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Research

Scale-dependent effects of conspecific negative density dependence and immigration on biodiversity maintenance

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Conspecific negative density dependence (CNDD) has been highlighted as a main driver of biodiversity maintenance. However, while there is general consensus on the scale-dependent and interacting nature of ecological processes, there is limited knowledge about the relative importance of CNDD across spatial scales and on its interaction with other processes, such as dispersal and immigration. While many studies have detected CNDD at local scales, it remains unknown whether its effects on biodiversity maintenance scale-up to landscapes and regions. Here, we use a generic dynamic and spatially-explicit simulation model to assess the interacting relative effects of local-scale CNDD and immigration from a metacommunity for biodiversity maintenance across spatial scales. For this purpose, we systematically varied immigration rates, the average strength and the variation of CNDD among species. We found that CNDD only determined species richness in strongly isolated communities with little or no interspecific variation in CNDD. In closed communities, plausible interspecific variation in CNDD led to a strong reduction in species richness. In open communities, realistic levels of immigration overwhelmed the effects of CNDD on diversity maintenance. From these results, we suggest that local CNDD is unlikely to be a main driver of biodiversity in real communities, especially at larger spatial scales. This study provides a first step towards improved integration of local-scale coexistence theory with large-scale metacommunity theory and highlights the importance of considering the interacting and scale-dependent nature of ecological processes.

Keywords: coexistence theory, immigration, interspecific variability, Janzen–Connell effect, metacommunity, scale dependence, spatial simulation model, species richness, species–area relationship, stabilizing mechanism

Introduction

Understanding the maintenance of biodiversity, especially in species-rich communities, such as tropical forests, grasslands and coral reefs, remains an area of interest and intense debate (Ricklefs 2015, Terborgh 2015). A large number of hypotheses

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have been levied to explain how species coexist and biodiversity is maintained (reviewed by Pianka 1966, Chesson 2000, Wright 2002, Willig et al. 2003, Fine 2015), including macroevolution and biogeographical processes (Ricklefs 1987, Wiens and Donoghue 2004) as well as local ecological processes, such as disturbances (Connell 1978), trophic interactions (Janzen 1970, Connell 1971) and resource competition (Tilman 1982). Importantly, the relative importance of different processes has been hypothesized to depend critically on the spatio–temporal scales in which observations are made. Ecological processes are thought to influence diversity maintenance at smaller scales, whereas historical biogeographic processes influence diversity at larger scales (Shmida and Wilson 1985, Turner and Tjørve 2005, Jetz and Fine 2012). Despite the clear recognition of the importance of scale for biodiversity patterns and processes, many studies still investigate the importance of a given process for biodiversity at a single and typically rather small scale, and then extrapolate the results found to biodiversity maintenance in general (i.e. across scales).

Here, we focus on the question of whether considering the spatial scale of biodiversity measurements (i.e. the sampling area) might change our perspective on a particular class of coexistence mechanisms that are jointly characterized by an increase of conspecific negative density dependence (CNDD) relative to heterospecific negative density dependence (HNDD). The increase of CNDD relative to HNDD results in a negative relationship between the average fitness of a species and its relative abundance. This demographic pattern is called negative frequency dependence and can foster the long-term coexistence of species (Chesson 2000, Adler et al. 2007).

An increase of conspecific relative to heterospecific density dependence can emerge from several ecological mechanisms, including high resource competition between conspecifics (Tilman 1982), as well as host specific consumers or pathogens (Janzen 1970, Connell 1971), including plant–soil feedbacks (Bever 2003, Mangan et al. 2010). These mechanisms act primarily when there are short distances between focal individuals and are thus considered as local-scale processes. Many previous studies refer to CNDD as driver of diversity maintenance, but implicitly focus on the ratio between CNDD and HNDD (Johnson et al. 2012, LaManna et al. 2017, Stump and Comita 2018). To keep terminology simple, we follow this convention and use the term CNDD to refer to a relative increase of CNDD versus HNDD.

There is ample empirical evidence for the occurrence of CNDD in tropical forests (Comita et al. 2010, Mangan et al. 2010, Bagchi et al. 2014, LaManna et al. 2017), temperate forests (Packer and Clay 2000, Johnson et al. 2012), grasslands (Petermann et al. 2008, Maron et al. 2016) and coral reefs (Marhaver et al. 2013). In addition, theory shows that CNDD can maintain high diversity in closed communities without immigration (May et al. 2009, Levi et al. 2019). The empirical support for local-scale CNDD is often considered as implicit evidence that the mechanisms behind CNDD are also important drivers of biodiversity maintenance at larger spatial scales. However, recent syntheses emphasized the large gap between demonstrating the existence of CNDD in a local neighbourhood versus understanding its consequences for diversity maintenance at larger spatial scales (Terborgh 2012, Comita et al. 2014). Yet, we do not know if and how local CNDD mechanisms (typically operating at neighbourhoods of meters) scale up to allow the coexistence of a large number of species at larger scales (e.g. tens to hundreds of hectares).

