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SYNTHESIS

Local Stabilising Density Effects in the Context of Ecological Disturbance and Community Assembly

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ABSTRACT

The maintenance of species diversity in ecological communities has many promising explanations, including certain types of local biotic interactions that generate differential effects on the performance of conspecific and heterospecific individuals. To date, most studies of these local biotic interactions have focused on relatively stable systems, such as mature forests or undisturbed grasslands. However, many ecosystems are far from a stable state, especially under accelerating global climate change. Here, we present a synthesis of local differences between conspecific and heterospecific interactions following disturbances—and how disturbances may alter the strength and scaling of these effects to population growth and species diversity. First, we clarify terminology and categorise disturbances based on their primary mode of impact on species interactions. Second, we leverage existing literature to develop a framework for understanding how disturbances may alter the strength and role of local biotic interactions in regenerating communities. Third, we use prominent examples of disturbance: drought, windthrow and wildfire, to highlight remaining gaps in knowledge. Finally, we discuss implications for future populations and communities in unstable states. We emphasise the need for empirical studies to further integrate disturbance and local conspecific density effects within broader ecological models of community assembly and functioning.

1 | Introduction

Ecosystems that generate global cultural and economic wellbeing are increasingly threatened by anthropogenic climate change and climate-related changes to natural patterns of ecological disturbance. Today, ecologists are concerned that unpredictable patterns and severity of disturbance events will erode key ecosystem services and diversity in future ecological systems (Lindenmayer et al. 2019; Seidl et al. 2017; Swanson et al. 2011). In part, this concern reflects uncertainty about how disturbance events alter the underlying processes generating and maintaining species diversity in regenerating ecosystems (Seidl and Turner 2022). To address this uncertainty, the need exists for synthesis of literature on ecological disturbance and the processes that affect species diversity. Here, we synthesise recent advances in interactions between ecological disturbances and one such process that can affect species diversity: local density-dependent species interactions.

Ecologists have a longstanding interest in determining relationships between ecological disturbances and species diversity (Clements 1916; King 1685; Turner 2010), which has often manifested in identifying the 'winners and losers' of abiotic change based on functional traits and life-history strategies (Keith et al. 2007; McKinney and Lockwood 1999; Noble and Slatyer 1980; see Tabarelli et al. 2012). The 'winner and losers' paradigm suggests that disturbances alter species composition and diversity by changing the availability and heterogeneity of both resources and competitors, which either stochastically (i.e., random dispersal, priority effects; Egler 1954; Horn 1974) or deterministically (i.e., succession trajectories, CSR theory; Fox 1982; Grime 1977; Peet and Christensen 1987) promote assemblages of species with disturbance-adapted strategies (*reviewed by* Pulsford et al. 2016). However, disturbances may also alter the occurrence and outcome of density-dependent mutualistic, antagonistic, and resource interactions—a nuance that has rarely been integrated with the 'winners and losers' paradigm (Andersen 2019; Gasith and Resh 1999; Post 2013). Given evidence for the prevalence of density-dependent interactions (Comita et al. 2014; Song et al. 2021) and their potential to affect local species diversity (Bagchi et al. 2014; Brown et al. 2020; LaManna et al. 2017, 2022; Mitchell et al. 2006), incorporating density-dependent interactions into frameworks of community regeneration and recovery following disturbance presents a key opportunity to bridge the gap between community and disturbance ecology.

One important conceptual area examining how density-dependent interactions influence species diversity is the study of local conspecific density dependence (CDD). Local CDD is defined as the relative influence of local conspecific densities on individual performance (i.e., growth, survival, reproductive rates) arising primarily from intraspecific competition and interactions with shared antagonists and/or mutualists (LaManna et al. 2024). To distinguish from single-species concepts of density-dependent population regulation, we adopt the term local 'stabilising' CDD to describe local density-dependent effects that may stabilise population growth and influence species diversity in the context of a multi-species community. For example, population growth may be stabilised by local CDD that generates a negative relationship between conspecific densities and individual performance relative to heterospecific densities (i.e., stronger negative effect of conspecifics than heterospecifics; Hülsmann et al. 2024). Alternatively, local CDD can also destabilise population growth under certain conditions where the relationship between conspecific densities and individual performance is positive relative to heterospecific densities (i.e., stronger negative effect of heterospecifics than conspecifics; Hülsmann et al. 2024). Local stabilising CDD is hypothesised to promote or stabilise local species diversity under certain conditions (Broekman et al. 2019; LaManna et al. 2017; Wright 2002), while local destabilising CDD is hypothesised to destabilise or erode local species diversity under certain conditions (Delavaux et al. 2023; Zahra et al. 2021). Hereafter, we use the term 'stabilising CDD' to refer to local conspecific density effects on individual performance that could scale to affect population growth and species diversity under certain conditions, regardless of whether the net effect is stabilising or destabilising. When discussing directional predictions for local CDD in the context of ecological disturbance (e.g., becoming more or less stabilising), we explicitly state the direction of change.

Ecological disturbances, which disrupt local abiotic properties and/or the density of organisms, likely alter the role of stabilising CDD in affecting individual performance and shaping local species diversity. However, the strength, directionality, and effects of stabilising CDD in disturbed environments remain critically unexplored (Comita and Stump 2020; LaManna et al. 2024). In part, this knowledge gap persists due to a lack of underlying predictions for understanding how the drivers of local stabilising CDD may be altered in disturbed environments. Moreover, studies integrating local stabilising CDD and disturbance are hampered by: (1) complex interactions between the underlying drivers of local stabilising CDD; (2) variability of disturbance effects due to system-specific resilience and susceptibility to rapid change; and (3) context-dependent factors affecting the outcome of interactions between individuals, including phylogenetic relatedness, resource requirements, and functional traits.

Here, we begin to bridge the gap between disturbance ecology and the study of local stabilising CDD using tree communities as a focal study system. First, we review recent observational and experimental studies of stabilising CDD along abiotic gradients. Next, we develop a conceptual framework for exploring how disturbances might impact the local drivers of stabilising CDD and how differences between conspecific and heterospecific effects may scale up to affect community assembly and diversity. Finally, we present critical gaps in knowledge and future directions for ecologists interested in integrating density-dependent interactions into frameworks of recovery and succession following disturbance.

2 | Evaluating the Drivers of Local Stabilising CDD in a Changing World

Over half a century has passed since Janzen (1970) and Connell (1971) first hypothesised that species diversity may be maintained by local, density-dependent interactions between relatively host-specific natural enemies (i.e., pathogens, herbivores, etc.) and their hosts. Since that time, ecologists have expanded this hypothesis to incorporate direct intraspecific competition (e.g., Adler et al. 2018), relatively host-specific mutualists (e.g., Bachelot et al. 2015; Delavaux et al. 2023; Kandlikar et al. 2019), and drivers that generate stabilising CDD across spatial and temporal scales (e.g., Swenson et al. 2023). Today, there is broad support for the ability of disproportionately strong or weak conspecific interactions within a local neighbourhood context to mediate performance, particularly among early life-stage plants (Comita et al. 2014; Hülsmann et al. 2021; Song et al. 2021). Debate continues to surround the ability of these local interactions to scale up and generate stabilising CDD in population growth rates at the community and regional scales, a requirement for local interactions to affect species diversity (Chesson 2012; Hubbell 2001; Hülsmann et al. 2021, 2024; LaManna et al. 2021, 2024). However, theory and simulation studies suggest that under certain scenarios stabilising CDD within local neighbourhoods should contribute to community composition, diversity and function (Chesson 2000; Levi et al. 2019; Smith 2022).

To distinguish between the types of local interactions capable of generating stabilising CDD in individual performance, we place each driver into one of three categories: apparent, allelopathic and resource interactions (Box 1, Figure 1). Each driver is hypothesised to generate either a negative (stabilising) or positive (destabilising) effect on conspecific relative to heterospecific performance. We highlight that each driver must be relatively

BOX 1 | Defining the drivers causing local CDD to be stronger than local heterospecific density dependence (HDD).

Hülsmann et al. (2021) categorise the mechanisms capable of generating local stabilising CDD (also negative CDD; CNDD) into three separate groups: (1) host-specific enemies, (2) abiotic niche differentiation, and (3) autotoxicity. Here, we additionally integrate the drivers capable of generating destabilising CDD including host-specific mutualists, allelopathy, and strong interspecific competition (Figure 1). We generalise these new categories to (1) apparent interactions, (2) resource interactions, and (3) allelopathic interactions. Importantly, stabilising and destabilising CDD are defined in relation to heterospecific densities, or the measurement of conspecific effects after accounting for the effects of heterospecifics (Hülsmann et al. 2024; LaManna et al. 2024).

