emigration. Some recent papers have used Ricker functions to measure stabilizing CDD for open local sub-populations, but in this case, stabilizing CDD can be confounded with dispersal. See Box 4 discussion of spatial data for solutions.

Analog in plant–soil feedback literature: Plant–soil feedback is measured with the equation:

$$I_s = \delta_{11} + \delta_{22} - \delta_{12} - \delta_{21} \qquad \text{(Eq 4)}$$

where I_s the pairwise feedback between two species, which is the difference between performance in conspecific-conditioned (δ_{11}, δ_{22}) and heterospecific-conditioned (δ_{12}, δ_{21}) soils (Bever, Westover, and Antonovics 1997). When density is explicit, this is analogous to stabilizing CDD.

Analogs to stabilizing CDD in resource competition and coexistence theory: Two-species Lotka–Volterra models have been parameterized for coexistence theory and can be used to demonstrate analogs to stabilizing CDD (Broekman et al. 2019; Chesson 2000):

$$\frac{1}{N_1}\left(\frac{dN_1}{dt}\right) = r_1\left(1 - \alpha_{11}N_1 - \alpha_{12}N_2\right) \qquad \text{(Eq 5)}$$

$$\frac{1}{N_2}\left(\frac{dN_2}{dt}\right) = r_2\left(1 - \alpha_{22}N_2 - \alpha_{21}N_1\right) \qquad \text{(Eq 6)}$$

where the left-hand sides of the two equations are the per-capita growth rates for each species, and the right-hand side shows how r_1 and r_2, the intrinsic rates of increase for each species, decrease with conspecific (α_{11}, α_{22}) and heterospecific (α_{12}, α_{21})

(Continues)

competition (or effects of natural enemies). The α terms are the per-capita competitive effects of conspecific and heterospecific individuals on the per-capita growth rate of each species. The inequality:

$$\alpha_{11}\alpha_{22} > \alpha_{12}\alpha_{21} \tag{Eq 7}$$

is analogous to stabilizing CDD; combined conspecific effects are greater than combined heterospecific effects. If measured at the population level, then this is the condition for stabilization.

The analog for destabilizing CDD would be the reverse of Equation 7:

$$\alpha_{11}\alpha_{22} < \alpha_{12}\alpha_{21} \tag{Eq 8}$$

Stable coexistence further requires each species to have a stronger effect on itself than on the other species, which can be evaluated using the inequality:

$$\sqrt{\frac{\alpha_{21}\alpha_{12}}{\alpha_{11}\alpha_{22}}} < \sqrt{\frac{\alpha_{22}\alpha_{21}}{\alpha_{11}\alpha_{12}}} < \sqrt{\frac{\alpha_{11}\alpha_{22}}{\alpha_{21}\alpha_{12}}} \tag{Eq 9}$$

or equivalently

$$\alpha_{11} > \alpha_{21} \text{ and } \alpha_{22} > \alpha_{12} \tag{Eq 10}$$

The middle term in Equation 9 represents the fitness ratio of the two species, or intrinsic fitness differences, and the left (and right) terms represent the ratio of interspecific to intraspecific effects (or the inverse on the right), also known as the niche difference. For stable coexistence, niche differences must exceed intrinsic fitness differences as discussed in Section 4.2.2.

We emphasize that a community with all species experiencing stabilizing CDD may still not be stably coexisting. For example, a breakdown of coexistence could occur when species have different intrinsic demographic rates, more complex competitive interactions that depend on the identity of all partners, or if stabilizing CDD varies among species (Broekman et al. 2019; Hülsmann, Chisholm, and Hartig 2021). However, the terms are motivated by the theoretical expectation that if species are equal in all other aspects, do not distinguish between heterospecific interaction partners, and are in a homogenous environment, then stabilizing CDD should allow species coexistence.

Throughout the manuscript, we will refer to "stabilizing CDD" in a general sense, meaning local CDD that is either stabilizing or destabilizing as defined above. If we use it in a directional sense, we will use "more/stronger stabilizing" or "more/stronger destabilizing," whichever is appropriate.

3 | Understanding Local Stabilizing CDD

A challenge in the study of stabilizing CDD is to disentangle the influence of mechanisms that have been the focus within different subfields of ecology. In this section, we synthesize these mechanisms and discuss how stabilizing CDD might interact with dispersal and influence plant species' spatial distributions. These interfacing mechanisms are important to determine the ways in which stabilizing CDD might scale up to influence populations and communities (which we focus on in Section 4).

3.1 | Understanding Other Causes of Variation in Local Conspecific Densities

To determine how local stabilizing CDD might scale up to shape community and regional biodiversity dynamics, we need to first consider other mechanisms like dispersal limitation or abiotic habitat preferences that affect the degree of conspecific aggregation or disaggregation in species' spatial distributions. Many seed dispersal studies have supported a general pattern of most seeds falling nearby conspecific adults with a long tail of relatively few individuals that are able to disperse greater distances (Beckman and Sullivan 2023; Clark et al. 1999; Janzen 1970; Nathan and Muller-Landau 2000; Thomson et al. 2011). Relatively host-specific natural enemies and mutualists are thought to operate on such initially high conspecific densities. Such antagonists should thin out high densities of conspecifics over time and allow space for other plant species (Murphy, Wiegand, and Comita 2017), whereas relatively host-specific mutualists would have the opposite effect, favoring greater plant performance in areas of high rather than low conspecific densities (Segnitz et al. 2020). For species with strong stabilizing CDD, young individuals that disperse farther from their parent or to areas of low conspecific density should have greater demographic performance than individuals that do not (the opposite is expected for species with destabilizing CDD).

Abiotic habitat preferences that differ among species also create variation in local conspecific densities. Plant species that favor particular light environments or soil characteristics (e.g., nutrients, soil moisture) should aggregate in areas with those conditions (Bagchi et al. 2011; Harms et al. 2001). Like dispersal limitation, abiotic habitat preferences affect variation in local conspecific densities that, in turn, influence how stabilizing CDD might scale up to influence populations and communities (Chesson 2012; Chesson et al. 2005). These effects need to be understood and accounted for when trying to understand how CDD works at the community scale.

3.2 | Mechanisms of Local Stabilizing CDD Across Subfields in Ecology

Multiple mechanisms can generate local stabilizing or destabilizing CDD. Disentangling these different mechanisms, which may all respond in different ways across spatial and temporal scales, may be critical for being able to understand how local CDD scales up to influence community dynamics. The Janzen–Connell hypothesis and subsequent studies focusing on local stabilizing CDD emphasized host-specific natural enemies and intraspecific competition as mechanisms generating local stabilizing CDD (Liu et al. 2015; Mangan et al. 2010; Packer and Clay 2000). However, an emerging consensus is that stabilizing CDD is the net outcome of many types of biotic interactions (Williams et al. 2021), including interactions with relatively host-specific mutualists, allelopathy, and the relative strength of competition among conspecifics and heterospecifics (Bachelot et al. 2017; Delavaux et al. 2023, 2024; Liang et al. 2015, 2021; McIntire and Fajardo 2014; Spear and Broders 2021).

The mechanisms generating stabilizing CDD are related to mechanisms studied in plant–soil feedback (PSF). Plant–soil feedback occurs when an individual plant conditions local soil environments such that the demographic performance of conspecific seedlings (or juvenile age classes more generally) are affected differently relative to heterospecific seedlings (Bennett and Klironomos 2019; Bever, Westover, and Antonovics 1997; Crawford et al. 2019; Eppinga et al. 2018). Thus, mechanisms generating PSF should also generate stabilizing CDD, but important differences exist in the ways in which mechanisms generating PSF and stabilizing CDD have been studied.

An advantage of PSF research is that its frameworks explicitly and separately consider different mechanisms that generate positive and negative feedback (Bever, Westover, and Antonovics 1997; Kandlikar et al. 2019), which correspond to destabilizing and stabilizing CDD, respectively. Many PSF studies can isolate a functional group (e.g., mycorrhizal fungi) and study that group's contribution to net feedback. PSF frameworks have also been extended to explicitly incorporate the densities of different types of relatively host-specific microbial organisms (Kandlikar et al. 2019), and the study of plant-phyllosphere feedback has recently gained attention (Whitaker et al. 2017; Box 1). Such work suggests that CDD research can benefit from adopting a more mechanistic focus on above- and below-ground agents and how those agents combine to influence the net magnitude of stabilizing CDD. For example, expansions of stabilizing CDD studies to more explicitly measure or model the dynamics of specific antagonist/mutualist communities, including density-dependent regulation of microbial communities (Bever et al. 2010; Kandlikar et al. 2019) and direct competition among plants (Lekberg et al. 2018), may be essential to explain high species diversity (Liu et al. 2015).