Hubbell et al. (2001), for example, argued that local-scale CNDD may not be sufficient to influence community wide patterns in tree composition. Recently, studies have shown that realistic degrees of interspecific variation in CNDD can drastically reduce diversity maintenance compared to scenarios where CNDD is equal for all species (Miranda et al. 2015, Stump and Comita 2018), since species with strong CNDD face a competitive disadvantage relative to species with low CNDD.

There is also limited knowledge of how local CNDD interacts with other diversity maintenance processes. From the perspective of metacommunity ecology (Leibold and Chase 2017), CNDD will interact with spatial processes such as dispersal, immigration and source–sink dynamics. The joint and interacting consequences of spatial processes and local-scale CNDD for the maintenance of species richness, however, are poorly understood. Specifically, while there is strong theoretical and empirical evidence for the importance of both CNDD (Adler et al. 2010, LaManna et al. 2017) and dispersal (Mouquet and Loreau 2003, Cadotte 2006) when considered in isolation, each process influences local diversity differently. Thus, it remains to be known which proportions of local diversity are maintained by local-scale CNDD one the one hand and by species immigration due to mass effects and source–sink dynamics on the other hand.

Few empirical studies have explicitly linked CNDD mechanism to coexistence and diversity maintenance, but most have been conducted at relatively small spatial scales (e.g. less than 1–100 m^2) (Wills et al. 2006, Levine and HilleRisLambers 2009, Adler et al. 2010, Mangan et al. 2010, Bagchi et al. 2014). At least two recent studies have suggested evidence for a relationship between local CNDD and large-scale biodiversity patterns in forests (Johnson et al. 2012, LaManna et al. 2017), but both are intensively debated with respect to unresolved methodological issues (Chisholm and Fung 2018, Hülsmann and Hartig 2018, Detto et al. 2019). While some theoretical studies have directly addressed the link between CNDD and community diversity, they were agnostic towards scale (Chisholm and Muller-Landau 2011, Yenni et al. 2012), focussed on a single scale (Adler and Muller-Landau 2005), or ignored interactions of CNDD with other potential processes of diversity maintenance (Levi et al. 2019).

Accordingly, the main goal of our study is to assess the relative effects of local-scale CNDD versus immigration from a metacommunity on the maintenance of species richness across spatial scales (i.e. across different sampling areas of biodiversity measurements). One possibility to address the scale-dependent consequences of interacting dynamic processes is to use spatially-explicit and individual-based simulation models (Brown et al. 2011, May et al. 2015). Here, we extend and use such a model that has been parameterized by field data from tropical forests (May et al. 2015, 2016) to address our research questions. We incorporated CNDD into the model by simulating recruitment success (i.e. the probability of establishment of new tree individuals) as a function of the distance and the density of con- and heterospecific adult neighbours. We consider two main scenarios in the simulations:1) isolated communities without immigration, and 2) open communities with different levels of immigration from a metacommunity. The metacommunity is modelled using a stable species composition, which assumes that mechanisms other than CNDD maintain diversity at the metacommunity scale, such as speciation (Hubbell 2001) and/or species sorting along environmental gradients (Whittaker 1962, Chase and Leibold 2003).

Overall, we found that the importance of CNDD for diversity maintenance strongly depended on immigration rates into a local community and on the spatial scale on which diversity was measured (ranging from 25 m^2 to 100 ha in this study). In isolated communities, CNDD completely maintained biodiversity and its effects increased with spatial scale. In contrast, in open communities immigration easily overwhelmed the effects of CNDD on biodiversity maintenance, especially at larger spatial scales. Given the high importance of dispersal, mass-effects and source–sink dynamics from the perspective of metacommunity ecology, these findings challenge the common perception of the general importance of CNDD for biodiversity maintenance.

Material and methods

The spatial simulation model CONFETTI

For this study, we extended the spatially-explicit model CONFETTI, which simulates mortality and recruitment of individuals in a local community (May et al. 2015, 2016). The model structure was inspired by previous community models (Hubbell 2001, Chave et al. 2002), but in contrast to many previous models, the locations of the individuals in CONFETTI are described in continuous space rather than on a discrete 2D-lattice and interactions are modelled using a spatial neighbourhood approach (Canham et al. 2004, Uriarte et al. 2004).

The community is simulated in a square plot with side length L that includes a certain number of individuals N, which represent adult trees. Each individual is characterized by its species identity and its x–y-coordinates. We assume that the number of individuals in the community remains constant over time (zero-sum dynamics). This is a simple way to model a fixed carrying capacity of the community (Hubbell 2001).

Every model step includes the death of one adult individual and the subsequent establishment of a new one. Mortality is simulated as random event (i.e. mortality is assumed to be independent of individuals' interactions and their species identity). As soon as an individual dies, a new one, called a 'recruit', is generated either as an immigrant from the metacommunity (with probability m) or as an offspring of another individual in the local community (with probability $1-m$). The parameter m is called the immigration rate (Hubbell 2001). Note that 'recruitment' refers here to the establishment of a new adult individual. In the case of local recruitment, we first randomly choose a mother individual from the simulated plot, and second, we determine the potential location of the recruit using either a radially-symmetric Gaussian distance kernel with mean distance d_m to simulate spatially restricted dispersal (Clark et al. 1999), or a random position to simulate spatially unrestricted (i.e. random) dispersal. To avoid edge effects, we used periodic boundary conditions if the random location of the recruit was outside of the plot, i.e. we treated the plot as a torus without edges.