Apparent Interactions

Local CDD in trees is most often stabilising and largely thought to be generated by negative apparent interactions with host-specific taxa in the phyllosphere and rhizosphere; including herbivores, root and leaf-associated fungi, and other microscopic organisms (apparent competition; Bagchi et al. 2010; Bachelot et al. 2020; Chen et al. 2019; Desprez-Loustau et al. 2006; Holt 1977; Liu et al. 2022; Mangan et al. 2010; Packer and Clay 2000; Song et al. 2018). However, local CDD can also be destabilising, driven by positive apparent interactions with mycorrhizal fungi and mutualistic foliar endophytes (apparent facilitation; Bachelot et al. 2015; Delavaux et al. 2023; Pu et al. 2022; Zahra et al. 2021). Together, antagonistic and mutualistic apparent interactions contribute to the net stabilising or destabilising effects of local CDD (Bever et al. 1997; Jiang et al. 2020).

Resource Interactions

Local stabilising CDD in trees can also be generated by strong intraspecific relative to interspecific competition. For example, many tree species exploit resources or habitat spaces in a manner that reduces the survival and growth of other nearby conspecific individuals, thereby generating local stabilising CDD (Comita et al. 2014; Johnson et al. 2017). Resource interactions often contribute to local stabilising CDD at both individual (Umaña et al. 2018) and population scales (Wiegand et al. 2021). While less common, resource interactions can also generate local destabilising CDD through stronger interspecific competition than intraspecific competition, which advantages demographic rates of clustered conspecifics relative to those near heterospecific individuals (e.g., resource facilitation such as hydraulic lift of limiting resources; Armas et al. 2010).

Allelopathic* Interactions

Less frequently invoked as a driver of local CDD are allelopathic compounds produced by trees. These compounds can generate locally stabilising or destabilising CDD by disproportionately impacting the growth and survival of conspecific individuals relative to heterospecific individuals (Mazzoleni et al. 2015; Hierro and Callaway 2021; Yuan et al. 2022). Allelopathic interactions are thought to be most often stabilising, such as chemical production that inhibits conspecific relative to heterospecific demographic rates. However, allelopathic interactions can also be destabilising when allelopathy benefits conspecific demographic rates relative to heterospecifics (e.g., pathogen suppression).

*In 1937, Molisch first presented the term allelopathy with the publication of *The influence of one plant on another: allelopathy* (Molisch 1937 [2001]). Although our modern use of *pathy* often exclusively refers to harmful, negative effects, Molisch's original definition sought to incorporate both positive and negative chemical interactions among plants. Here, we use the original meaning of Molisch's term *allelopathy*, and distinguish directionality with ‘positive’, ‘negative’, or ‘neutral’ (*as described by* Hierro and Callaway 2021).

host-specific, meaning it causes disproportionate effects on the performance of conspecific individuals relative to heterospecific individuals. For these purposes, host-specificity does not necessarily represent host-adaptation or preference (Bever 2002). Additionally, functional or relative host-specificity, as opposed to absolute host-specificity, is sufficient to generate differential effects across hosts and therefore contribute to local stabilising CDD (Spear and Broders 2021).

Ecologists are increasingly interested in how abiotic gradients affect the relative importance and strength of drivers that generate local stabilising CDD (Comita and Stump 2020; LaManna et al. 2024). In general, local CDD appears to become more stabilising in areas with low light, high soil moisture, and aseasonal climates (Table 1; Augspurger and Kelly 1984; Brown et al. 2021; LaManna et al. 2016; Lebrija-Trejos et al. 2023; Lin et al. 2012; Milici et al. 2020; Song et al. 2018). On broader spatial scales, local stabilising CDD also appears to weaken with increasing elevation and latitude (Fibich et al. 2021; Hülsmann et al. 2024; LaManna et al. 2017, 2021, 2022). Together, these studies indicate that local CDD may vary predictably along abiotic gradients, suggesting common mechanisms contributing to patterns of plant performance.

Assigning mechanisms to correlations between local stabilising CDD and abiotic gradients is challenging. For example, abundant shade, humidity, and resources may generate stronger local stabilising CDD by increasing host-specific antagonist loads (Inman-Narahari et al. 2016; Kobe and Vriesendorp 2011), or by altering the spatial heterogeneity of resources (Johnson et al. 2017). Similarly, gradients of local stabilising CDD may result from increased relative host-specific facilitation under abiotic stress, such as interactions between plants and mycorrhizal fungi (Delavaux et al. 2023; Fajardo and McIntire 2011; Maestre et al. 2009). Finally, gradients of local stabilising CDD may result from stress-mediated allelopathic or resource interactions, although these possibilities remain less explored (Devaney et al. 2018; Record et al. 2016). Given increasing uncertainty

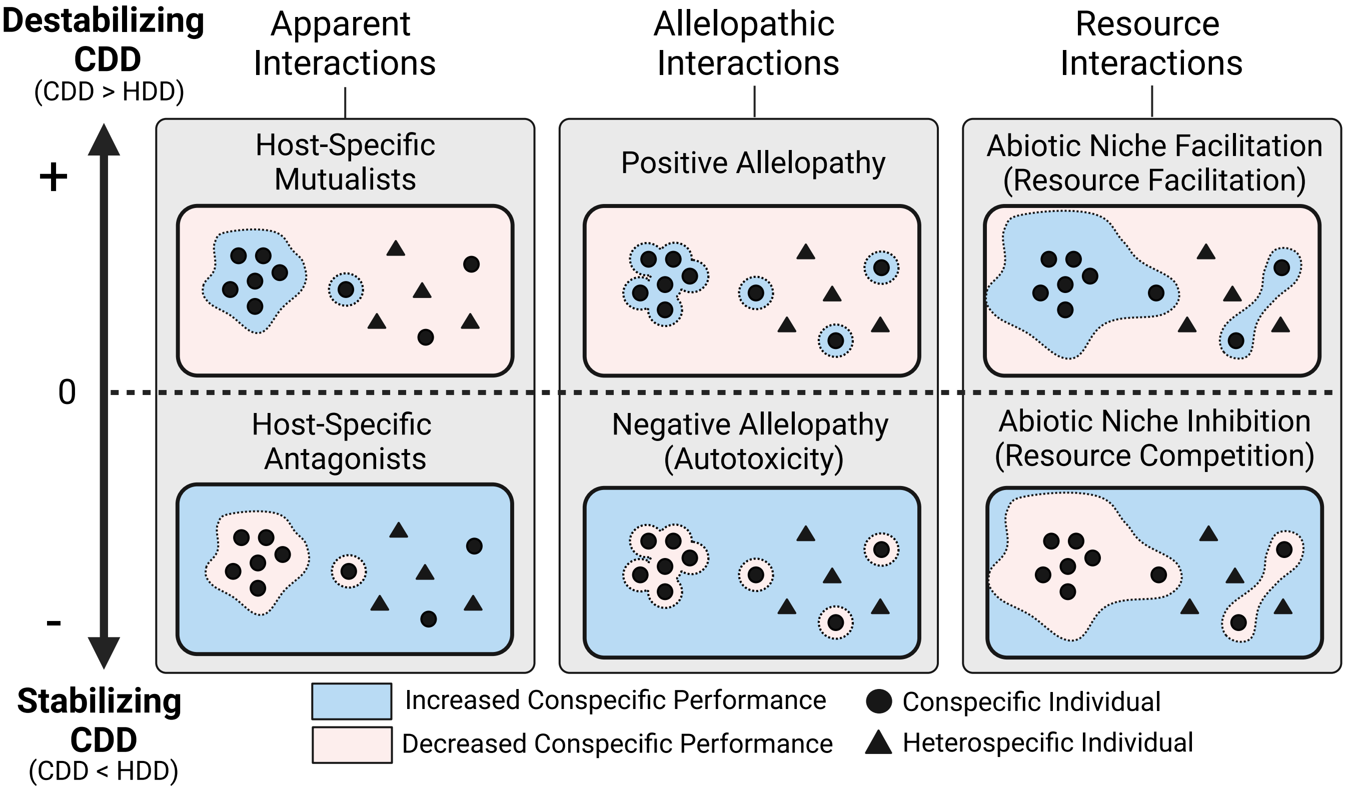

FIGURE 1 | Contribution of apparent, allelopathic, and resource interactions to stabilising or destabilising local CDD. The drivers of local CDD can be divided into three categories: Apparent, allelopathic, and resource interactions. Each of these interaction types may have positive (destabilising) density effects on conspecific performance (circles, blue areas) or negative (stabilising) density effects on conspecific performance (circles, pink areas). The net strength of stabilising or destabilising CDD, therefore, corresponds to the net strength and directionality of each interaction category. Importantly, local CDD is measured in reference to heterospecific densities. Heterospecific neighbours are represented as triangles. While the functional result of all drivers of local CDD remains constant (i.e., suppression or bolstering of local conspecific performance) the spatial patterns of these effects may vary with category. For instance, in forests trees draw down resources from their surrounding areas—often extending beyond root area via mycorrhizal networks. Allelopathic interactions, however, are almost always restricted to canopy crown area. This figure illustrates the similarities between apparent, allelopathic, and resource interactions, as well as how they may differ in spatial effects and contribution to net local CDD. For examples of each, refer to Box 1.

over the future of abiotic conditions and stressors (Seidl and Turner 2022), understanding the mechanisms underlying central ecological processes such as local stabilising CDD will be important for predicting the effects of future disturbance patterns under climate change.