We acknowledge that measuring every interaction among plant species and their biotic agents is often impractical. A potential solution to this dilemma might be for future studies to determine which are the most impactful mechanisms generating stabilizing CDD in their systems and attempt to parse the separate contributions of these impactful mechanisms to generating net stabilizing CDD. We also recommend that future studies attempt, whenever possible, to integrate large-scale observational studies with field and greenhouse experiments that disentangle the relative contributions of different functional groups to net stabilizing CDD. For example, studies could observe changes in the strength of stabilizing CDD across nutrient limitation gradients and pair that with greenhouse experiments that test the contributions of different agents to generating stabilizing CDD across nutrient treatments. Moreover, plant–soil feedback studies could help bridge findings and concepts with stabilizing CDD by more explicitly linking the role of distance and density to plant feedback; thus helping translate results between different approaches (Kandlikar et al. 2019; Ke and Wan 2020, 2023). Explicit study of species densities is important to consider because recent theoretical and simulation studies have indicated that traditional PSF models incorporating relative frequencies instead of absolute densities may not be able to account for multispecies coexistence (Miller, Lechón-Alonso, and Allesina 2022).

3.3 | Effects of Stabilizing CDD on Spatial Distributions of Species

An alternative way to evaluate stabilizing CDD is via spatial patterns. Local stabilizing CDD can erode local aggregation of conspecific individuals over time through mortality of individuals in high conspecific density areas (Connell 1971; Janzen 1970). Thus, species that exhibit strong local stabilizing CDD might show decreased conspecific aggregation in older relative to younger age classes or relative to other species that do not exhibit strong local stabilizing CDD (Murphy, Wiegand, and Comita 2017; but see Marchand et al. 2020). In contrast, local destabilizing CDD is expected to promote conspecific aggregation because it should increase the performance of individual plants that fall below parents or disperse into areas of high conspecific density. This is readily observed in monodominant forest stands characterized by tree species associated with relatively host-specific ectomycorrhizae (e.g., dipterocarp forests; Segnitz et al. 2020).

Earlier studies that used complete spatially random null models to evaluate the spatial patterns of tree species found evidence for widespread conspecific aggregation, which raised doubt about the importance of local stabilizing CDD to spatial distributions (e.g., Condit et al. 2000; Harms et al. 2001). However, more recent approaches have advocated using null models based on empirically observed seed dispersal. These studies indicate spatial patterns consistent with moderate to strong dispersal limitation that is counteracted by strong local stabilizing CDD (Kalyuzhny et al. 2023; LaManna, Mangan, and Myers 2021). While we advocate null-model approaches that use empirical dispersal information to compare spatial patterns expected by dispersal alone to patterns expected under stabilizing CDD, we also caution that empirical information on dispersal may be incomplete which could introduce bias. Care should also be taken to account for variability in empirical estimates of dispersal.

An important challenge with studying spatial patterns expected from stabilizing CDD is disentangling the influence of different mechanisms. For example, if spatial aggregation of conspecifics is detected, is this due to dispersal limitation, positive biotic interactions, environmental filtering, or their interaction? Ideally, pattern-based approaches might be paired with local-scale field experiments or surveys to enable researchers to distinguish between alternative mechanisms (Ledo and Schnitzer 2014). Null model approaches can improve our confidence that these patterns are robust to other non-biotically mediated mechanisms (Detto and Muller-Landau 2016; Kalyuzhny et al. 2023).

3.4 | Interplay Between Stabilizing CDD and Seed Dispersal

Because local stabilizing CDD favors individuals that disperse far from high conspecific density areas, dispersal-associated traits that enhance a plant's ability to escape from such areas should be favored in species with local stabilizing CDD (Beckman and Sullivan 2023; Howe and Smallwood 1982; Schupp, Jordano, and Gómez 2010). Therefore, local stabilizing CDD will not only reduce conspecific aggregation through direct mortality of plants in high conspecific density areas but also should reduce conspecific aggregation by exerting strong directional selection for traits that enable greater dispersal distances (Eck et al. 2019). This selection for greater dispersal capabilities in species with local stabilizing CDD has important consequences for the evolution of seed dispersal as well as trade-offs with other life-history traits (Stump and Comita 2020). Likewise, strong destabilizing CDD should favor shorter dispersal distances and mutualist-dependent trees may be constrained by the dispersal capabilities of their mutualists (Delavaux et al. 2024).

The timing and mode of seed dispersal also determine if seedlings can establish in areas of high or low conspecific density. For example, reproductive phenology is often synchronized so that animal dispersers travel from one conspecific fruiting tree to another, dispersing seeds into areas of high conspecific density (Beckman and Sullivan 2023; Hirsch et al. 2012; Vander Wall and Beck 2012). Evidence also indicates that animal seed dispersal results in different spatial configurations, indicating that plant or seed traits favoring one group of dispersers over another alter dispersal patterns and proximity to conspecifics and heterospecifics (Fedriani, Wiegand, and Delibes 2010; Martínez, García, and Obeso 2008; Rogers et al. 2021). For example, contagious seed dispersal, which happens when primates deposit seeds into latrines or birds rest on favored perches, can lead to interspecific association in seedling recruitments (Wright et al. 2016). There is a need to evaluate the potential for such interplay between dispersal strategies and stabilizing CDD, which has been rarely studied. Comparisons for future study include how dispersal phenology, distance, and mode (and other dispersal-associated traits) are related to local stabilizing CDD across species.

4 | Scaling up Impacts of Local Stabilizing CDD on Communities and Metacommunities

Another persistent challenge to studying local CDD is a limited understanding of the implications of local stabilizing CDD for community-level density and frequency dependence as well as metacommunity dynamics (Chisholm and Fung 2020; Levi et al. 2019; Schupp 1992; Smith 2022). This research gap is due in part to the long-lived nature of some plants (especially trees) and the multiple mechanisms that could lead to similar stabilizing CDD patterns at different spatial and temporal scales. This research gap is also due in part to missed attempts for explicit upscaling of local stabilizing CDD into population- and community-scale models used in broader ecological theories (e.g., Chesson's scale transition theory; Chesson 2012; Chesson et al. 2005).

Local stabilizing CDD might scale up to generate stabilizing CDD for an entire plant community or metacommunity (Chesson et al. 2005; but see May et al. 2020). Yet, the possibility exists that local-scale stabilizing CDD may be counteracted by processes at large scales (e.g., predator satiation) or that stabilizing CDD might emerge from processes that occur at larger scales even if it does not occur at local scales (e.g., bark beetles responding to variation in host density at the landscape scale, spatial storage effects). In this section, we synthesize the implications of local stabilizing CDD for community and metacommunity dynamics.

4.1 | Placing Local Stabilizing CDD in the Context of Broader Ecological Theories

To determine the implications of local stabilizing CDD for community and metacommunity dynamics, we first place it within the context of broader ecological theories. Box 2 uses mathematical formulae to link stabilizing CDD to these broader ecological theories. Resolutions to several prominent CDD-related misconceptions about how CDD relates to broader ecological theories are offered in Box 3. Box 4 provides a roadmap to recent literature advances and debates on stabilizing CDD.

4.1.1 | Local Stabilizing CDD in the Context of Modern Coexistence Theory

Modern coexistence theory conceptualizes species coexistence as mediated by two phenomenological forces: interspecific fitness differences (linked to equalizing mechanisms) and niche differences (linked to stabilizing mechanisms; Chesson 2000). Stabilizing mechanisms give species an advantage when rare and equalizing mechanisms reduce intrinsic fitness differences. The probability of species coexistence increases when niche differences exceed fitness differences. Local stabilizing CDD can be thought of as a stabilizing mechanism (the demographic signature of "niche differences") at local scales if it is assumed that rare species will mostly experience density effects from heterospecific neighbors, while common species will mostly experience density effects from conspecifics (Adler, HilleRisLambers, and Levine 2007; HilleRisLambers et al. 2012; Kraft, Godoy, and Levine 2015). Local stabilizing CDD may promote species

BOX 3 | Clarifying CDD-related misconceptions.