In the case of immigration from the metacommunity, a random mother species is chosen from the metacommunity and the immigrant is placed at a random position within the simulated plot. The metacommunity is represented by a static species abundance distribution, i.e. every species has a fixed relative abundance in the metacommunity. This reflects the assumption that metacommunity dynamics are much slower than local community dynamics (Hubbell 2001). We modelled the metacommunity by drawing random deviates from a log-normal abundance distribution with mean and standard deviation as model parameters ($meta_m$, $meta_{sd}$), followed by standardization of the random deviates so that the relative abundances sum to 1.

After the species identity and the position of a potential recruit have been simulated, the model considers neighbourhood interactions as determinant of the establishment probability to mirror the assumptions of Janzen (1970) and Connell (1971). Accordingly, we assume that the recruit is affected during its juvenile stage by competition from all adult individuals within a certain neighbourhood distance r_{max}. We calculate a neighbourhood competition index (NCI) that considers the species identities and distances to all individuals within a circle with radius r_{max}.

$$\mathrm{NCI}_i = \frac{1}{\pi r_{\max}^{2}} \sum_{j=1}^{n} \frac{c_{ij}}{r_{ij}} \tag{1}$$

where n is the number of neighbour trees within r_{max}, c_{ij} is the competition coefficient between the species of recruit i and the species of neighbour j, and r_{ij} is the distance between recruit i and neighbour individual j. This NCI represents a simplified version of the index used in Canham et al. (2004) and Uriarte et al. (2004). In contrast to these studies, we do not consider size differences among individuals. We standardize the neighbourhood competition index by neighbourhood area ($\pi \times r_{max}^2$) to disentangle the effects of the strength of neighbourhood competition versus the range of neighbourhood interactions. Finally, we convert the NCI into a probability of successful establishment p_i:

$$p_i = 1 - \frac{\mathrm{NCI}_i}{a_{\mathrm{rec}} + \mathrm{NCI}_i} \tag{2}$$

where a_{rec} represents a model parameter that is equal to the NCI value that reduces establishment probability by 50%. When an establishment event is not successful, a new position is tested until there is a successful establishment. However, while several positions can be tested for an establishment event, the choice between immigration and local recruitment is only made once to assure that the correct proportions of immigrants and local recruits are simulated.

Model parameterization

An increase of conspecific relative to heterospecific negative density dependence (CNDD versus HNDD) is incorporated in the parameterization of the species' competition coefficients c_{ij} (Eq. 1). We assumed that interspecific competition is equal for all species pairs. Accordingly we used $c_{ij} = 1$ for all cases where species $i \neq$ species j. Increased CNDD results whenever intraspecific competition is higher than interspecific competition. In our model this means there is higher CNDD than HNDD when $c_{ii} > 1$. To consider interspecific variation in CNDD we draw species-specific c_{ii} values from a truncated normal distribution with mean C_{m} and coefficient of variation C_{cv} (= standard deviation/mean). The distribution was truncated at 1 at the lower tail to exclude positive density dependence ($c_{ii} < 1$). With this parameterization, we can independently vary the strength of CNDD by increasing C_{m} and interspecific variation in CNDD by changing C_{cv}. In preliminary simulations, we also used a log-normal distribution to model interspecific variation in CNDD. Since results (not shown) were highly consistent with both distributions and the parameterization with mean and coefficient of variation is more intuitive for normal distributions, we focussed our detailed analysis on simulations using the truncated normal distribution.

To place our study into a plausible ecological context, we used a reference parameter set (Table 1) that is adopted from studies where a model version that represents neutral community dynamics (i.e. with CNDD equal to HNDD) was parameterized using spatially-explicit census data from tropical forest plots (May et al. 2015). Specifically, we used model optimization techniques to derive parameter estimates that resulted in close agreement between model predictions and field observations from a 50 ha forest plot on Barro Colorado Island (Panama) with respect to community patterns including total species richness, species abundance distribution, pair–correlation function, species–area relationship and distance decay of community similarity (May et al. 2015).

To investigate the scale-dependent consequences of local CNDD and immigration in a generic way, we conducted theoretical simulation experiments by systematically extending the parameter space around our reference parameter set (Table 2). As we are primarily interested in the interacting effects of immigration, the mean strength and the interspecific variation of CNDD, we systematically varied the relevant parameters (m, C_{m}, C_{sd}) over wide ranges. With respect to parameter values for immigration rates, Chisholm and Lichstein (2009) provide an approach to estimate the immigration rate based on the perimeter and area of the plot that contains the local community and the mean dispersal distance of the focal species. For tropical and temperate forests, mean seed dispersal distances between 10 m and 100 m have been estimated (Greene et al. 2004, Muller-Landau et al. 2008), which translates into immigration rates between 0.013 and 0.13 for the 1000 × 1000 m plot used here. This range corresponds to the higher values of the parameter set simulated here (Table 1, 2), which means we simulated values that are conservatively low as well as values that are realistic for forest communities. An overview of all model parameter values used in this study is provided in Table 1. The model CONFETTI is implemented in C++ with an R interface and the code is available on GitHub (<https://github.com/FelixMay/confettiRbasic>)

Table 1. Model parameters used in thus study.