3 | Categorising Disturbances by Primary Effects on Forest Structure

Ecological disturbances have long been understood to influence community structure and dynamics across spatial and temporal scales (Cooper 1926; Pickett et al. 1985; White 1979). However, developing inclusive definitions of disturbance that integrate a variety of causes, scales, and consequences for community structure and diversity remains a prominent challenge. Over the past century, the term 'disturbance' has often been used to generally describe an event that disrupts any ecological level, environmental component, or the organisational status of organisms (Pickett et al. 1989). Alternatively, disturbance can be defined as external events that influence ecosystem processes such as energy cycling, biomass accumulation, and hydrological patterns (Sousa 1984; Swanson et al. 2011). More recently, explicit definitions of disturbances based on their spatial scale and/or level of ecological organisation they affect have been proposed (i.e., local vs. regional disturbances; Battisti et al. 2016; Levin 2000). We acknowledge that clearly defining disturbance is central to understanding disturbance effects on local stabilising CDD. Towards that goal, we present generalisable categories of ecological disturbance tailored to exploring their potential impacts on the interactions that generate local stabilising CDD in forest ecosystems.

The function and structure of forest ecosystems are defined by the spatial composition and age distribution of trees (Ammer 2019). It is no surprise, therefore, that ecological disturbances in forests are often defined by their primary mode of influence on trees—either directly causing tree mortality or indirectly altering compositions through rapid changes to resources, habitats, and/or competitive environments. Forests experience a wide spectrum of naturally occurring disturbance events, including drought, windthrow, wildfire and insect outbreaks, among others. Here, we group these individual disturbance types into three categories based on their primary mode of influence on trees: interference, destruction, and combined disturbances (Box 2). Interference disturbances,

TABLE 1 | Empirical studies of local CDD along abiotic gradients (selected publications).

Paper	System	Life stage	Study type	Interactions between environmental variable and conspecific density effects (M = mortality, G = growth)
Light				
Augspurger and Kelly (1984)	Tropical forest	Seedlings	Obs.	Weakens local stabilising CDD (M)
Holík et al. (2021)	Temperate forest	Seedlings	Obs.	Weakens local stabilising CDD (M)
Inman-Narahari et al. (2016)	Tropical forest	Seedlings	Obs.	Weakens local stabilising CDD (M)
Kobe and Vriesendorp (2011)	Tropical forest	Seedlings	Obs.	Weakens local stabilising CDD (M)
McCarthy-Neumann and Ibanez (2013)	Tropical forest	Seedlings	Exp.	Weakens local stabilising CDD (M)
Record et al. (2016)	Tropical forest	Seedlings	Obs.	Weakens local stabilising CDD (M)
Brown et al. (2021)	Temperate forest	Saplings (2- to 12.7-cm DBH)	Obs.	Weakens local stabilising CDD (G)
Song et al. (2021)	Tropical forest	Seedlings	Obs.	Weakens local stabilising CDD (G)
Soil nutrients				
Brown et al. (2021)	Temperate forest	Saplings (2- to 12.7-cm DBH)	Obs.	Weakens local stabilising CDD (G)
LaManna et al. (2016)	Temperate forest	Seedlings and saplings (< 10-cm DBH)	Obs.	Strengthens local stabilising CDD (M)
Record et al. (2016)	Tropical forest	Seedlings	Obs.	Weakens local stabilising CDD (M)
Zang et al. (2021)	Tropical forest	Adults (≥ 1-cm DBH)	Obs.	Strengthens local stabilising CDD (M)
Moisture/precipitation				
Bachelot et al. (2020)	Tropical forest	Seedlings	Obs.	No distinct effect on local stabilising CDD (G & M)
Lebrija-Trejos et al. (2023)	Tropical forest	Seedlings	Exp.	Strengthens local stabilising CDD (M)
Lin et al. (2012)	Tropical forest	Seedlings	Obs.	No distinct effect on local stabilising CDD (G & M)
Milici et al. (2025)	Tropical forest	Seedlings	Exp.	Strengthens local stabilising CDD (G & M)
O'Brien et al. (2017)	Tropical forest	Seedlings	Exp.	Strengthens local stabilising CDD (G)
Song et al. (2020)	Tropical forest	Seedlings	Obs.	Strengthens local stabilising CDD (M)
Song et al. (2024)	Tropical forest	Seedlings	Obs.	Strengthens local stabilising CDD (M)
Uriarte et al. (2018)	Tropical forest	Seedlings	Obs.	Strengthens local stabilising CDD (M)
Temperature/warming				

(Continues)

TABLE 1 | (Continued)

Paper	System	Life stage	Study type	Interactions between environmental variable and conspecific density effects (M = mortality, G = growth)
Bachelot et al. (2020)	Tropical forest	Seedlings	Exp.	Weakens local stabilising CDD in M but strengthens local stabilising CDD in G
Germain and Lutz (2022)	Temperate forest	Adults ($\geq$1-cm DBH)	Obs.	Weakens local stabilising CDD (M)
Liu and He (2021)	Temperate forest	Seedlings	Exp.	Strengthens local stabilising CDD (M)
Liu and He (2022)	Tropical forest	Seedlings	Exp.	Weakens local stabilising CDD (M) for one of two focal species
Song et al. (2018)	Tropical forest	Seedlings	Obs.	Strengthens local stabilising CDD (M)
Elevation				
Fibich et al. (2021)	Temperate forest	Saplings ($<$15-cm DBH)	Obs.	Weakens local stabilising CDD (M)
LaManna et al. (2022)	Temperate forest	Adults ($\geq$5-cm DBH)	Obs.	Weakens local stabilising CDD (M), particulary for 5- to 15-cm DBH class
Xu and Yu (2014)	Subtropical forest	Seedlings	Obs.	Weakens local stabilising CDD (M)

such as nutrient depletion, initially impact the availability of resources such as nutrients, light, and space while leaving competitive densities relatively undisturbed in the short term. Destruction disturbances, such as windthrow, initially impact tree abundance, density, and/or health while leaving resource availability relatively undisturbed in the short term. Finally, combined disturbances, such as wildfires, have initial impacts on both aboveground tree structures and resource environments in the short term.

While the initial effects of interference, destruction, and combined disturbances differ, each triggers a complex recovery timeline with cascading consequences for both the availability of nutrients and competitive densities. Here, we focus explicitly on predicting local stabilising CDD through initial and late recovery phases following disturbance. We define initial recovery as the period immediately following disturbance, characterised by rapid changes in community composition and ecosystem processes as organisms respond to altered abiotic conditions. Late recovery is defined as the subsequent period when community composition begins to stabilise, characterised by slower rates of change and increasing functional redundancy (Chang and Turner 2019). We acknowledge two important caveats to this approach. First, not all disturbances fall cleanly into any one category (Box 2). Second, recovery phases are complex, and our predictions may need future refinement to account for system-specific successional trajectories. We highlight that most literature on local CDD along abiotic gradients focuses on one component of abiotic change (Table 1), and therefore categorising disturbances by their initial abiotic effects represents a natural first step towards a more inclusive understanding of disturbance-CDD dynamics.

4 | How Disturbances May Affect Local CDD in Individuals, Populations and Communities

4.1 | Primary Effects of Disturbance on Apparent, Allelopathic, and Resource Interactions

The primary mechanism by which disturbances might alter local stabilising CDD is by strengthening or weakening the effects from its underlying drivers. Apparent, resource, and allelopathic interactions (Box 1, Figure 1) may all be altered by disturbance, which may increase or decrease the difference between local conspecific and heterospecific effects on performance depending on the primary effects of disturbance (Figure 2A). For example, combustion from wildfires reduces the abundance and colonisation rates of many tree-associated mycorrhizal fungi (DeVan et al. 2023; Dove and Hart 2017). Reduced facilitation from mycorrhizal fungi following wildfire may cause stronger local stabilising CDD because relatively host-specific benefits from mycorrhizal fungi should otherwise counteract stabilising effects from shared pathogens. Alternatively, if wildfire were to disproportionately reduce the abundance of host-specific pathogens relative to host-specific mutualists, then wildfire may weaken local stabilising CDD, even to the point of generating local destabilising CDD (Hewitt et al. 2023). Understanding how the underlying drivers of local stabilising CDD respond to different categories of disturbance across time is key to estimating the

BOX 2 | Defining categories of ecological disturbance for understanding disturbance effects on CDD.

In 1985, Edward Rykiel proposed four categories for ecological disturbances: interference, destruction, decomposition, and suppression (Rykiel 1985). Here, we adapt these categories to delineate how different disturbances may have differing effects on the underling apparent, allelopathic, and resource interactions generating local stabilising CDD in forests.

Interference

- *Rykiel 1985 Definition*: Matter/energy/information exchange processes are inhibited.
- *Working Definition*: An *event* or *agent* that primarily alters nutrient availability or chemical properties in the system while leaving plant competitive densities and compositions relatively intact.
- *Examples*: In trees this category of disturbance most often influences soil nutrient, water, and light availability. Prominent examples of interference include drought, nutrient depletion, and nutrient decomposition—all of which primarily act by altering the availability and compositional heterogeneity of resources.