Observing density-dependent patterns does not allow inference on the underlying mechanism(s): Observing local stabilizing CDD in demographic performance does not imply a particular mechanism. For example, observing increased mortality in seedlings at higher conspecific densities does not mean soil pathogens are responsible. Mutualists (e.g., mycorrhizae, pollinators) and impacts of plants on their local abiotic environment (e.g., autotoxicity, allelopathy) can produce destabilizing or stabilizing CDD patterns (Bever, Westover, and Antonovics 1997; Chen et al. 2019; Torti, Coley, and Kursar 2001). Species' abiotic habitat preferences can also result in the appearance of destabilizing CDD (i.e., higher growth/survival in preferred habitats with higher abundances). Alternatively, the absence of expected spatial patterns from stabilizing CDD does not preclude the operation of density-dependent mechanisms (e.g., separate mechanisms generating destabilizing or stabilizing CDD may yield no net CDD). Ultimately, net stabilizing CDD is determined by the net effect of multiple interacting biotic and abiotic mechanisms that respond to (or are correlated with) local densities of plant species, including below and aboveground enemies and mutualists as well as intraspecific competition and density-dependent alteration of the local abiotic environment.

For stabilizing CDD to be present, strict host-specificity is not required: Local stabilizing CDD does not require strict host specificity (Spear and Broders 2021) and can occur as long as there are differential effects of the interactions across hosts (Sedio and Ostling 2013). The lack of strict host-specificity and a focus on the relative effects of natural enemies and mutualists is more explicit in plant–soil/phyllosphere feedback theory (Bever, Westover, and Antonovics 1997).

Local stabilizing CDD is not necessarily frequency dependence: Local stabilizing CDD is a response to local population density of conspecifics relative to heterospecifics. On the other hand, frequency dependence is a response to the relative abundance of species in a community. While both must be considered relative to the frequency or density dependence of that response in other species in that community to allow any inference relevant to stabilization, information about total community abundances or densities is lost when using frequencies (Broekman et al. 2019). However, frequency and density-dependence are sometimes used interchangeably (especially in forest ecology) because total abundance is often assumed fixed by space and light limitations.

CDD must be compared to heterospecific density dependence (HDD) to distinguish it from overall density dependence: Many local interactions are not specialized (e.g., generalist pathogens/herbivores). In early and mid-seral forests, predictable negative relationships between tree density and growth rates are evident and referred to as self-thinning or crowding. However, only when CDD is greater than HDD do these processes have the potential to affect population regulation and species coexistence via local stabilizing CDD. For example, classic studies measuring distance dependence often do not test whether CDD < HDD.

Stabilizing CDD in a particular demographic rate or life stage does not necessarily translate to stabilizing CDD in population growth rates: Even if local stabilizing CDD is observed for a particular demographic rate and/or life stage, the population growth rate may not exhibit stabilizing CDD. This is because individual demographic rates capture only one component of plant fitness. Stabilizing and destabilizing CDD in separate demographic rates (e.g., reproduction, recruitment, mortality) or across different life stages (e.g., seed, seedling, sapling, adult) can counteract one another. Therefore, evidence for local stabilizing CDD in a single demographic rate at a particular life stage is consistent with, but should not be taken as definitive evidence of, population regulation.

Stabilizing CDD in population growth does not necessarily maintain diversity or lead to coexistence: While stabilizing CDD in *population growth rates* is stabilizing (CDD < HDD), it is still not sufficient for species coexistence (Broekman et al. 2019). Stabilizing CDD must also overcome any intrinsic fitness differences among species (Chesson 2000) to lead to coexistence. One frontier in this field is the production of tools for scaling the effects of stabilizing CDD in vital rates through coexistence (see also (Eppinga et al. 2018; Hülsmann, Chisholm, and Hartig 2021; Chesson 2012)).

Stronger mean stabilizing CDD in a community does not necessarily lead to higher diversity: Several theoretical studies have shown that even when on average a community exhibits stabilizing CDD, variation among species in the strength of stabilizing CDD may increase fitness differences among species, potentially leading to a reduction in diversity (Hülsmann et al. 2024; Miranda, Carvalho, and Dionisio 2015; Stump and Comita 2018). However, if stabilizing CDD varies among species such that it is stronger for species with higher intrinsic fitness, diversity maintenance should be enhanced (Stump and Comita 2018).

coexistence in the presence of intrinsic fitness differences, whereas local destabilizing CDD may hinder coexistence (Box 2).

Both local stabilizing CDD and frequency dependence (Box 1) have the potential to measure aspects of stabilization, although careful consideration should be given to each of these measures and the way they relate to stabilization (Broekman et al. 2019). Density and/or frequency dependence at the population/community scale tends to measure how population growth rates change with an increasing density or frequency of a species within an entire community and often at landscape to regional scales (Chesson 2000; Yenni, Adler, and Ernest 2017). In contrast, local stabilizing CDD measures how demographic performance changes in neighborhoods with increases in local conspecific relative to heterospecific densities. These are important differences that have led to the emerging conclusion that local stabilizing CDD is not necessarily the same as negative density or frequency dependence at the population/community scale (e.g., Chesson 2012; Ellner

BOX 4 | Roadmap to recent debates and advances in stabilizing CDD literature.

Evidence for local stabilizing CDD using dynamic data on individual performance: Many studies have found evidence of stabilizing CDD using data on individual performance (survival/growth) between at least two time periods. In trees, meta-analyses show that seedlings tend to exhibit the strongest levels of stabilizing CDD (Comita et al. 2014; Song et al. 2021), although not all studies in these meta-analyses explicitly compared conspecific to heterospecific effects. Recent meta-analyses of plant–soil feedback (PSF) studies also show pervasive negative feedback (Jiang et al. 2024), which is analogous to stabilizing CDD. Collectively, these studies support the idea that stabilizing CDD is widespread among plant species. Stabilizing CDD observed using dynamic data on individual performance can be confounded with habitat-associated influences on individual performance, e.g., soil chemistry, topography, and aridity. Such habitat affinities should ideally be modeled explicitly (Chen et al. 2010; Krishnadas et al. in prep).

Evidence for local stabilizing CDD using spatial data: Spatial data has been used to evaluate predictions of stabilizing CDD, including tests for the influence of stabilizing CDD on spatial patterns of sapling recruitment (LaManna, Mangan, et al. 2017; LaManna, Mangan, and Myers 2021) and on spatial patterns of seedling cohorts through time (Murphy, Wiegand, and Comita 2017). However, tests for stabilizing CDD in local recruitment or population growth (which includes recruitment) are prone to confounding influences of not only habitat affinities but also dispersal (Hülsmann and Hartig 2018). Long-distance dispersal can resemble stabilizing CDD, and short-distance dispersal can resemble destabilizing CDD. If empirical information on dispersal and spatial distributions (i.e., habitat affinities) is available, null models can be used to disentangle the influence of dispersal and habitat associations from stabilizing CDD (Kalyuzhny et al. 2023; LaManna, Mangan, and Myers 2021). But whenever available, dynamic data (multiple time points) are a stronger test than static data (single time point; Detto et al. 2019).

Does stabilizing CDD differ across mycorrhizal types? While stabilizing CDD seems more prevalent than destabilizing CDD from meta-analyses, evidence also suggests that mutualists such as mycorrhizae mediate the strength of stabilizing CDD across plant species. Dynamic and spatial studies have found that CDD is less stabilizing for plant species associated with ectomycorrhizal fungi (EcM) than species associated with arbuscular mycorrhizae (AM) (Bennett et al. 2017; Delavaux et al. 2023; Jiang et al. 2020; Liang et al. 2021).

How does local stabilizing CDD differ between tropical and temperate forests? A recent study using dynamic data on sapling tree survival found that there is no overall significant difference in local stabilizing CDD between tropical and temperate forests (Hülsmann et al. 2024). However, this and other studies have found that species at low to moderate abundances experience stronger stabilizing CDD than common species in tropical but not temperate forests (LaManna, Mangan, and Myers 2021). Simulation studies suggest that strong stabilizing CDD for species at lower abundances can lead to their long-term persistence in systems (Yenni, Adler, and Ernest 2012). Together, these findings suggest that stabilizing CDD may be regulating abundances of tree species in tropical forests, with stronger stabilizing CDD for low to moderately abundant species in tropical forests potentially reducing their local extinction rates and enhancing diversity there over time. Emerging work also places mutualists as important mediators of larger scale patterns of biodiversity, such as the latitudinal biodiversity gradient (Delavaux et al. 2024). Ongoing studies are evaluating whether other life stages of trees, including seedlings, might exhibit latitudinal differences in stabilizing CDD. These and other forthcoming empirical and theoretical studies may allow more firm conclusions on whether and how stabilizing CDD contributes to the latitudinal diversity gradient.