Parameter	Description	Standard value	Range used in simulations
L	Size of simulated plot (side length of square)	1000 m	–
N	Number of individuals	40 000	–
metaSR	Species richness of the metacommunity	500	–
metaCV	Coefficient of variation (= sd/mean) of relative abundances in the metacommunity	100%	–
m	Immigration rate	0	0–0.1
r_{max}	Neighbourhood radius of tree interactions	10 m	5 m – ∞
a_{rec}	Coefficient for strength of interactions	0.005	–
d_{m}	Mean distance of recruitment kernel	40 m	40 m or random
C_{m}	Mean strength of intraspecific competition – a value of 1 indicates that intraspecific is equal to interspecific competition	10	1–20
C_{cv}	Interspecific variation of intraspecific competition (coefficient of variation among species = standard deviation/mean)	0	0–1

Table 2. Design of simulation experiments. This table only reports the parameters values that were systematically varied in simulation experiments. The constant reference values are provided in Table 1.

	Immigration from the metacommunity	Interspecific variation in CNDD	Parameter variations
Simulations in the main text			
Set 1 (Fig. 1)	No	No	Full factorial design of $r_{\max}$ in {5, 10, 20, ∞} and C_m in {1, 2, 5, 10, 20}
Set 2 (Fig. 2)	No	Yes	Full factorial design of C_m in {1, 2, 5, 10, 20} and C_{cv} in {0, 0.1, 0.2, 0.4, 0.6, 0.8, 1.0}
Set 3 (Fig. 3)	Yes	No	Full factorial design of C_m in {1, 2, 5, 10, 20} and m in {0, 0.001, 0.01, 0.1}
Simulations in the supplementary material			
Set 1a (Fig. A1)	No	No	Same as in Set 1, but with unrestricted dispersal, i.e. $d_m = \text{random}$
Set 3a (Fig. A2)	Yes	No	Same as in Set 3, but with unrestricted dispersal, i.e. $d_m = \text{random}$
Set 3b (Fig. A3)	Yes	No	Same as in Set 3, but with unlimited interaction range, i.e. $r_{\max} \rightarrow \infty$

Simulation experiments

We designed and conducted three sets of simulation experiments that address our three main questions. 1) How is species richness determined by CNDD in the absence of immigration and without interspecific variation in CNDD? 2) How does biodiversity maintenance change with interspecific variation in CNDD? 3) How do immigration from a metacommunity and CNDD jointly and interactively influence species richness across spatial scales? An overview of all our simulation experiments is provided in Table 2.

Isolated communities

First, we investigated how many species can be maintained by CNDD in isolated communities without immigration from the metacommunity ($m = 0$). To this end, we varied the strength of CNDD (C_m) and the range of neighbourhood interactions ($r_{\max}$) (Table 2, Set 1). In the variation of $r_{\max}$, we also included the extreme assumptions that all trees in the simulated forest plot contribute to the NCI value for a potential recruit and that their distances to the recruit do not matter ($r_{\max} \rightarrow \infty$). That means we considered the plot-scale abundances instead of the local neighbourhood in the evaluation of Eq. 1 and ignored the distances between recruit and neighbour trees (r_{ij}).

Within this first set of simulations, we assumed that there are no interspecific differences in CNDD (i.e. $C_{cv} = 0$). However, there is empirical evidence that species differ substantially in the response to conspecific neighbours (Comita et al. 2010, Mangan et al. 2010). Accordingly, we simulated a second set of scenarios with varying interspecific differences in CNDD. For these simulations, the neighbourhood radius of tree interactions was kept at its reference value of $r_{\max} = 10$ m (Table 2, Set 2).

Open communities with immigration

Finally, we conducted simulations of open communities, which consider immigration from a metacommunity (Loreau and Mouquet 1999, Hubbell 2001) and assessed the interacting effects of CNDD and immigration rate. Accordingly, we simulated a full factorial design for different immigration rates m combined with several levels of the strength of intraspecific competition (C_m). For these scenarios, we did not consider interspecific differences in CNDD and again kept the radius of tree interactions ($r_{\max}$) at its reference value (Table 2, Set 3). To assess the generality of our simulations, we also used the plot-scale abundances of species to calculate competition ($r_{\max} \rightarrow \infty$) analogue to the simulations for isolated communities and conducted all simulations with spatially restricted ($d_m = 40$) and spatially unrestricted recruitment ($d_m = \text{random}$) (Table 2, Set 3a–b).