Destruction

- *Rykiel 1985 Definition*: Existing biomass is reduced in quantity (*see also* Grime 1979).
- *Working Definition*: An *event* or *agent* that dramatically alters plant competitive densities and compositions, or lowers mean plant health, while leaving nutrient and chemical properties largely intact.
- *Examples*: Prominent examples of plant disturbances include logging, windthrow (treefall), and epidemics caused by disease or herbivory—all of which primarily act by altering aboveground tree structures.

Combined (Discomposition)

- *Rykiel 1985 Definition*: Particular populations are selectively eliminated, reduced, added, or expanded.
- *Working Definition*: An *event* or *agent* that comprehensively alters plant composition, nutrient availability, and mean plant health.
- *Examples*: Prominent examples of combined disturbances include wildfire and geologic disturbances that initiate primary succession. These disturbances act by altering nutrients, habitat availability, and pre-disturbance tree composition.

While useful for understanding locally mediated biotic interactions, we acknowledge that many ecological disturbances do not cleanly fall into interference or destruction disturbance categories. Many disturbances, including windthrow and drought, have secondary implications for both nutrient availability and aboveground tree structures. We emphasise that categories are based on their primary mode of impact on forests—which has consequences for community assembly, successional trajectories, and the net effect of disturbance on local biotic interactions through recovery.

relative differences between conspecific and heterospecific effects on individual performance.

A central challenge with generalising the primary effects of disturbance on local interactions is that species do not monolithically respond to disturbance. Instead, individual performance in disturbed environments differs on life-history, stress tolerance, and functional trait axes (Lavorel et al. 1997), which together alter the apparent, allelopathic, and resource interactions generating local stabilising CDD in recovering communities (Brown et al. 2020; Pu et al. 2020; Zang et al. 2021). For example, fast-growing tree species benefit from increased light (Seidl et al. 2014) but are often more susceptible to natural enemies due to reduced investment in physical and chemical defences compared to slow-growing tree species (McCarthy-Neumann and Kobe 2008; Zhu et al. 2018; Zang et al. 2021). The strength of apparent, allelopathic, and resource interactions of fast-growing and slow-growing tree species may therefore vary with life-history strategies and functional traits through community assembly and recovery.

4.2 | Primary Effects of Disturbance on Local Stabilising CDD in Populations and Communities

While not central to our synthesis, we highlight that disturbances may also alter the effect of local stabilising CDD at the population and community scales by altering fitness hierarchies, selecting for closely-related species, and limiting conspecific densities (Figure 2B,C). Such factors at higher levels of ecological organisation likely influence the extent to which local stabilising CDD scales up to impact populations and communities, and we highlight Scale Transition Theory as a potentially useful framework for understanding the scaling of local CDD effects (Chesson 2012). Given that disturbances occur along variable spatial and temporal scales, creating complex feedbacks between individual-level processes and population-level outcomes, these factors are important considerations for future studies.

Local stabilising CDD is thought to stabilise populations that otherwise would not coexist due to intrinsic fitness differences, disadvantaging performance of otherwise dominant species and maintaining local diversity (Adler et al. 2007; Chesson 2000). As disturbances alter the availability of space and resources (nutrients, light, space, etc.), they likely confer competitive advantages to species with disturbance-adapted traits–thereby generating novel fitness hierarchies in multi-species communities (Figure 2B; Loehle 2000). The performance of disturbance-adapted species may be released from otherwise strong local stabilising CDD if disturbances accentuate intrinsic fitness differences.

Additionally, disturbed environments favour species that share similar adaptations—potentially increasing phylogenetic relatedness among recovering communities (Burns and Strauss 2011). Increased relatedness may affect the degree to which heterospecific apparent, allelopathic, and resource interactions influence conspecifics, and vice versa. For example, many tree-associated taxa (i.e., herbivores, mycorrhizal fungi,

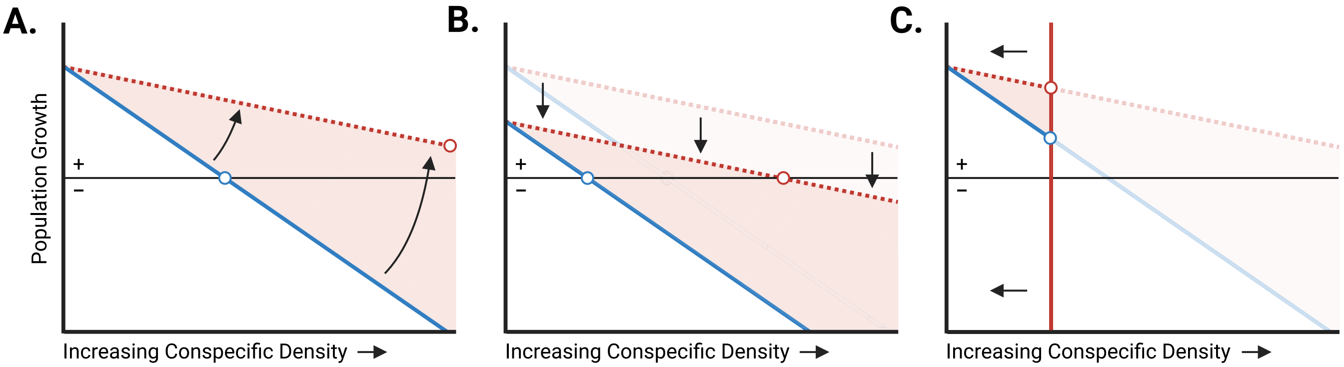

FIGURE 2 | Effects of disturbance on local stabilising CDD. Local stabilising CDD, arising from relatively host-specific interactions (Figure 1), is depicted here as the slope of the relationship between local population growth rate and local conspecific density (blue line). While not always negative (CDD < HDD), local stabilising CDD is often hypothesized to maintain species diversity by maintaining species abundances at equilibrium where sloped growth-density lines cross zero. We acknowledge that these slopes may be positive (CDD < HDD) but simplify to negative effects here for brevity. Disturbances may affect the relationship between conspecific density and population growth (A) by altering the relatively host-specific interactions generating local stabilising CDD. These may be small perturbations, or large to the point where population growth is no longer limited by density (no equilibrium abundance, red-dotted line). Disturbance-altered local CDD may be further affected by novel intrinsic fitness differences (B). Novel patterns of resource availability (light, space, nutrients, etc.) confer advantages to disturbance-adapted species and disadvantages for disturbance-sensitive species along functional trait and life history axes. Depicted is an average decline in fitness (population growth when conspecific density = 0, which decreases equilibrium abundance). Finally, repeat disturbance events or dramatic abiotic changes may reduce the effects of disturbance-altered local CDD on community dynamics by limiting conspecific densities (C; solid red line). Even if local stabilising CDD is strong, severely limited conspecific densities would reduce the effects of local CDD on recovery. Here, we focus on the effects of disturbance on the underlying drivers of local CDD (A), but acknowledge that disturbances may alter the intercept and population growth equilibriums while not interfering with the underlying relationship between conspecific density and population growth (B, C).

etc.) are clade or genera-specific (Novotny et al. 2002; Gilbert and Webb 2007), which can lead to stabilising density effects at higher taxonomic levels (e.g., con-mycorrhizal density dependence; Averill et al. 2022; Delavaux et al. 2023; Zhu et al. 2015). Generally, we expect that increased relatedness could strengthen local stabilising CDD by intensifying competitive interactions among related species—unless functional traits are uncorrelated with phylogeny (Bunker and Carson 2005; Mayfield and Levine 2010; Kraft et al. 2015).

Finally, disturbance-altered local stabilising CDD may have limited effects on community dynamics due to lower local densities following disturbances (Figure 2C; Kobe and Vriesendorp 2011). For example, strong local stabilising CDD may fail to influence populations or communities if disturbed conditions limit conspecific densities or interactions. Limited conspecific densities may have long-term consequences for community assembly driven by declines in relative host-specificity among interactions. Altered fitness hierarchies, phylogenetic relatedness, and limited conspecific densities are important considerations for examining local CDD at the population and community scales—but fall outside the scope of our synthesis, which is primarily focused on the underlying interactions generating local stabilising CDD in individual performance.

5 | Disturbance Severity and Biological Legacies

The effects of disturbance on ecological communities depend on the severity as well as the spatial and temporal regime of disturbance (Figure 3; Turner 2010). Disturbances range from spatially and temporally discrete (e.g., wildfire, hurricanes) to spatially and temporally ambiguous, often overlapping in time and space (e.g., nutrient deposition, extreme heat events, drought; Graham et al. 2021; Reyer et al. 2015). These spatial and temporal disturbance regimes likely have long-term consequences for local conspecific and heterospecific densities as well as fitness hierarchies defining the effects of local CDD on community structure (Comita and Stump 2020). Generally, we predict that high frequencies or severities of disturbance are expected to limit conspecific densities and select for stress-tolerant species that generate less stabilising conspecific density effects, thereby reducing the overall effect of local CDD on community assembly (Figure 3A,B; Vázquez and Simberloff 2002). Still, severity and frequency are not sufficient to explain variations of local CDD along abiotic gradients, as the category of disturbance (i.e., interference, destruction, combined) plays a significant role in determining community dynamics through recovery (Box 2).