Does local stabilizing CDD change with other environmental factors? Recent studies have found evidence that CDD becomes more stabilizing in wetter conditions (Bennett and Klironomos 2019; LaManna et al. 2022; Lebrija-Trejos, Hernández, and Wright 2023), and plant–soil feedback meta-analyses suggest that feedback is more positive (less stabilizing) with increasing aridity (Jiang et al. 2024). This pattern was predicted because relatively host-specific pathogens that generate stabilizing CDD are more abundant in wetter conditions whereas relatively host-specific mutualists, such as ectomycorrhizae, that generate destabilizing CDD are more important/essential to plant performance in arid environments (LaManna et al. 2022; Milici et al. 2020). Further studies are needed to determine the prevalence of this mechanism.

Legacy stabilizing CDD: Recent studies suggest not only living conspecifics generate stabilizing CDD but also dead conspecifics (Magee et al. 2024). More empirical and theoretical work is needed to assess the prevalence of this effect and its influence on diversity maintenance.

et al. 2022). For example, if rare species experience strong local stabilizing CDD but are spatially aggregated on the landscape due to another aggregating process, they may not exhibit negative frequency dependence at the population level because they, like common species, experience strong negative density effects from nearby conspecifics (Ellner et al. 2022). It remains a challenge to determine under which circumstances rare species with strong stabilizing CDD might nonetheless aggregate and how we can include this effect in theory. Within tropical tree communities, stabilizing CDD is stronger for species at lower abundances, suggesting that their abundances are regulated by stabilizing CDD (Hülsmann et al. 2024). Tropical tree species also show more dispersed spatial patterns than can be explained by empirically observed dispersal alone (Kalyuzhny et al. 2023). These empirical findings support the idea that strong local stabilizing CDD generates more dispersed local spatial distributions (Fricke and Wright 2017), which might facilitate negative frequency dependence and a rare species demographic advantage at community scales, all else being equal.

4.1.2 | Local Stabilizing CDD in the Context of Resource Competition Theory

Local stabilizing CDD has connections to broader ecological theories on resource competition, apparent competition, and niches (Chase and Leibold 2003; Letten, Ke, and Fukami 2017; Levine and HilleRisLambers 2009). These theories are related to coexistence theory but rely on specific biological mechanisms of resource competition or other mechanisms of niche differentiation. Coexistence mechanisms based on resource competition generally rely on the idea that two or more species can coexist if they have niche differences related to trade-offs in resource use (Chase and Leibold 2003; Letten, Ke, and Fukami 2017; Tilman 1988). Coexistence occurs because each species consumes more of the resource that most limits its population growth (Letten, Ke, and Fukami 2017; Tilman 1982, 1988), generating stronger intra- than interspecific competition and local stabilizing CDD. Contemporary niche theory has extended the idea of resource niches to incorporate other types of potential niche differentiation (Letten, Ke, and Fukami 2017), including natural enemies and mutualists (Grover and Holt 1998; Holt 1977; Holt and Bonsall 2017; Koffel, Daufresne, and Klausmeier 2021; Peay 2016; Thompson et al. 2020). The extent to which species compete more strongly with conspecifics than heterospecifics for limiting resources or the extent to which natural enemies are relatively host-specific will tend to increase the strength of local stabilizing CDD. Local stabilizing CDD could also be generated if heterospecifics with shared natural enemies have different defenses (Endara et al. 2017). Thus, local stabilizing CDD can be thought of as a demographic signature of niche differentiation that can promote coexistence by favoring competitive or apparent competitive interactions among conspecifics, all else being equal. Host-specific mutualists can also be viewed as a form of niche differentiation and can expand potential niche breadths of species (Bulleri et al. 2016) but may also generate local destabilizing CDD and erode diversity in the absence of other processes (Bever 1999; Koffel, Daufresne, and Klausmeier 2021; Peay 2016; Valdovinos and Marsland 2021).

4.1.3 | Synthesizing Predictions and Tests of Theories Related to Local Stabilizing CDD

To scale up the influence of local stabilizing CDD on larger scale processes such as community dynamics, it is necessary to synthesize across different frameworks. Local stabilizing CDD has been studied in the context of Janzen–Connell effects, plant–soil feedback, resource competition, and coexistence. To integrate local stabilizing CDD within broader ecological theories and provide solutions for how one might evaluate its potential influences on larger level processes, we summarize these predictions in Table 1, highlight the caveats and limitations of each prediction, and provide examples of studies examining each prediction. One outcome of this synthesis is the acknowledgment that theoretical frameworks with different underlying mechanisms often predict similar outcomes at the individual, population, and community levels (Table 1; Chave, Muller-Landau, and Levin 2002). Therefore, we advise caution when inferring mechanism from a pattern, and additional predictions should be tested where possible to disentangle alternative mechanisms.

Some of the predictions in Table 1 have been extensively tested, while others represent important gaps for future research. Predictions at three levels of biological organization are explored in Table 1: individual, population, and community. Predictions for the effects of local stabilizing CDD on individual performance have received far more empirical attention than predictions at the population and community scales, likely because studies at that scale are more feasible. For example, the prediction that individual performance decreases with increasing conspecific density or frequency (Prediction 1) has received substantial empirical support, although we emphasize that this finding does not indicate stabilizing CDD without comparison to heterospecific density effects. Predictions 2 to 4 (individual scale)—stronger conspecific than heterospecific density effects, biotic environments have a stronger effect on the performance of conspecifics than heterospecific, and plant–soil feedback varies with phylogenetic distance—have also received substantial support. Predictions 5 and 6 (individual scale)—shared defense traits and mycorrhizal types—are gaining more support as research turns to these potential drivers of local stabilizing CDD. Some important challenges at the individual scale remain, including: translating findings across field-based and greenhouse experiments (Beals et al. 2020; Beckman, Dybzinski, and Tilman 2023); distinguishing between mechanistic drivers of local stabilizing and destabilizing CDD; and mitigating a bias toward short-lived plant species and early life stages. We discuss challenges evaluating predictions at the population and community levels below.

4.2 | Scaling up Effects of Local Stabilizing CDD on Population, Community, and Metacommunity Patterns and Processes

Ecological scaling theories can be used to examine the impacts local stabilizing CDD might have on communities and metacommunities. One such theory, scale-transition theory, advocates an integrated research program involving analytics, simulations, experiments, and observational studies to examine how local and often nonlinear demographic processes, such as local stabilizing CDD, scale up to influence populations, communities, and metacommunities (Chesson 2012; Chesson et al. 2005). This theory suggests that factors like covariance between performance and density across localities, spatial variation in species distributions and the underlying environment, and nonlinear relationships between performance and conspecific density (common in CDD studies) can either dampen or amplify how stabilizing CDD at local levels scales up to influence stabilizing CDD at larger-spatial scales (Figure 1).

While we recommend researchers attempt to apply scale-transition theory and similar scaling approaches to determine the effects of local stabilizing CDD on populations, communities, and metacommunities, several challenges and misconceptions remain that have hampered progress in CDD research. In this section, we discuss these key challenges.

TABLE 1 | Synthesis of predictions from the Janzen–Connell hypothesis (JC), feedback theory (FT), resource-competition theory (RC), and coexistence theory (CT) that are related to stabilizing CDD.