Model evaluation and scheduling

Each model simulation used the following scheduling. First, we sampled the fixed relative abundances of all species in the metacommunity from a log-normal distribution. The initial state of the local community was derived by sampling N (= 40 000) random individuals from the metacommunity that are placed at random positions in the simulated arena. The initial state always contained 499 or 500 species. That is, our simulation results of isolated communities are not biased by low initial species richness. Next, the sequence of birth–death events was iterated until one of the following two criteria was fulfilled, but at least for 10 000 generations. The simulation was stopped, if either just one species survived in the local community, or the species richness and species abundance distribution reached an equilibrium. The first criterion of only one remaining species was only relevant for scenarios without immigration, because species richness was always higher with immigration from the metacommunity. We assessed the second criterion, by calculating the Shannon-diversity $H = -\sum p_i \times \log(p_i)$ after every 1000 generations, where p_i is the relative abundance of species i and the sum is over all species in the local community. We assumed convergence to a dynamic equilibrium and stopped the simulation if the coefficient of variation of Shannon-diversity over the last 10 000 generations dropped below 0.01. For each parameter set, we conducted 100 replicate simulations. From the community at the end of each simulation run we derived species–area relationships (SAR) using non-overlapping squares that cover the entire plot and vary in size from 25 m^2 up to the plot size of 100 ha. For each scenario, we averaged the SARs (i.e. the species richness values for all sizes of the non-overlapping squares) over the replicate runs. In addition, we recorded Shannon-diversities calculated from the abundances at the 100 ha scale at the end of the simulation runs.

Results

Isolated communities

As expected, CNDD can maintain a reasonable number of species in isolated communities. Species richness increased with increasing mean strength of CNDD (C_m). The strength of the positive effects of CNDD increased with spatial scale, most likely because small scales can only harbour a limited number of individuals and thus also only few species. At the same time, species richness also increased with increasing radii of neighbourhood interactions (r_{max}), especially for scenarios with strong CNDD (Fig. 1). With spatially unrestricted dispersal in the local community species richness reached an asymptote at slightly lower sampling areas compared to restricted dispersal, but otherwise results are highly consistent between the scenarios with spatially restricted versus unrestricted dispersal (Supplementary material Appendix 1 Fig. A1).

We found that species richness across all scales sharply declined with interspecific variation in CNDD (Fig. 2). As soon as the coefficient of variation of CNDD (C_{cv}) was equal to, or larger than 0.4, just one species dominated the plot over the long run. The results considering Shannon-diversity at the 100 ha scale are highly consistent with the analysis of the species–area relationships (Supplementary material Appendix 1 Fig. A2, A3).

Open communities with immigration

In simulations with immigration from a metacommunity, we investigated how the consequences of CNDD vary with immigration rate as well as across spatial scales. When there was no or very little immigration, species richness clearly benefited from CNDD, but this effect vanished with increasing immigration. With high immigration rates, there was no difference comparing scenarios with or without CNDD (Fig. 3). These findings were robust to an unlimited interaction range within the plot and spatially unrestricted recruitment ($r_{max} \rightarrow \infty$, d_m = random, Supplementary material Appendix 1 Fig. A4, A5) and were consistent when we analysed Shannon-diversity instead of species richness (Supplementary material Appendix 1 Fig. A6).

With respect to the effects of CNDD on species richness at different spatial scales, we found that the positive effect of CNDD on species richness (measured as log-response ratio between species richness with and without CNDD) increased with spatial scale and converges to an asymptote in isolated communities (Fig. 4). In open communities, however, the effects of CNDD on species richness drastically decreased even with low levels of immigration and were completely overruled with high immigration rates. Interestingly, with low to immediate immigration rates the effect of CNDD showed a unimodal relationship with spatial scale (Fig. 4). That means CNDD contributed most to species richness maintenance at intermediate scales around 4–6 ha.

Discussion

In this study, we investigated the interacting relative effects of conspecific negative density dependence (CNDD) and immigration from a metacommunity on species richness across spatial scales. Overall, we found that CNDD only contributed significantly to biodiversity maintenance if immigration was absent or very low and when there was little or no interspecific variation in CNDD (Levi et al. 2019).

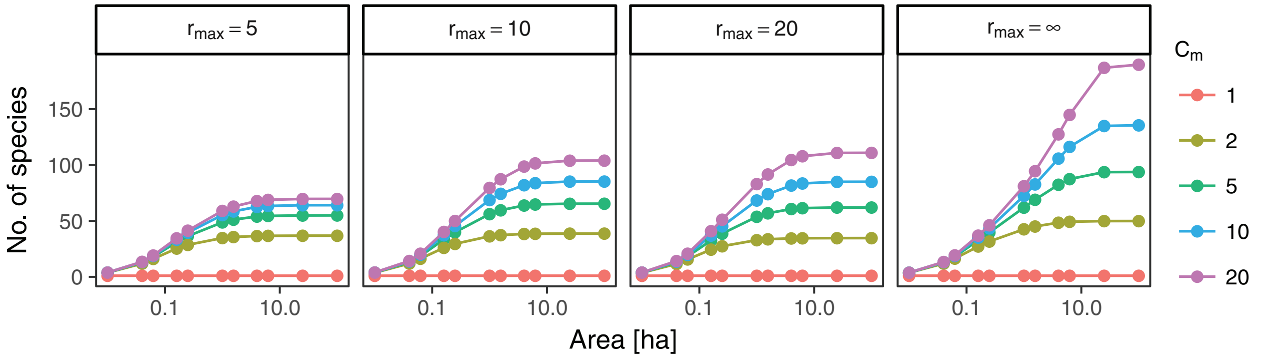

Figure 1. Species–area relationships (SARs) for different combinations of the strength of CNDD (C_m) and different neighbourhood radii of local interactions (r_{max}) in isolated communities without immigration from a metacommunity. The lines show average values of 100 replicate models runs. Note that $C_m = 1$ means that there is no CNDD and therefore the species number always converges to one species. The panel to the right ($r_{max} = \infty$) considers a model with spatially unlimited interactions, i.e. individuals interact with all other individuals in the plot and the distances among trees do not matter for their interactions.