Recovery and successional trajectories are frequently mediated by persisting abiotic properties, species compositions, and disturbance refugia—a phenomenon known as biological legacies or legacy effects (Bowd et al. 2021; Cuddington 2011; Jacquet and Altermatt 2020). Biological legacies are a primary pathway by which local stabilising CDD may persist following disturbance. For example, root structures of damaged or dead trees may provide important refugia for host-associated natural enemies and mutualists (Mayer et al. 2022), which remain able to influence performance among neighbouring conspecific individuals (Magee et al. 2024). Similarly, legacies of resource and allelopathic interactions may persist through disturbance and alter the recovery of both conspecific and heterospecific individuals. Thus, legacy effects are an important consideration for predicting local stabilising CDD through initial and late recovery.

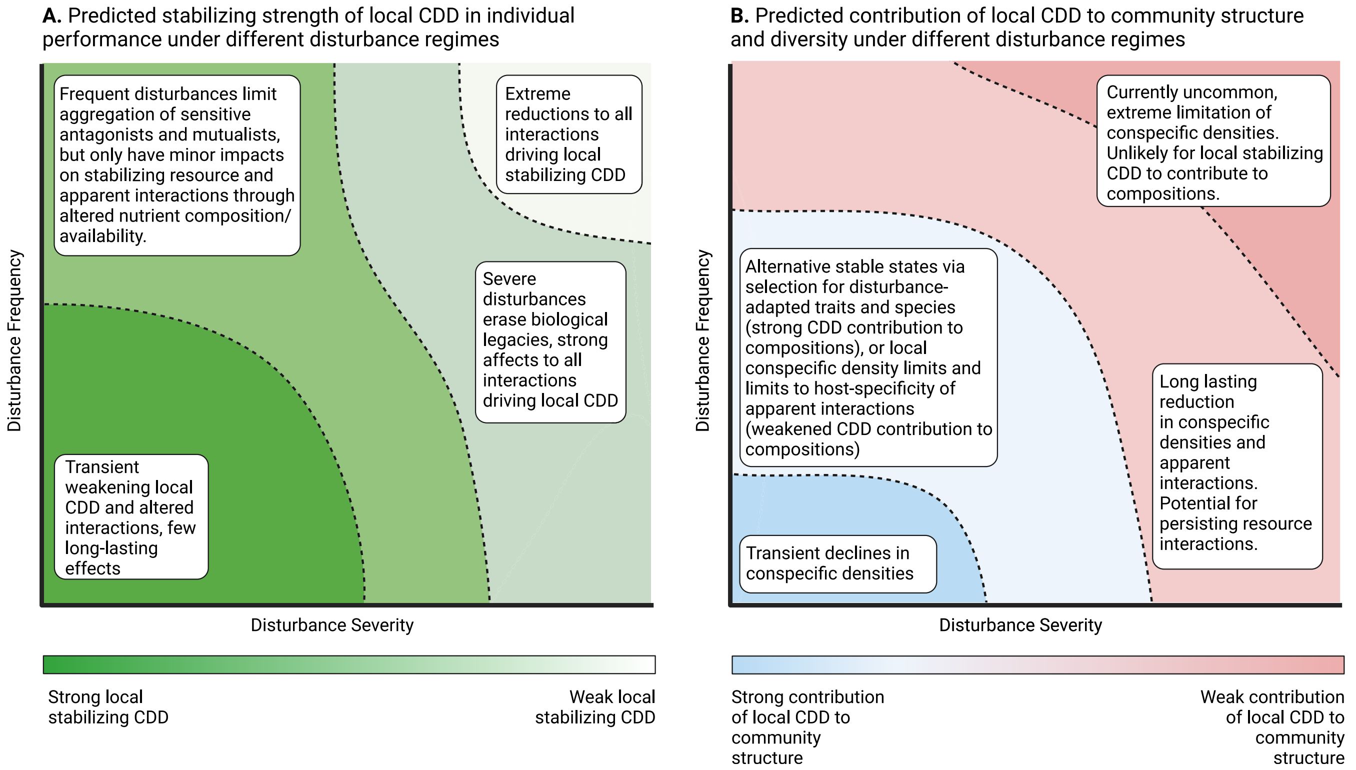

FIGURE 3 | Heatmaps of predicted impacts of disturbance regimes on the relative stabilising strength of local CDD (A), as well as the contribution of local CDD to patterns of community assembly (B). Disturbance regimes, defined as patterns of disturbance severity and frequency, are expected to generally reduce the stabilising effect of local CDD in individual performance as well as the contribution of local CDD to community structure and assembly (A). We predict that local stabilising CDD will generally decrease in strength (become less stabilising, green to white) with increasing disturbance severity and frequency. Along with disturbance effects on the stabilising strength of local CDD, we predict that increases to disturbance frequency and severity decrease the potential for local CDD to affect community structure and assembly (B). In red regions, we predict that local CDD is unlikely to overcome novel fitness hierarchies and/or local conspecific density limits.

In the following sections we discuss the implications of the three disturbance categories, interference, destruction, and combined, for local stabilising CDD (Figure 4). In each disturbance category we (1) synthesise studies of local CDD along observational or experimental abiotic gradients, (2) predict the generalisable effects of disturbance on local stabilising CDD, and (3) present a prominent disturbance example to explore CDD-disturbance relationships in more detail. In each example we further specify the implications of local stabilising CDD through initial and late recovery—highlighting gaps in knowledge and generating predictions where possible.

6 | Effects of Interference Disturbance on Local Stabilising CDD

Interference disturbances, which primarily alter abiotic conditions without immediately impacting tree species composition, are common and expected to increase in frequency and intensity over the next century (Box 2; Cook et al. 2018; Seidl et al. 2017). Initially, interference alters the availability and spatial heterogeneity of key limiting resources, such as water, nutrients, and light. Classic examples of interference include organic matter depletion (Federer et al. 1989), nitrogen deposition (Janssens et al. 2010), extreme rain events (Margrove et al. 2015), and drought. Given that many mechanisms driving local stabilising CDD are directly related to resource availability or are impacted by resource-related stress, we emphasise that interference may have strong cascading effects on local stabilising CDD in forest systems. To synthesise and highlight knowledge gaps, we focus on the primary effects and implications for recovery of a prominent natural interference disturbance: drought.

6.1 | Initial Effects of Drought on Local Stabilising CDD

The initial mechanism by which drought alters local interactions is by reducing water availability, which likely affects the negative apparent interactions driving local stabilising CDD. Moisture is a central requirement for the germination and dispersal of many pathogenic host-associated taxa (fungi, bacteria, oomycetes, etc.), and reduced moisture is associated with reduced pathogen loads and pathogen spread between conspecifics (Milici et al. 2020; Boczoń et al. 2021). However, pathogenic host-associated taxa and herbivores also induce mortality at higher rates in drought-stressed adult trees compared to controls (Anderegg et al. 2016; Bell et al. 2020; Caldeira 2019; Gely et al. 2020; Oliva et al. 2014). To date, most relevant studies of local stabilising CDD have focused on small observational or experimental reductions in precipitation, finding that local stabilising CDD weakens, even to the point of becoming destabilising, with decreasing precipitation (Figure 4A; Bachelot et al. 2020; Jiang et al. 2024; Lebrija-Trejos et al. 2023;