	Theory						
Prediction	**JC**	**FT**	**RT**	**CT**	**Mechanisms**	**Challenges and caveats**	**Examples of studies**
Scale 1: Individuals							
(1) Performance decreases (JC, neg. feedback, RC) or increases (pos. feedback) with conspecific density or frequency	X	X	X	X	Relatively host-specific plant enemies, mutualists, or intraspecific competition for resources affect plant performance at high conspecific density or frequency	Intraspecific & interspecific effects may be caused by multiple mechanisms (e.g., competition, enemies, facilitation, mutualists, habitat requirements); effects on individual performance (e.g., growth) may or may not scale up to influence population-level fitness or growth rates (Prediction 7)	M: (Hyatt et al. 2003) R: (Carson et al. 2008) M: (Comita et al. 2014) R: (Hülsmann, Chisholm, and Hartig 2021) E: (Hülsmann et al. 2024) M: (Song et al. 2021)
(2) Conspecific effects on performance are more negative (JC, neg. feedback, RC) or positive (pos. feedback) than heterospecific effects on performance (stabilizing and destabilizing CDD, respectively)	X	X	X	X			R: (Connell 1983) R: (Schoener 1983) R: (Goldberg and Barton 1992) M: (Gurevitch et al. 1992) M: (Adler et al. 2018) T: (Chesson 2000) E: (Hülsmann et al. 2024)
(3) Local biotic environments have a stronger negative (JC, neg. feedback) or positive (pos. feedback) effect on the performance of conspecifics than heterospecifics (stabilizing and destabilizing CDD, respectively)	X	X			Relatively host-specific plant enemies or mutualists have differential effects on the performance of conspecific & heterospecific plants	Difficult to compare results from the field versus greenhouse studies, isolate effects of resource competition from effects of soil microbes, isolate driving microbial functional groups & include large numbers of species	R: (Bever, Mangan, and Alexander 2015) E: (Whitaker et al. 2017) E: (Hülsmann et al. 2024) T: (Eppinga et al. 2018) M: (Crawford et al. 2019) R: (Bennett and Klironomos 2019) M: (Beals et al. 2020)
(4) Neg. or pos. feedback (stais stronger among pairs of distantly related than closely related species		X	X		Closely related plant species share similar enemies, mutualists, or resource requirements	Assumes strong phylogenetic signal in host ranges of enemies & mutualists or resource use	M: (Crawford et al. 2019) E: (Stein and Mangan 2020)
(5) Performance decreases with increasing similarity of neighbor defense traits or resource-acquisition traits	X	X	X		Neighboring plants with more similar defense or resource-competition traits have lower performance due to shared enemies or interspecific competition, respectively	Assumes (1) host ranges of enemies are determined by host–defense traits (e.g., chemical defenses), (2) interspecific differences in resource-acquisition traits correlate with competitive ability	R: (Sedio 2017) E: (Sedio et al. 2021) E: (Forrister et al. 2019) E: (Umaña et al. 2018)

(Continues)

TABLE 1 | (Continued)

	Theory						
Prediction	**JC**	**FT**	**RT**	**CT**	**Mechanisms**	**Challenges and caveats**	**Examples of studies**
(6) Performance decreases with conspecific density relative to heterospecific density more strongly for arbuscular mycorrhizal (AM) than ectomycorrhizal (EM) plant species	X	X			EM plants experience weaker stabilizing CDD because their roots are better defended against below-ground enemies, and/or because they form mycorrhizal associations with higher specificity, both of which may counteract pathogen-driven stabilizing CDD. EM are also better at acquiring organic nutrients that are largely inaccessible to AM (Johnson, Clay, and Phillips 2018; Phillips, Brzostek, and Midgley 2013)	The mycorrhizal type is often inferred (often phylogenetically) instead of being observed for each species. Further, some plants form both AM and EM, or associate with other mycorrhizal types, complicating expectations. Mycorrhizal relationships are very dependent on local conditions, which may alter patterns	R: (Connell and Lowman 1989) R: (Laliberté et al. 2015) E: (Bennett et al. 2017) E: (Chen et al. 2019)
Scale 2: Populations							
(7) Per-capita recruitment or population growth rate decreases (JC, neg. feedback, RC) or increases (pos. feedback) with increasing conspecific density or frequency relative to heterospecific density or frequency	X	X	X	X	Relatively host-specific plant enemies, mutualists, or intraspecific competition affect recruitment or population growth at high conspecific relative to heterospecific density or frequency	Difficult to test with long-lived species; estimates of stabilizing CDD in recruitment using a power function can be biased by regression dilution (Detto et al. 2019)	R: (Siepielski and McPeek 2010) E: (Zhu, Woodall, et al. 2015) T: (Chesson 2000)
(8) Intraspecific aggregation decreases with increasing stabilizing CDD or increasing neg. feedbacks through space or time	X	X	X	X	Relatively host-specific plant enemies or intraspecific competition reduce spatial aggregation of conspecifics by decreasing recruitment or increasing mortality	Aggregation is also caused by other processes (e.g., dispersal limitation, abiotic habitat associations)	E: (Hubbell 1979) E: (Detto and Muller-Landau 2016) E: (Murphy, Wiegand, and Comita 2017) R: (Wiegand et al. 2017) T: (Wiegand et al. 2021) E: (Kalyuzhny et al. 2023)
Scale 3: Communities							
(9) Local species diversity increases/ decreases with neg./ pos. frequency dependence within a community through time	X	X	X	X	Specialized plant enemies or intraspecific competition increases diversity via neg. frequency-dependent selection, mutualists decrease (or increase) diversity via pos. (or neg.) frequency-dependent selection	Often requires models to simulate long-term population & community dynamics; assumes neg. frequency dependence is strong enough to overcome average fitness differences among species; difficult to test with long-lived species	E: (Wills et al. 2006) E: (Levine and HilleRisLambers 2009) E: (Adler, Ellner, and Levine 2010)

(Continues)

TABLE 1 | (Continued)

Prediction	Theory				Mechanisms	Challenges and caveats	Examples of studies
	JC	FT	RT	CT			
(10) Species diversity increases/decreases with stabilizing/destabilizing CDD or neg./pos. frequency dependence across communities through space	X	X	X	X	Stronger stabilizing CDD maintains higher diversity; stronger destabilizing CDD decreases diversity	Often examined indirectly by comparing stabilizing CDD among plant species at temperate and tropical latitudes (e.g., (HilleRisLambers, Clark, and Beckage 2002)	E: (Harms et al. 2000) E: (Johnson et al. 2012) E: (Bagchi et al. 2014) E: (LaManna, Mangan, et al. 2017) R: (Hülsmann, Chisholm, and Hartig 2021) T: (Levi et al. 2019)
(11) Stabilizing/destabilizing CDD causes local species evenness (an important component of species diversity) to increase/decrease as a cohort of individuals ages from early to later life stages	X		X	X	Specialized enemies or intraspecific competition increases diversity in later life stages via stabilizing CDD at earlier life stages	Increases in diversity from early to later life stages could be caused by higher recruitment or survival of rare than common species	E: (Harms et al. 2000) E: (Wills et al. 2006)
(12) Relative abundance is correlated with stabilizing CDD or feedback strength	X	X	X	X	Stronger stabilizing CDD from specialized enemies or intraspecific competition may keep a species rare and/or allow species to persist when they become rare	Causal relationship unclear; stabilizing CDD may affect abundance, or vice-versa	E: (Comita et al. 2010) E: (Mangan et al. 2010) E: (Bachelot, Kobe, and Vriesendorp 2015) E: (Zhu, Woodall, et al. 2015) E: (LaManna, Mangan, et al. 2017; LaManna, Mangan, and Myers 2021) E: (Hülsmann et al. 2024) T: (Stump and Comita 2018, 2020)
(13) Site-to-site variation in community composition (beta diversity) decreases with stronger stabilizing CDD	X	X	X		Stabilizing CDD from specialized enemies or intraspecific competition allows more species in the regional pool to co-occur in local communities, decreasing beta-diversity among communities	Prediction may depend on how stabilizing CDD influences regional (gamma) diversity	E: (LaManna, Belote, et al. 2017)
(14) Stabilizing CDD is stronger in warmer, wetter, less-seasonal, or more productive climates	X	X			Warmer, wetter, less-seasonal, or more productive climates promote higher diversity, greater specialization, and/or greater virulence of enemies	Assumes effects of enemies vary systematically with environmental conditions	M: (Comita et al. 2014) LaManna, Belote, et al. 2017) E: (LaManna et al. 2022)

(Continues)

TABLE 1 | (Continued)