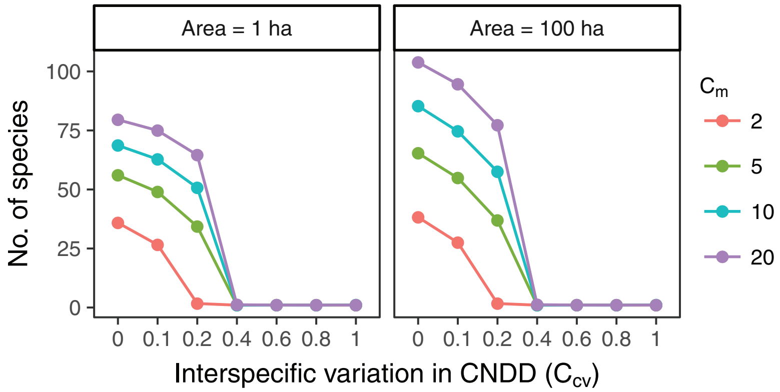

Figure 2. Consequences of interspecific variation in CNDD on species richness in isolated communities at two different spatial scales. The lines show average values of 100 replicate models runs. Interspecific variation in CNDD is measured by the coefficient of variation in CNDD among species (C_{cv}). The neighbourhood interaction radius (r_{max}) was set to be 10 m for these simulations.

In this scenario, CNDD fosters diversity far beyond the range of direct neighbourhood interactions. However, we argue that the assumptions of very low interspecific differences in CNDD and of very low immigration are too restrictive and unrealistic for natural communities, as discussed below.

We found that the relative importance of CNDD for biodiversity maintenance drastically decreased as soon as there were realistic levels of immigration. Considering our model assumption of a static metacommunity with fixed species richness, it is clear that a sufficiently high immigration rate will overwhelm any local processes. (In the limit of immigration rate $m = 1$, there are essentially no local dynamics anymore). Accordingly, the relevant question is not if immigration outperforms local CNDD, but at which rate of immigration this happens. Seed dispersal distances of forest trees derived in tropical and temperate forests translate into immigration rates between 0.013 and 0.13 for a 1000 × 1000 m plot (Chisholm and Lichstein 2009). This range corresponds to the higher values of the parameter set simulated here (Table 1), and thus clearly falls within the range where immigration overwhelmed the effect of local CNDD on species richness in the simulations. However, even an order of magnitude smaller immigration rates drastically reduced the effect of CNDD on biodiversity maintenance in our simulations. We presume that communities other than forests might differ substantially in their immigration rates. For instance, herbaceous communities likely experience lower immigration rates due to lower mean dispersal distances (Thomson et al. 2011, May et al. 2013), while communities of mobile animals might have higher immigration rates. Due to the wide range of immigration rates simulated here, and the strong effects of immigration on the relative importance of CNDD, we are confident that our findings are not biased by unrealistic parameter choices and are relevant for ecosystems other than forests.

Overall, our findings suggest that CNDD may be rather unlikely to be a major driver of diversity maintenance in real communities, especially at large spatial scales. This clearly contrasts with the widespread perspective that local CNDD is a key mechanism of diversity maintenance (Wright 2002, Adler et al. 2010, Comita et al. 2010, Terborgh 2012). However, it is important to note that our findings do not contradict studies that provided evidence for local CNDD (e.g. studies reviewed by Comita et al. 2014). Our results do

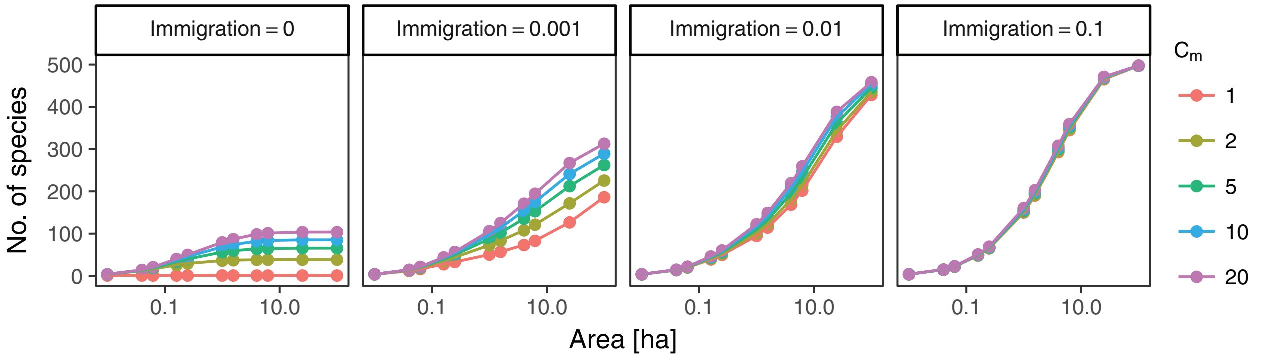

Figure 3. Species–area relationships for different combinations of the strength of CNDD (C_m) and the immigration rate (in different panels). The lines show average values of 100 replicate models runs. Note that $C_m = 1$ means that there is no CNDD. The neighbourhood interaction radius (r_{max}) was set to be 10 m for these simulations. Corresponding figures with unlimited interaction range ($r_{max} \to \infty$) in the simulated communities are provided in the Supplementary material Appendix 1 Fig. A5.