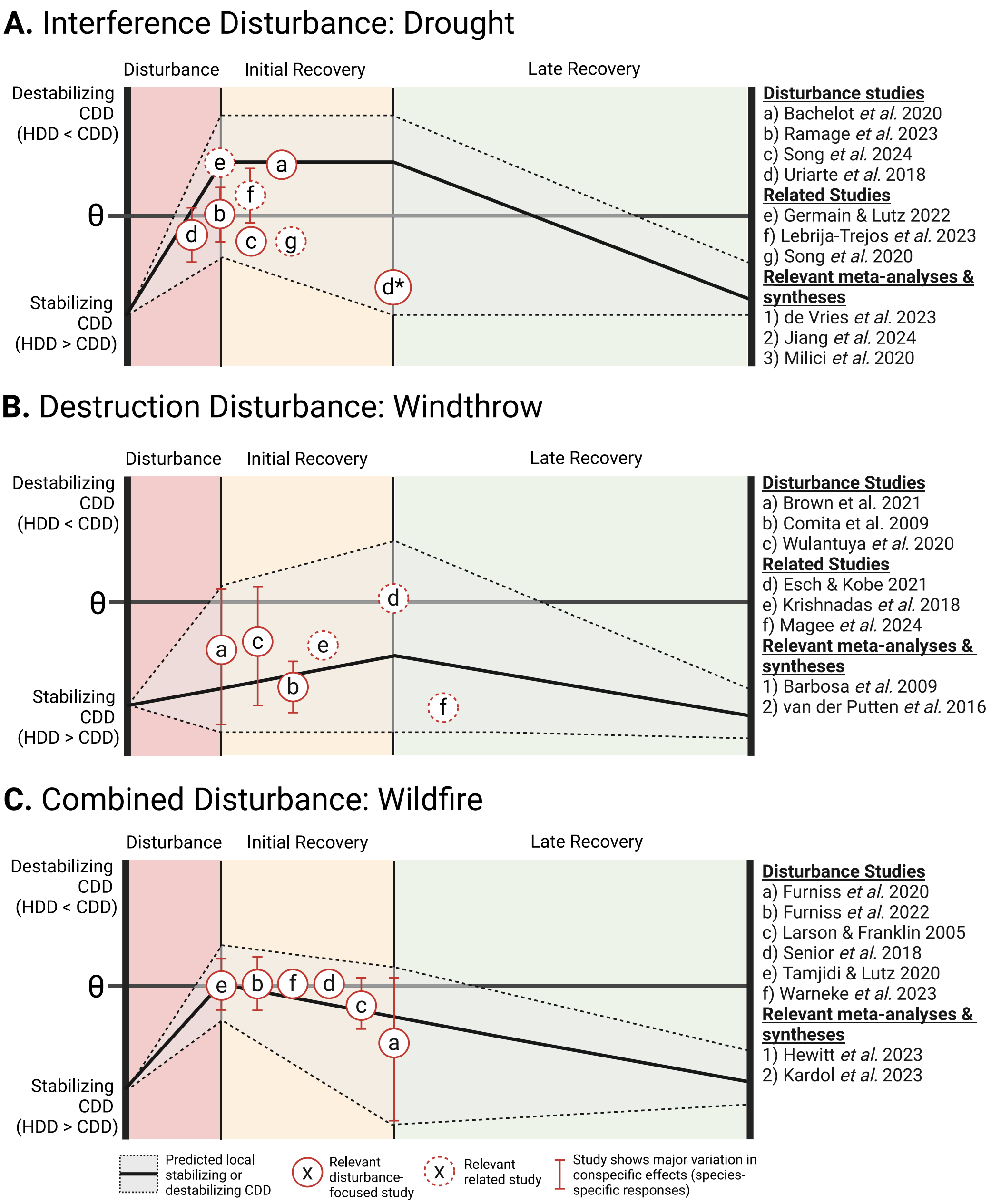

FIGURE 4 | Predicted primary effects of (A) interference, (B) destruction, and (C) combined disturbances on local stabilising CDD, and implications through short and long-term recovery. Disturbances have category-specific effects on the underlying drivers of local stabilising CDD: Apparent, allelopathic, and resource interactions, which may lead to category-specific strength and directionality of local stabilising CDD through various stages of recovery. For each disturbance category, the black line represents our predictions for the relative strength and directionality of local CDD through disturbance and recovery. Grey shaded areas correspond to our relative confidence in predicted effects and highlight areas where more study is warranted. To formulate these predictions (and confidence intervals) we rely on selected studies of disturbance and environmental change across plant–soil feedback, conspecific density dependence, and frequency dependence literature. Letters correspond to specific studies on the right of each panel and are offset from one another for visual clarity—not to indicate relative differences in study timeline. When few empirical studies were available, we relied on related studies of conspecific density effects across changing environmental conditions to generate our predictions. These relevant non-disturbance studies are outlined in a dashed-line circle instead of a solid-line circle. If the selected study found evidence for both positive and negative (destabilising and stabilising) effects, we included a red confidence interval to highlight uncertainty. Uriarte et al. (2018) find weakened conspecific density effects in dry years (Panel A, study D) and enhanced conspecific density effects at dry sites (Panel A, study D*). Additionally, our predictions were informed by several meta-analyses and syntheses which we include on the right side of each panel. We acknowledge that in certain systems local CDD begins as destabilising but opt to begin our predictions at the most common observation: Strong stabilising CDD (CDD < HDD).

Milici et al. 2025; Ramage et al. 2023; Song et al. 2020; Song et al. 2024; Uriarte et al. 2018). There remain uncertainties over the degree to which this trend is generalisable across functional traits and life histories, and how drought severity and recovery timelines impact local stabilising CDD (Bachelot et al. 2015; Milici et al. 2020).

Key to understanding drought effects on local stabilising CDD is the relative impact of reduced water availability on the abundance of host-specific natural enemies relative to generalists. Certain tree-associated pathogenic microorganisms are more protected from drought, including endophytic pathogens which colonise intercellular apoplastic spaces. Other pathogenic microorganisms, such as externally attached epiphytic pathogens, are likely more drought sensitive (Sohrabi et al. 2023). Little is known of the relative host-specificity of epiphytic and endophytic pathogens associated with tree roots (Barrett and Heil 2012), and our understanding is complicated by microorganisms that switch from pathogenic to mutualistic, and endophytic to epiphytic, over life stages (Redman et al. 2001).

General support for weakened local stabilising CDD, or even local destabilising CDD, under drought conditions may be caused by increasing effects of mutualistic interactions paired with declines in pathogen spread between conspecifics (Milici et al. 2020). For example, mycorrhizal fungi and leaf endophytes both confer drought tolerance by providing physical protections against water loss and pathogen infection as well as upregulating exchange of mineral ions and water (Augé et al. 2015; Püschel et al. 2021). Strong destabilising apparent interactions with mutualists may therefore contribute to weaker local stabilising CDD immediately following drought (Figure 4A; Bachelot et al. 2015; de Vries et al. 2023). Additionally, relative differences in host-specificity among mycorrhizal fungal types and leaf endophytes, along with functional trait variety in tree hosts, may underlie species-specificity in initial drought effects on local stabilising CDD (Lebrija-Trejos et al. 2023; Liu and He 2022; Ramage et al. 2023; Song et al. 2021; Uriarte et al. 2018).

For example, the contribution of mycorrhizal fungi to local stabilising CDD under drought likely varies between dominant eco-physiological types: ectomycorrhizal (EcM) and arbuscular mycorrhizal (AM; de Vries et al. 2023). AM fungi form arbuscules within root cell walls and therefore are thought to be more drought resistant than EcM fungi, which form sheaths around root structures and between root cells (Osonubi et al. 1991; Wu and Zou 2017; Kilpeläinen et al. 2017). AM fungi are also thought to be less relatively host-specific than EcM fungi; therefore, they contribute less to local stabilising CDD (Laliberté et al. 2015). Local stabilising CDD may be disproportionately weakened in EcM trees relative to AM trees under drought, although the degree to which mycorrhizal type alters drought tolerance and recovery timelines remains uncertain.

Along with apparent interactions, the ratio of intraspecific to interspecific competition under drought appears to vary, likely contributing to local destabilising CDD in some cases (Gazol and Camarero 2016; Lin et al. 2012), and local stabilising CDD in others (O'Brien et al. 2017; Jourdan et al. 2020). These context dependencies are likely a product of novel fitness hierarchies under drought (Castagneri et al. 2022; Hommel et al. 2016). For example, species with disturbance-adapted traits may experience stronger stabilising effects as spatially aggregated conspecifics compete for increasingly limited water and mobile soil nutrients. Future studies should consider interactions between intraspecific competition, functional traits, and the implications of reduced plant defences under drought conditions as factors affecting the strength and directionality of local stabilising CDD.

6.2 | Effects of Drought on Local Stabilising CDD Through Late Recovery

As forest communities recover from drought, increased adult mortality rates open forests canopies and reduce microclimatic buffering—increasing sub-canopy temperatures and incident radiation levels (Hanson and Weltzin 2000). Increased temperatures may be particularly relevant for early ontogenetic stages such as seedlings, where local stabilising CDD effects on performance are generally strongest (Comita et al. 2014; Song et al. 2021). Among seedlings, there appears to be no generalizable effects of warming on local stabilising CDD (Table 1; Bachelot et al. 2020; Germain and Lutz 2022; Liu and He 2021; Song et al. 2018). Disparity among prior studies may point to nonlinear functional responses to drought depending on the intensity of warming. For example, Bachelot et al. (2020) find evidence for increased survival for conspecific seedlings under strong warming (4°C) while Liu and He (2021) find decreased survival for conspecific seedlings under weaker warming conditions (1.2°C ± 0.5°C). There also appears to be a role for functional traits (Song et al. 2021) and tolerance among host-associated taxa (Liu and He 2022) in mediating warming effects on local CDD.

Beyond warming effects, the relative strength of apparent, allelopathic, and resource interactions through late recovery remains largely underexplored. Uriarte et al. (2018) found evidence for stabilising local CDD in dry tropical sites, but not for wet tropical sites under drought conditions, which may indicate that short- and long-term drought have different implications for community assembly. Reduced plant defences under drought may persist through late recovery (Xu et al. 2010), increasing the stabilising effect of antagonists. Reduced defences may also contribute to increased stabilising apparent interactions through the proliferation of secondary antagonists that specifically target weak, stressed trees (Jactel et al. 2012). However, decreased defences may not always translate to stronger stabilising effects, such as when reduced production of negative allelopathic compounds weakens local stabilising CDD in regenerating seedlings (Hasanuzzaman et al. 2013). Moreover, the implications of weakened tree defences and additional secondary antagonists for local stabilising CDD may or may not be additive and may vary between leaf and root structures where drought severity and recovery timelines also vary (Milici et al. 2020; de Vries et al. 2023). We highlight interactions between reduced defences, reduced allelopathy, and increased virulence of primary and secondary antagonists as important considerations for future studies assessing local stabilising CDD under drought.