Prediction	Theory				Mechanisms	Challenges and caveats	Examples of studies
	JC	FT	RT	CT			
(15) Interspecific trade-offs in resource requirements or host specificity of enemies	X	X	X	X	Interspecific differences in resource requirements or specificity of enemies define niche differences that underlie stabilizing CDD & neg. frequency dependence	Resource competition (e.g., RC) and host specificity of enemies are difficult to measure empirically & for large numbers of plant species	T: (Tilman 1982, 1988) T: (Chase and Leibold 2003)
16) Host ranges of enemies increase with latitude	X				Enemies are more specialized to host plant species at tropical than temperate latitudes, resulting in stronger stabilizing CDD in the tropics	Most studies have examined host ranges (diet breadth) of insect herbivores, but fewer have examined host ranges of microbial pathogens	E: (Novotny et al. 2006) E: (Dyer et al. 2007) E: (Forister et al. 2015)
(17) Plant defense traits or resource-acquisition traits are overdispersed at the community scale	X	X	X		Plants with more similar defense or resource-competition traits are excluded from local communities due to shared enemies or interspecific competition, respectively	Lower statistical detection power, even if the underlying process is strong (Vellend 2016)	T: (Weiher and Keddy 1995) E: (Kraft and Ackerly 2010) E: (Endara et al. 2022)
(18) Local species diversity increases with the spatial variance in resource ratios			X	X	Intermediate ratios of limiting nutrients in the environment are less likely to lead to competitive exclusion		T: (Tilman 1982, 1988) E: (Hubbell 2009)
(19) Species relative abundance varies across gradients of limiting resources or resource ratios			X	X	Species have the highest abundance in habitats where they are the best competitor		T: Tilman (1982, 1988) E: (Hubbell 2009)

Note: All four theories make predictions about outcomes of local species interactions—such as interactions between plant hosts and relatively specialized natural enemies (JC), differential effects of conspecific and heterospecific plants on soil/phyllosphere properties (FT), intraspecific/interspecific competition for limiting resources within and among plant species (RC), and niche and fitness differences within communities (CT)—on stabilizing conspecific density dependence (CDD) and frequency dependence (FD) across three scales of biological organization: Individual plant performance (Scale 1), populations (Scale 2), and communities (Scale 3). Each major prediction is listed below, followed by associated mechanisms, challenges or caveats, and examples of supporting literature (E = empirical study; T = theoretical study; M = meta-analysis; R = review). When applicable, we include predictions for both stabilizing and destabilizing CDD, as well as negative (neg.) and positive (pos.) frequency dependence or feedback.

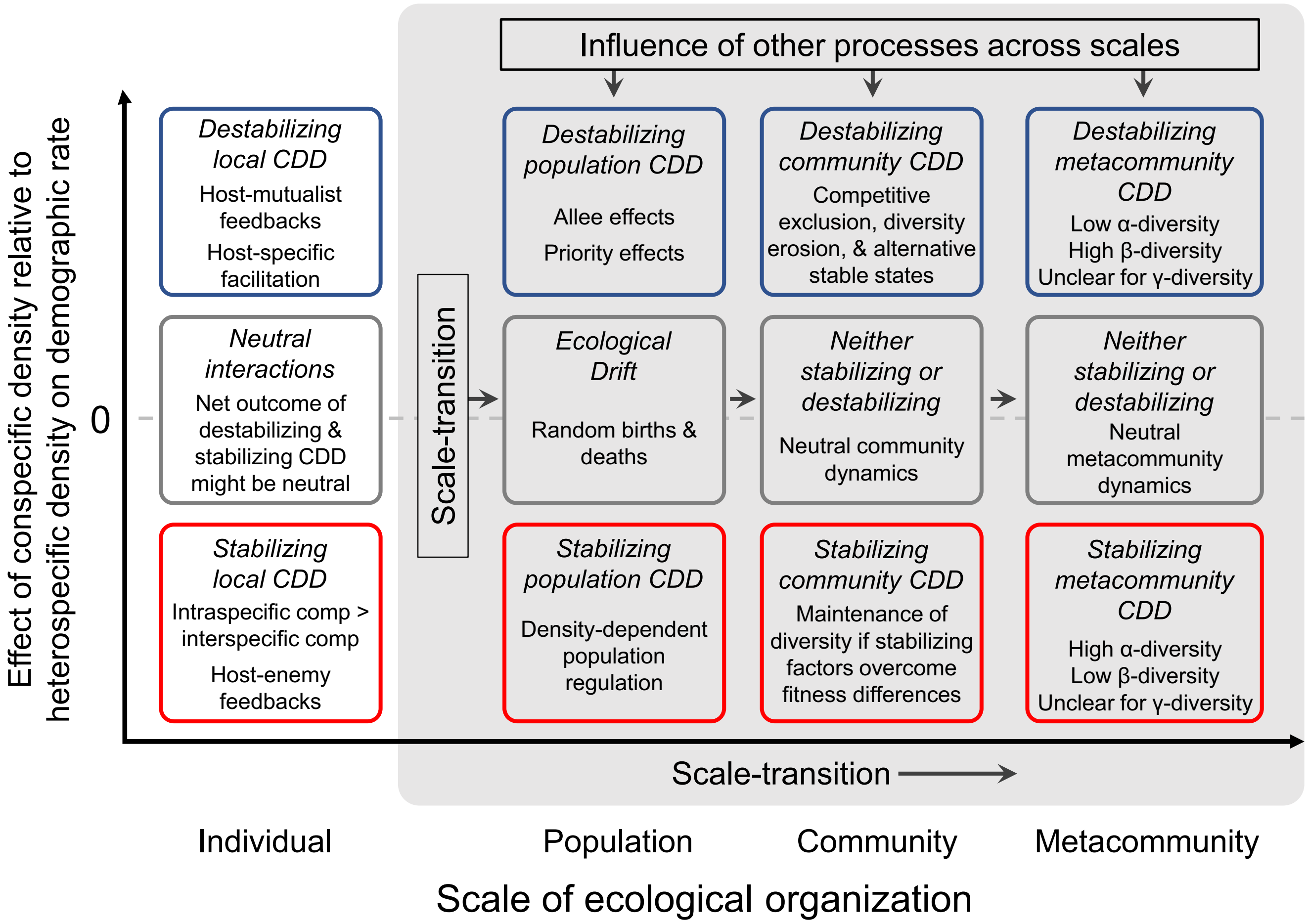

FIGURE 1 | Up-scaling stabilizing CDD from individuals to populations to communities to metacommunities. Ways in which stabilizing/destabilizing CDD in individual demographic performance (e.g., the relationship between survival, growth, etc. and conspecific relative to heterospecific density) might scale up to influence stabilizing/destabilizing CDD in population growth rates and community and metacommunity dynamics. Examples of stabilizing, destabilizing, or neutral CDD are given at individual, population, and community scales. Emergent metacommunity properties might be influenced by stabilizing CDD, and hypothesized effects of stabilizing CDD on metacommunities are provided. Because of scale-transition and the influence of larger scale processes, stabilizing CDD measured at the individual level may or may not translate into stabilizing CDD at higher levels of ecological organization (See Section 4).

4.2.1 | Integrating Stabilizing CDD Effects Across Life Stages

Studies of local stabilizing CDD focusing on one life stage or demographic rate have led to great advances. Yet the influence of these effects on individual fitness remains unclear because stabilizing CDD at one life stage may be offset or reversed by destabilizing CDD at another (O'Brien et al. 2022). For example, destabilizing CDD in seed production (greater seed production at high conspecific density) is expected for outcrossed plant species (Jones and Comita 2008) but is logistically difficult to measure and rarely studied in trees. A difficult but helpful goal would be studies that determine how local stabilizing CDD varies as well as covaries across multiple life stages and vital rates for some focal species and communities. This approach would help us to better understand how local stabilizing CDD at particular life stages influences overall population growth rates. This avenue is critical for future research because the effects of local stabilizing CDD on population growth rates will ultimately be a driver of how density-dependent effects scale up to influence community and metacommunity properties (Chesson et al. 2005; Thompson et al. 2020).