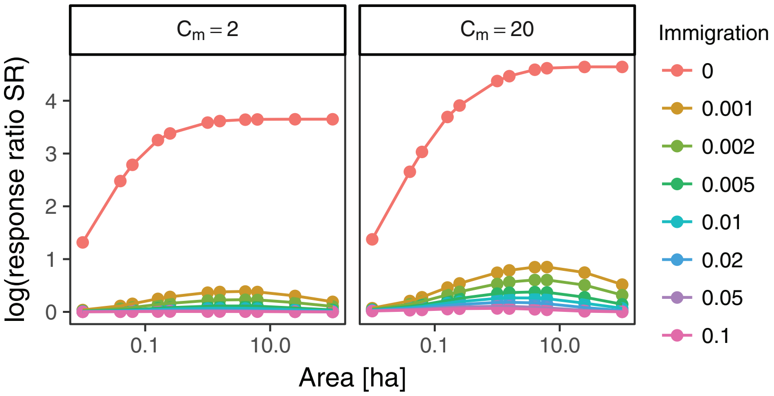

Figure 4. Effect size of CNDD on species richness in open communities at different scales and for different immigration rates. The effect sizes were calculated as log-ratio of species richness (SR) for scenarios with CNDD ($C_m > 1$) compared to scenarios without CNDD ($C_m = 1$), but with equal values for all the other parameters including immigration. The effect sizes were calculated from average species–area relationships of 100 replicate model runs (Fig. 3).

not imply that CNDD does not exist, but instead, we show that even if CNDD is active, its effects on biodiversity can be easily overwhelmed by immigration. Of course, immigration can only overwhelm local-scale CNDD when there are additional mechanisms of biodiversity maintenance at larger spatio-temporal scales. It is important to keep in mind that the large majority of CNDD studies that found significant negative effects of conspecific neighbours on focal individuals were conducted at small spatial scales and often on a limited number of species. These effects were then speculatively extrapolated to the community level (Freckleton and Lewis 2006). We are only aware of two studies conducted with annual plants (Levine and HilleRisLambers 2009) and within a shrub- and grassland community (Adler et al. 2010), which directly assessed the contribution of stabilizing niche differences and thus of CNDD on biodiversity maintenance. Both studies found that CNDD is essential for biodiversity maintenance in the respective systems, but focussed on small scales in communities with low overall species richness. What is urgently lacking are empirical tests of the importance of CNDD for biodiversity maintenance across a larger range of spatial scales and in highly diverse communities.

Our results illustrate that metacommunity processes at larger spatial scales can easily swamp the effects of local CNDD. Interestingly, the effect of CNDD was largest in model versions that correspond to non-spatial 'mean-field' approximations with spatially unrestricted recruitment and an unlimited interaction range within the community (Fig. 1, Supplementary material Appendix 1 Fig. A1), while the assumptions of spatially restricted dispersal, local interactions, interspecific variability in CNDD, and immigration drastically reduced the ability of CNDD to maintain high levels of species richness. This also suggests that classic coexistence theory that tended to ignore spatial patterns and the spatial scales of ecological processes, as well as metacommunity dynamics, is likely to be insufficient to understand how species coexist and diversity is maintained in real ecosystems (Leibold et al. 2004, Leibold and Chase 2017, Wiegand et al. 2017).

Implications of model assumptions

The simulation approach used here is well suited to investigate the propagation of CNDD effects across scales, but of course, every model includes simplifying assumptions. In what follows, we discuss the implications of model assumptions and parameter choices for the scale-dependent effect of CNDD on diversity.

Scaling behaviour of biodiversity

In closed communities without immigration, we found that species richness maintained by CNDD increased across spatial scales. This result is in general agreement with a recent simulation study that addressed the consequences of CNDD in the absence of other potential mechanisms of biodiversity maintenance and without interspecific variation in CNDD (Levi et al. 2019). However, we found that species richness in closed communities showed a sigmoidal relationship with area, while Levi et al. (2019) found monotonous increases according to a power law (compare Fig. 1 in this article to Fig. 5 in Levi et al. 2019). This apparent contradiction can be explained by the different methods to construct these scaling relationships: We sampled smaller areas within a given 100 ha plot, whereas Levi et al. (2019) simulated community dynamics in plots of increasing size. Comparing species–area relationships that were derived with consistent methods from simulations of both models, might be an interesting follow up study to improve our understanding of the scaling behaviour of biodiversity with CNDD, but is beyond the scope of this study.