6.3 | Predictions and Gaps for Local Stabilising CDD and Interference Disturbances

Interference disturbances are thought to have wide-ranging implications on the underlying apparent, allelopathic, and resource interactions driving local stabilising CDD. We predict that local CDD becomes generally destabilising following interference and returns to stabilising as recovery progresses (Figure 4A). There are several important limitations to our predictions. First, most studies of local CDD under interference rely on short-term variations or seasonal differences in precipitation, nutrients, and temperature and disproportionately examine seedling mortality in tropical systems (Table 1). Interference effects may be limited among seedlings when nearby canopy adults buffer against macroclimatic extremes (de Frenne et al. 2021), an effect which may only erode under severe interference (Davis et al. 2019). Studies of interference under buffered canopies may miss critical interactions with light availability, warming, and seedling performance that only emerge when disturbance is severe or prolonged. Second, recovery from interference involves factors that may not be present following short-term interference, including secondary antagonists and compound disturbance events (e.g., insect outbreaks following wildfire; Gely et al. 2020; Littell et al. 2016). Additionally, functional trait and life history variety among individuals in local communities is likely to modulate the effects of interference on local stabilising CDD, although this has received relatively little attention in the literature. We emphasise the need for observational and experimental studies of population dynamics under severe and long-term interference to increase our confidence in predicting future community responses to drought and other interference disturbances.

7 | Effects of Destruction Disturbance on Local Stabilising CDD

Destruction disturbances primarily alter plant competitive densities, compositions, and conditions, while having limited initial effects on nutrient and chemical properties (Box 2). Destruction disturbances are highly variable in spatial scale, ranging from local windfall events or pathogen infections that create patches of downed trees to landscape-scale destructive disturbances such as hurricanes or massive pathogen outbreaks. Destruction disturbances are often associated with biological legacies in the form of remnant trees, residual organisms (e.g., microbes, herbivores), propagules, and abiotic conditions (e.g., allelopathy, spatial resource patterns) influenced by previous plant compositions (Johnstone et al. 2016). To date, the degree to which destruction and biological legacies interact to influence local stabilising CDD remains largely unstudied. Chan et al. (2023) simulate that local stabilising CDD may be relatively unaffected by destruction disturbance if legacies of conspecific density are strong. Magee et al. (2024) corroborate this prediction, finding that local stabilising CDD among adult trees remains strong and even becomes more stabilising when individual mortality events are considered. Still, others find that biological legacies may erode quickly after destruction disturbances—or even flip from stabilising to destabilising (Figure 4B; Brown et al. 2021; Esch and Kobe 2021). To synthesise and highlight knowledge gaps, we focus on how local stabilising CDD responds both in initial and late recovery from a prominent destruction disturbance: windthrow.

7.1 | Initial Effects of Windthrow on Local Stabilising CDD

Windthrow generates canopy gaps and structural heterogeneity, reducing host availability and indirectly altering resource environments (Ulanova 2000). To date, few studies have focused explicitly on local stabilising CDD in gaps despite their ubiquity and potential to affect forest structure (but see Brown et al. 2021; Comita et al. 2009; Wulantuya et al. 2020). For species with root functional traits conferring resistance to wind damage, such as deep root systems or roots that spread laterally into regions of dense soil (Dupuy et al. 2005; Ray and Nicoll 1998), windthrow may increase the ratio of intraspecific resource competition relative to interspecific competition. Shared functional traits and life history strategies among wind-resistant trees may translate to increased intraspecific competition for limiting resources—although these effects may be muted by an overall release from competitive interactions.

We predict that windthrow effects on local stabilising CDD through initial recovery largely depend on the spatial patterns and scale of disturbance. Small windthrow events, where atmospheric and light conditions remain relatively unchanged, likely maintain stronger biological legacies (Sicoe et al. 2023). In contrast, larger events may create edge-like conditions where local stabilising CDD is typically weaker (Krishnadas et al. 2018). Patch connectivity further influences these dynamics—larger and more connected patches maintain more diverse communities of host-specific organisms (Johnstone et al. 2016), while the arrangement of fallen trees can create corridors or barriers affecting organism movement between patches (Franklin et al. 2000). In areas with numerous canopy gaps, Brown et al. (2021) found that local CDD varied from stabilising to neutral to destabilising among sapling species—potentially pointing to the importance of functional traits in determining disturbances responses. Wulantuya et al. (2020) found similar functional variety, with shade-tolerant trees experiencing more stabilising local CDD in gaps relative to shade-intolerant species. We expect small-scale windthrow disturbances to have limited initial effects on the apparent and allelopathic interactions contributing to local CDD. Allelopathic compounds likely persist in relatively unaltered soils, particularly where fallen trees create dense patches of woody debris. Similarly, apparent drivers of local stabilising CDD, such as microbial communities and herbivores, likely persist in undisturbed soils and gap refugia (Seidl et al. 2014).

7.2 | Effects of Windthrow on Local Stabilising CDD Through Late Recovery

The persistence of biological legacies of local stabilising CDD through recovery likely depends on system-specific decomposition and nutrient cycling rates (Johnstone et al. 2016; Ke and Levine 2021). For example, microbial compositions appear to quickly match pre-disturbance compositions in some systems (Mayer et al. 2022), and follow priority effects towards alternative stable states in others (Jacquet and Altermatt 2020; Miller et al. 2021). Rapid turnover may contribute to findings that legacies of local stabilising CDD in seedling mortality erode rapidly following destruction (Esch and Kobe 2021). However, legacies of local stabilising CDD may persist longer in adults, particularly after small-scale individual mortality events (Magee et al. 2024). Since successional stages are correlated with distinct microbial compositions (Liang et al. 2022), future studies of local stabilising CDD following destruction disturbance should consider life and successional stages, microbial priority effects, and system-specific turnover rates.

Late recovery following windthrow disturbance is characterised by increased light availability and radiation and decreased moisture and microclimatic buffering (Mitchell 2013), which likely reduces the abundance and spread of natural enemies—and may amplify the effects of mutualists on individual performance (Wulantuya et al. 2020). Locally dry and hot conditions, coupled with mechanical damage, likely increase the susceptibility of trees to secondary antagonists (Bouget and Duelli 2004), which could strengthen local stabilising CDD. Ultimately, we expect that correlated changes to abiotic conditions and apparent interactions will have significant implications for remnant tree health and local stabilising CDD through recovery.

During long trajectories of recovery, repeated windthrow events can promote structural complexity, which may have emergent effects on local stabilising CDD at both individual and community scales. Windthrow-generated structural heterogeneity can persist for extended periods (Ulanova 2000; Marra et al. 2014), creating diverse microhabitats that promote local diversity and could contribute to stronger local stabilising CDD. However, repeated windthrow events may also limit conspecific densities and reduce the effects of local CDD on community dynamics (Kobe and Vriesendorp 2011). We emphasise that structural heterogeneity, biological legacies, and microclimatic conditions generated by windthrow are all important factors to consider when assessing local stabilising CDD in destruction-disturbed forests.

7.3 | Predictions and Gaps for Local Stabilising CDD and Destruction Disturbances

Destruction disturbances present interesting opportunities for studying how biological legacies and spatially heterogenous disturbance patterns affect local stabilising CDD. We predict that local CDD may initially remain strongly stabilising following destruction disturbances, especially if injured trees enhance the stabilising effect of antagonists and intraspecific competition (Figure 4B). As recovery progresses, we predict that strong legacies of local CDD may slowly weaken as abiotic conditions become less favourable to tree-associated microbiomes and new spatial patterns of tree hosts emerge. Several important knowledge gaps remain. First, the relative importance of biological legacies versus remnant-tree populations in maintaining local stabilising CDD following destruction is poorly understood. Second, the spatial scale at which destruction affects local stabilising CDD requires further study, particularly how the size and distribution of gaps influences apparent interactions (Brown et al. 2021). Finally, the interaction between destruction and other disturbances (e.g., insect outbreaks triggered by damaged trees) may have complex effects on local stabilising CDD that warrant investigation. To address these gaps, we highlight the need for long-term studies and experimental manipulations of the interactions between gap size, biological legacies, and local stabilising CDD following destruction disturbance.

8 | Effects of Combined Disturbance on Local Stabilising CDD

Combined disturbances are defined as ecological disturbances with initial effects on abiotic conditions as well as plant densities, compositions, and/or mean plant condition (Box 2). In forests, combined disturbances alter the physical structure and composition of trees, soil properties, and the nutrient-cycling processes that define community structure and function (Huston 2014). Many combined disturbance events, such as wildfires, are increasing in frequency, extent, and intensity with climate change (Ellis et al. 2022). To date, little is known about how combined disturbances interact with local stabilising CDD. The prevailing paradigm is that combined disturbances decrease the relative importance of biotic interactions relative to functional traits and abiotic conditions (Hollingsworth et al. 2013; Kardol et al. 2023). In the following section, we highlight how this paradigm may be useful—and yet insufficient—to explain conspecific density effects in combined disturbance settings using a prominent example: wildfire.