Some studies of relatively short-lived plants have integrated CDD effects across many or all life stages (Goldberg et al. 2001; Silva-Matos, Freckleton, and Watkinson 1999). However, few studies focusing on long-lived plants have measured local stabilizing CDD on all or nearly all demographic rates/transitions across life stages for an organism at the same location (Table 1). One key finding of select studies that have attempted to study local stabilizing CDD across life stages of long-lived plants is that strong local stabilizing CDD at earlier life stages tends to weaken at older life stages (LaManna et al. 2022; Zhu, Comita, et al. 2015, 2018; but see Chu and Adler 2015). Future studies might examine covariation in stabilizing CDD across life stages to determine if certain life stages are predictive or representative of stabilizing CDD in other life stages. If so, research might focus on those critical or representative life stages. When necessary auxiliary information is available, studies looking at adult-to-adult transitions across generations may be able to directly measure stabilizing

CDD as integrated across life stages without having to measure stabilizing CDD at each individual life stage.

Studies seeking to examine stabilizing CDD across different life stages might also integrate local stabilizing CDD effects on demographic performance across life stages with matrix models, integral projection models (IPMs; Ellner, Childs, and Rees 2016), or spatially explicit individual-based models (IBMs; DeAngelis and Grimm 2014) that allow for updated conditions throughout ontogeny and across multiple generations (Kinlock 2021). Different vital rates can be conditioned on local conspecific and heterospecific densities so that implications for population and community dynamics might be inferred. At any life stage, the signature of local destabilizing CDD may also emerge due to species habitat preferences or dispersal limitation (Box 3), emphasizing the need to explicitly assess the additive influence of the abiotic environment when examining stabilizing CDD in field-based studies (Chen et al. 2010; Johnson et al. 2017).

4.2.2 | Stabilizing CDD and Intrinsic Fitness Differences Among Species

Consideration of local stabilizing CDD in the context of coexistence theory highlights the possibility that intrinsic fitness differences among species at one or more life stages may be too great, potentially reducing or nullifying any potential diversity-maintenance effects of local stabilizing CDD (Barabás, Michalska-Smith, and Allesina 2016; Chesson 2000; Chisholm and Fung 2020; Yan, Levine, and Kandlikar 2022). In addition, species within a community commonly differ in the degree to which they experience stabilizing CDD, such as the finding that common species experience weaker stabilizing CDD than rare species in tropical forests (Comita et al. 2010; Hülsmann et al. 2024; Mangan et al. 2010). Several theoretical studies have demonstrated that variation in stabilizing CDD among species can in some circumstances enhance intrinsic fitness differences among species, weakening the ability of stabilizing CDD to maintain species diversity in a community (May et al. 2020; Miranda, Carvalho, and Dionisio 2015; Stump and Comita 2018). However, if stabilizing CDD is stronger for species with higher intrinsic fitness, fitness differences among species are expected to decrease and thereby enhance diversity maintenance (Stump and Comita 2018).

To address these possibilities, we recommend that future studies not only report local stabilizing or destabilizing CDD but also the possible impacts stabilizing or destabilizing CDD might have on fitness or competitive hierarchies in a community (e.g., Hülsmann et al. 2024). If possible, this might involve carefully designed studies or experiments to measure demographic performance along density gradients for multiple species in a community (Ke and Wan 2020, 2023). A combination of careful empirical measurements with modeling and simulations could also be used to evaluate fitness hierarchies in the context of local stabilizing CDD. Scale-transition theory could then be applied to evaluate the extent to which fitness hierarchies and local stabilizing CDD affect the likelihood of coexistence at community and metacommunity scales (Chesson 2012; Chesson et al. 2005). Only in the context of scale-transition theory or similar frameworks can firm inferences be made about the potential of local stabilizing CDD to impact communities or metacommunities.

4.2.3 | Pairwise Interactions, Lumped Heterospecifics, and Multispecies Systems

Other barriers to scaling up the influence of local stabilizing CDD on community dynamics involve simplifying assumptions used to make calculations more tractable, including the common practice of lumping heterospecific density effects when comparing them to conspecific density effects (see Hülsmann, Chisholm, and Hartig 2021; but see Volkov et al. 2009). Lumping heterospecifics to examine their density effects may be justified when assuming that specialized biotically-mediated interactions are particularly likely to occur between conspecifics, but this approach assumes that the host-specificity is absolute and that heterospecific effects are approximately homogenous. These simplifying assumptions are often necessary for highly diverse communities and for theoretical applications when the interest is treating each species as interacting with the average background of other species (e.g., O'Dwyer and Chisholm 2014). Generally, researchers should at least acknowledge and ideally evaluate whether differences among heterospecifics are important. For example, closely related heterospecifics can have effects that are more similar to conspecifics than more distantly related heterospecifics (Liu et al. 2012; Webb, Gilbert, and Donoghue 2006; Weiblen et al. 2006) due to, for example, phylogenetic signal in pathogen host-range (Gilbert and Webb 2007). This is not always the case, however, such as the finding of greater similarity in defense chemistry among more distantly related congeners (Forrister et al. 2019).

Developing analytical approaches to handle the vast numbers of species interactions in diverse communities should be a research priority, with potentially transformative impacts on our understanding of stabilizing CDD and coexistence (Gibbs, Levin, and Levine 2022). However, the first pragmatic step would be to determine the extent to which heterospecific density effects differ, why they differ, and the implications for coexistence. For example, instead of estimating all possible heterospecific effects separately, future studies could explicitly consider separate density effects for different functional groups of heterospecifics (Delavaux et al. 2023). Other options include factorial experiments, sparse-data Bayesian hierarchical modeling (Weiss-Lehman et al. 2022), modeling heterospecific effects with hyperparameters, or approaches leveraging network theory (Bimler et al. 2023; Kinlock 2021). However, intensive modeling approaches risk overfitting or obscuring a biologically relevant signal of stabilizing CDD.

More explicit consideration of pairwise feedback may enhance our ability to test predictions (Table 1) and empirically link studies of stabilizing CDD and plant–soil feedback (Broekman et al. 2019). However, the implications of pairwise interactions for community dynamics involving more than two species are less clear (Eppinga et al. 2018; Song, Barabás, and Saavedra 2019). Ultimately, several difficulties remain in determining the implications of local stabilizing CDD or coexistence frameworks for spatiotemporal community and metacommunity patterns, including a need to better incorporate stochasticity, further develop models for more-than-two-species coexistence (Jeltsch et al. 2019; Saavedra et al. 2017), and incorporate higher order and more complex species-interaction structures (e.g., intransitive competition; Allesina and Levine 2011; Gibbs, Levin, and Levine 2022; Kleinhesselink et al. 2022; Levine et al. 2017). Stochastic simulation models parameterized by empirical data on density-dependent effects may be a tractable and pragmatic path forward (Jeltsch et al. 2019).

4.3 | Spatial and Temporal Variation in Local Stabilizing CDD

A persistent challenge of scaling the effects of stabilizing or destabilizing CDD on community and metacommunity dynamics relates to how stabilizing CDD changes across environmental gradients and through time. Decades of research have shown that the abiotic environment strongly influences the fitness and distribution of biotic agents that generate or ameliorate stabilizing CDD, including herbivores (Coley, Bryant, and Chapin 1985), pathogens (Burdon, Jarosz, and Kirby 1989; Garrett 1970; Givnish 1999; Swinfield et al. 2012), and mutualists (Bertness and Callaway 1994; David, Thapa-Magar, and Afkhami 2018; Fajardo and McIntire 2011; Maestre et al. 2009). In the face of global change, explicitly testing how the strength of stabilizing CDD changes with environmental conditions both across space and time will become increasingly integral to forecasting downstream consequences of climate change on coexistence, diversity, and ecosystem function (Comita and Stump 2020).

Spatial and temporal variation in stabilizing CDD associated with climatic factors has potential implications for population and community responses to global change. Climate and land-use changes modify local microclimates as well as physiological stress levels and resource availability, which may, in turn, influence the role of local stabilizing CDD in promoting population stability and maintaining species diversity (Comita and Stump 2020). Ecosystem resilience depends in part on the ability of each species to tolerate and adapt to novel environmental conditions. To the extent that local stabilizing CDD might maintain species diversity, it can potentially increase the probability that a particular community harbors species that can survive and thrive in future conditions. Currently, little is known about how future extreme and unstable climatic conditions as well as more intensive land-use changes may influence local stabilizing CDD and biodiversity. Insights from statistically controlling the additive effects of the environment suggest that the effects of warming on plant–host interactions are uncertain; interactions may intensify (Liu and He 2021) or weaken (Bachelot et al. 2020) stabilizing CDD. Evidence suggests that stabilizing CDD weakens in dryer conditions (Comita et al. 2014; Jiang et al. 2024; LaManna et al. 2022; Lebrija-Trejos, Hernández, and Wright 2023; Uriarte, Muscarella, and Zimmerman 2018) and near forest edges relative to forest interiors (Krishnadas et al. 2018), which may result in less diverse and/or resilient communities in highly fragmented forests or under intensifying drought. More empirical and theoretical studies in disturbance-modified landscapes and the resulting effects on stabilizing CDD are needed.