8.1 | Initial Effects of Wildfire on Local Stabilising CDD

Wildfires initially induce tree mortality through combustion and lethal tissue temperatures, reducing conspecific densities and surging nutrient availability, particularly in the form of pyrogenic carbon (Bodí et al. 2014). Reduced conspecific densities, altered nutrient availability, and mortality among organisms generating stabilising or destabilising apparent interactions appear to generally neutralise local stabilising CDD (HDD = CDD; Figure 4C; Senior et al. 2018; Warneke et al. 2023). Influxes of pyrogenic carbon associated with wildfires can also neutralise allelopathic compounds (Zackrisson et al. 1996), potentially reducing the stabilising effect of negative allelopathy on local CDD. However, species-specific susceptibility to wildfire and the conditions created by the post-fire environment challenge generalisations (Furniss et al. 2022; Tamjidi and Lutz 2020). For example, wildfire likely reduces stabilising resource interactions by increasing resource availability, which may advantage the performance of fire-adapted species (such as those with functional advantages to survival in high-light, low moisture environments) over fire-susceptible species (Andreu et al. 2001; Burkle et al. 2015; Spasojevic et al. 2016). However, relative intraspecific competition among fire-adapted species and increased phylogenetic relatedness in the post-fire environment may intensify local stabilising CDD through initial recovery.

Along with altered abiotic conditions and spatial patterns of nutrient availability, wildfires also have primary effects on belowground microbial communities of natural enemies and mutualists that drive apparent interactions between conspecific individuals. Increased nutrient availability and decreased allelopathic chemical concentrations following wildfire generally result in saprotroph-dominated fungal communities (Hewitt et al. 2023; Rodriguez-Ramos et al. 2021). Much remains uncertain surrounding the effects of wildfire on soil microbial communities that influence plant performance, including the degree to which wildfires impact host-specific antagonists relative to generalist antagonists and whether dead, remnant wood (e.g., debris and standing snags) provides refugia for host-specific antagonists (Senior et al. 2018; Warneke et al. 2023). Among mutualists, ectomycorrhizal fungi are thought to be disproportionately susceptible to wildfire-induced mortality due to external root sheathing (Dove and Hart 2017; Mirzaei et al. 2023). Therefore, ectomycorrhizal trees may experience more stabilising local CDD than pre-fire conditions—although these effects would be muted in community assembly if coupled with dramatic reductions in conspecific densities (Figures 3B and 4C).

8.2 | Effects of Wildfire on Local Stabilising CDD Through Late Recovery

Limited studies indicate that the effects of conspecific adult density on community assembly through recovery are species- and context-specific (Furniss et al. 2020; Larson and Franklin 2005). Context-specificity may arise due to system-specific soil compositional changes, such as erosion, compaction, and changing nutrient abundances along with biological legacies (Bowd et al. 2021). Additionally, wildfire-produced charcoal from different tree species can have unique structural and chemical traits (Pluchon et al. 2015) that may have consequences for spatial relationships between conspecific densities and nutrient availability through recovery. Moreover, context-specific nutrient availability likely mediates novel spatial patterns of host-specific antagonists and mutualists (Hewitt et al. 2023; Pulido-Chavez et al. 2021) in ways that may alter local stabilising CDD (Furniss et al. 2022).

We predict that some species-specificity in local stabilising CDD through long-term recovery from wildfire arises from emergent effects of phylogenetic relatedness and shared tree-associated taxa. For example, ectomycorrhizal fungi are more likely to disperse, establish, and thrive in burned areas relative to other tree-associated fungi that lack the ability to decompose organic matter (Day et al. 2020). If post-fire communities are closely phylogenetically related and associate with ectomycorrhizal fungi, then local stabilising CDD may be weak or destabilising through recovery. To date, studies of microbial function and compositional changes following wildfire indicate a wide spectrum of resiliency among functions of the microbiome (e.g., nutrient cycling), and long-lasting priority effects on microbial community structure (Hewitt et al. 2023; Pérez-Valera et al. 2020). We emphasise that understanding changes to the tree-associated microbiome through late recovery is essential to estimating the strength and role of local stabilising CDD.

8.3 | Predictions and Gaps for Local Stabilising CDD and Combined Disturbances

Combined disturbances present unique challenges for understanding local stabilising CDD due to their simultaneous effects on conspecific densities and abiotic conditions. We predict that local stabilising CDD is initially neutralised following most combined disturbances, which reduce conspecific densities and remove biological legacies (Furniss et al. 2022; Tamjidi and Lutz 2020; Senior et al. 2018; Warneke et al. 2023). Through late recovery, the strength and direction of local stabilising CDD likely depend on interactions between pyrogenic carbon, disturbance refugia, and the success of antagonists relative to mutualists in colonising disturbed sites (Furniss et al. 2020; Larson and Franklin 2005). Several critical knowledge gaps remain. First, the relative host-specificity of early-colonising microbes following combined disturbances, and their effects on remnant tree hosts, requires further study (Nelson et al. 2022). Second, the degree to which novel nutrient compositions alter apparent and allelopathic interactions through initial and later recovery remains poorly understood. Finally, the severity and spatial heterogeneity of combined disturbance may create complex mosaics of local stabilising CDD with unpredictable or emergent effects at population and community scales. We emphasise that research should focus on long-term studies across gradients of severity and incorporate the effects of refugia and successional trajectories on local stabilising CDD.

9 | Special Considerations for CDD-Disturbance Dynamics

9.1 | Biological Invasion

A related conservation concern associated with ecological disturbances is the establishment and proliferation of naturalised taxa. Ecological disturbances open niche space and alter fitness hierarchies, priming disturbed areas for invasion (Hobbs and Huenneke 1992; Lembrechts et al. 2016). This is reflected in the life histories and functional traits of many prominent naturalised plants, which thrive in high-light, low-nutrient disturbed environments. The potential effects of invasion on local stabilising CDD have received relatively more attention in the literature than the drivers of ecological disturbance discussed here (*see* Klironomos 2002; Mitchell et al. 2006; Reinhart and Callaway 2006; Sullivan et al. 2017; Taylor and Hastings 2005). Much like interference disturbances, biological invasions alter interactions between trees and their surrounding environment. Invading taxa are often released from natural enemies, negative resource interactions, and negative allelopathic interactions, and therefore are expected to exhibit destabilising CDD (enemy-release hypothesis; Williamson 1996; Williams and Levine 2018). However, enemy release likely correlates with mutualist release, a potential limit to local diversity (Delavaux et al. 2024). Future studies of the enemy-release hypothesis in the context of local stabilising CDD could shed light on the degree to which invasion success is mediated by the underlying drivers of local CDD and the role of functional similarity or phylogenetic relatedness in driving invasion patterns.

9.2 | Temporal Variation and Climate Change: A Split Perspective

We know little about how novel disturbance regimes under climate change may affect the strength and role of local stabilising CDD. Warming and novel disturbance regimes are likely to increase average physiological stress and phenological mismatches (Keeler et al. 2021), potentially weakening the underlying drivers of local stabilising CDD and generating cascading negative impacts on species diversity, productivity, and carbon storage (Broekman et al. 2019; Germain and Lutz 2022). Additionally, increasing interannual climate variability may weaken local stabilising CDD by exposing individuals to novel and extreme abiotic conditions (Germain and Lutz 2020). However, there remains the possibility that warming and altered climatic regimes may benefit pathogens driving local stabilising CDD (Delgado-Baquerizo et al. 2020; Pugnaire et al. 2019), as well as the possibility that species with similar functional traits (i.e., 'winners' of climate change) may contribute to communities where intraspecific competition is disproportionately strong (de Bello et al. 2021). Predictions of forest composition and diversity under future climate scenarios should consider how stabilising factors like local CDD may mediate community responses to a rapidly changing world.

10 | Conclusions

Understanding how ecological disturbances influence the organisms that interact to generate local stabilising CDD is critical to understanding individual performance, population growth, and local diversity across spatial and temporal scales. Our synthesis reveals that different categories of disturbance—interference, destruction, and combined—have distinct implications for the underlying drivers of local stabilising CDD and their ability to influence community assembly. While interference disturbances weaken local stabilising CDD and even generate destabilising CDD, destruction disturbances may maintain stronger biological legacies of local stabilising CDD, and combined disturbances often neutralise local stabilising CDD entirely. Moving forward, empirical studies that integrate local stabilising CDD within broader ecological frameworks of disturbance and recovery will be essential for predicting community responses to novel disturbance regimes. Particular attention should be paid to species-specific responses, spatial heterogeneity of disturbance effects, and the persistence of biological legacies through recovery—all of which may fundamentally alter how local biotic interactions contribute to maintaining species diversity in an era of accelerating global change.

Author Contributions

C.J.D. and J.A.L. conceived the ideas. C.J.D. wrote the first draft of the manuscript, and both 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 analysed for the current study.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70118.

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