The importance of understanding how spatial and temporal changes in abiotic environments influence stabilizing CDD has encouraged empirical tests (Bachelot et al. 2020; Browne et al. 2021; HilleRisLambers, Clark, and Beckage 2002; Johnson et al. 2017; LaManna et al. 2016, 2022; LaManna, Mangan, and Myers 2021; Lebrija-Trejos, Hernández, and Wright 2023; Lin et al. 2012; Song et al. 2020). These studies provide some early support for the hypothesis that CDD is more stabilizing with increases in moisture and decreases in seasonality across space and time (Comita et al. 2014; Lebrija-Trejos, Hernández, and Wright 2023). These differences may be due to enhanced pathogen loads and dispersal in wetter, less seasonal conditions (Givnish 1999; Milici et al. 2020), but more empirical studies are needed to evaluate this hypothesis. Other predictions for how stabilizing CDD might differ with the abiotic environment across space and time include stronger stabilizing CDD in warmer, more productive areas/times (Table 1; Box 4). Ecologists interested in abiotic environmental effects on stabilizing CDD could turn to plant–soil feedbacks, reciprocal transplants, herbivore exclosures, and/or observational studies across land use and/or disturbance gradients to examine interactions between biotic factors, abiotic environmental factors, and plant performance (Dudenhöffer, Luecke, and Crawford 2022; Germany, Bruelheide, and Erfmeier 2019; Krishnadas et al. 2018; Van der Putten et al. 2013).

5 | Conclusions

The study of local stabilizing CDD has sustained strong interest for decades and has important implications for species coexistence and the maintenance of species diversity. Many gaps remain in our understanding of how these effects scale up to influence larger scale biodiversity patterns and community dynamics. Here, we offer a conceptual synthesis of local stabilizing CDD as well as solutions to help move the field forward (Box 5).

A combination of dynamic data, static patterns, targeted experiments, and simulations should be leveraged to push our empirical and theoretical understanding forward and validate those insights with checks against longer time series. Tests of emergent patterns have thus far concentrated mainly on responses of demographic performance, spatial patterns, and species diversity (Table 1). However, the list of patterns to be considered should be extended to include all common metrics used in community and metacommunity ecology, including species spatial and temporal turnover (LaManna, Belote, et al. 2017), and species-area and species-abundance relationships (Chave, Muller-Landau, and Levin 2002; Volkov et al. 2005). We suggest that studies use multiscale frameworks that explicitly acknowledge the scale at which stabilizing CDD is being examined and how it might interact with other ecological processes across scales (e.g., scale-transition theory). Such multiscale frameworks allow for a more comprehensive study of the different spatial and temporal patterns that might be expected from stabilizing CDD at various levels of biological organization.

The study of locally stabilizing CDD may also have important implications for evolutionary processes as well as ecosystem functions such as water and carbon fluxes, carbon sequestration, and biogeochemical cycles (e.g., Schnitzer et al. 2011). How local stabilizing and destabilizing CDD may influence ecosystem function and evolutionary processes should be the focus

BOX 5 | Challenges in stabilizing CDD research and proposed solutions.

Challenge: CDD does not necessarily imply multi-species comparisons.

Solution: Use the terms stabilizing or destabilizing CDD when referring specifically to CDD as it compares to general density (i.e., non-species-specific) effects. We emphasize that a community with species experiencing stabilizing CDD will not necessarily be stably coexisting (Box 3).

Challenge: Locally generated stabilizing CDD may be masked or counteracted by processes occurring at larger spatial scales.

Solution: Adopt multiscale frameworks to evaluate processes affecting stabilizing CDD at larger spatial scales. If possible, integrate larger scale observational studies with field and greenhouse experiments focused on disentangling the relative contributions of different mechanisms to net stabilizing CDD.

Challenge: Stabilizing CDD research has largely focused on density effects from particular types of natural enemies (e.g., pathogens), and the community dynamics of enemy populations are often treated as static.

Solution: Adopt a more mechanistic focus on different types of above- and belowground agents, and how those agents might interact dynamically to influence the net magnitude of stabilizing CDD. Also consider other mechanisms that have received less attention (e.g., allelopathy) that generate plant feedback (De Long et al. 2023).

Challenge: Strong local stabilizing CDD should exert strong directional selection for traits that enable greater dispersal distances.

Solution: Examine the potential for such interplay between dispersal strategies and stabilizing CDD, which has been rarely studied. Interesting comparisons include how dispersal phenology, distance, and mode (and any other dispersal-associated traits) differ across tree species as a function of their local stabilizing CDD.

Challenge: Many stabilizing CDD studies have focused on testing predictions at the individual level of biological organization (Table 1).

Solution: When possible, evaluate predictions for stabilizing CDD at population and community levels in addition to testing predictions at the individual level (Table 1). Scale-transition theory can be used to relate local and larger scale stabilizing CDD (Chesson 2012).

Challenge: Studies of local stabilizing CDD have largely focused on one life stage or demographic rate. Yet stabilizing CDD at one life stage may be offset or reversed by destabilizing CDD at another (O'Brien et al. 2022).

Solution: Measuring all life stages of a long-lived plant is logistically difficult. When possible, examine covariation in stabilizing CDD across life stages to determine if certain life stages are predictive or representative of other life stages. When necessary auxiliary information is available, studies looking at adult-to-adult transitions may be able to get at population-level effects without assessing stabilizing CDD at each life stage. We also suggest combining studies of different life stages of the same species when possible (e.g., with matrix models, integral projection models, and spatially explicit individual-based models).

Challenge: Intrinsic fitness differences among species may be too great, potentially reducing any potential diversity-maintenance effects of local stabilizing CDD (Barabás, Michalska-Smith, and Allesina 2016; Chesson 2000; Chisholm and Fung 2020; Yan, Levine, and Kandlikar 2022). Species within a community might also differ in the degree to which they experience stabilizing CDD (Comita et al. 2010; Hülsmann et al. 2024; Mangan et al. 2010).

Solution: We recommend that future studies not only report local stabilizing CDD but also the possible impacts stabilizing CDD might have on fitness or competitive hierarchies in a community (Hülsmann et al. 2024). If possible, this might involve carefully designed studies or experiments to measure demographic performance along density gradients for multiple species in a community (Ke and Wan 2020, 2023).

Challenge: Studies using statistical modeling to estimate the performance of individual plants often lump heterospecific effects (Hülsmann et al. 2024), a simplifying assumption used to make calculations more tractable.

Solution: While this is often necessary in highly diverse communities, researchers should at least acknowledge and ideally evaluate whether differences among heterospecifics are important. Future studies could consider separate density effects for different functional groups of heterospecifics instead of separate effects for each species (Delavaux et al. 2023). Other options include factorial experiments, sparse-data modeling, hyperparameters, or network theory.

Challenge: We lack a clear understanding of how stabilizing CDD changes across space and time.

Solution: Predictions for how stabilizing CDD might differ with the abiotic environment include stronger stabilizing CDD in wetter, warmer, and more productive areas/times (Table 1). Researchers could turn to plant–soil feedback, reciprocal transplants, herbivore exclosures, pathogen-specific exclusion, and/or observational studies across environmental, land use, and/or disturbance gradients to examine interactions between biotic factors, abiotic factors, and plant performance. Long-term studies of stabilizing CDD are recommended to determine how it changes with climatic conditions through time.

of future research and synthesis (Slade et al. 2019; Turnbull et al. 2013). Ultimately, uncovering the drivers of local stabilizing CDD and their effects on population, community, and metacommunity dynamics will help us better understand the processes driving biodiversity in a changing world.

Author Contributions

All authors conceived the ideas in this paper as part of a working group on density dependence. Joseph A. LaManna, Camille S. Delavaux, Florian Hartig, Jonathan A. Myers, Robert P. Freckleton, Matteo Detto, Akshay Surendra, and Cole J. Doolittle wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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Data Availability Statement

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

Peer Review

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