Interspecific variation of CNDD

In close agreement with recent studies, we found that interspecific variation in CNDD drastically reduced species richness, because there is a competitive advantage for species with low and a disadvantage for species with high CNDD (Miranda et al. 2015, Stump and Comita 2018). This means, interspecific variation in CNDD essentially introduces fitness differences among species, which foster competitive exclusions, when they are not balanced by stabilizing mechanisms (Chesson 2000). In our simulations, there was no coexistence at coefficients of variation of CNDD larger than 0.3–0.4. However, empirical studies typically found large variation of CNDD among species in forests (Comita et al. 2010, Johnson et al. 2012) and in grasslands (Petermann et al. 2008, Maron et al. 2016). Direct estimates of the variation in CNDD are rarely provided, but the observed variation is likely higher than the threshold found in our study. This means that in real communities, there must be additional mechanisms and trade-offs that maintain diversity and balance the disadvantage of high species-specific CNDD. Theoretical analyses indicated that coexistence might be fostered by a tradeoff between species-specific CNDD and growth rate when rare (Chisholm and Muller-Landau 2011). While such a tradeoff is potentially able to reduce the negative effects of interspecific differences in CNDD, to our knowledge we so far lack empirical support on tradeoffs between species-specific CNDD and other important demographic parameters.

Fitness differences

Our simulations include the assumption that all species share the same rates of mortality and recruitment in the absence of competition. In the terminology of coexistence theory, this means there are no fitness differences among species (Chesson 2000) other than potential interspecific differences in CNDD as discussed above. Accordingly, our model with equal CNDD for all species represents a system with zero fitness differences and equal stabilizing niche differences among all species pairs (Adler et al. 2007). This represents a strongly simplifying assumption, but based on coexistence theory, there is a clear prediction of what happens when these assumptions are relaxed. Introducing interspecific variation in density-independent mortality and/or recruitment is expected to result in increasing fitness differences among species (as long as the variation does not corresponds to the unlikely case of a perfectly equalizing tradeoff). However, coexistence theory indicates that any additional fitness differences will further reduce biodiversity maintenance if stabilizing niche differences remain constant (Adler et al. 2007).

We only considered interspecific variation in CNDD, but not in heterospecific negative density dependence (HNDD). Similarly, to the preceding arguments, we presume that adding variation to HNDD among species would result in additional fitness differences and thus in decreasing biodiversity. Testing this expectation with additional simulations could be an interesting follow-up investigation to the analysis presented here. In general, we argue that our findings are rather conservative, because we did not consider fitness differences other than interspecific differences in CNDD and any such fitness differences would reduce the positive effects of CNDD on biodiversity

Binary distinction between con- and heterospecifics

Furthermore, we only distinguish conspecific versus heterospecific neighbours in our model, which means that all heterospecific neighbours are assumed to have equal effects on a focal individual irrespective of their identity. From the perspective of niche theory, the fitness of individuals might be suppressed more by neighbours with similar traits and/or from closely related species than by neighbours with different traits or from distantly related species (Kraft and Ackerly 2010). These negative effects can be mediated by the same mechanisms as CNDD, for example, by strong overlap of resource requirements (MacArthur and Levins 1967) or by shared pathogens or herbivores (Freckleton and Lewis 2006). In this context, it has been recently shown that strong host-specificity (or highly species specific resource requirements, respectively) are required for significant diversity maintenance due to CNDD (Sedio and Ostling 2013). Accordingly, a relaxation of the simplified binary distinction between con- and heterospecifics in our model would represent a lower host-specificity and result in lower diversity. Therefore, we conclude that our general results will not change with a more realistic scenario of competition and negative density dependence based on trait differences or phylogenetic relatedness.

Diversity maintenance at the metacommunity scale

In our simulations, we considered a static metacommunity with a fixed species richness and species abundance distribution. In this way, we explicitly excluded potential feedbacks of local CNDD to the metacommunity and implicitly assume that diversity in the metacommunity is maintained by mechanisms other than local CNDD. Clearly, these assumptions are critical for the interpretation of our results, which show that if there is a diverse metacommunity, then immigration easily exceeds the effects of local CNDD on biodiversity maintenance. Ultimately, the key question in this context is: how plausible is diversity maintenance at the metacommunity scale by mechanisms other than local CNDD? From our perspective, the two most plausible candidate mechanisms are species-sorting due do different habitat requirements in a heterogeneous environment (Mouquet and Loreau 2002, 2003, Leibold et al. 2004) as well as speciation events that balance extinctions at large biogeographic scales (Hubbell 2001, Rosindell et al. 2010).

There is ample evidence that community composition and diversity at larger scales is influenced by environmental heterogeneity (Cottenie 2005, Kreft and Jetz 2007, Stein et al. 2014) and that the relative importance of heterogeneity increases with the spatial scale considered (Chase 2014, Garzon-Lopez et al. 2014). In the context of species distributions in heterogeneous environments, immigration corresponds to dispersal among local communities and the establishment of source sink dynamics (Pulliam 1988, Mouquet and Loreau 2003). Accordingly, our study is in close agreement with previous findings that dispersal among local communities can be a main driver of local diversity maintenance (Loreau and Mouquet 1999, Turnbull et al. 2000, Cadotte 2006). At even larger spatio–temporal scales, neutral theory shows that even comparably low speciation rates can balance extinction rates and maintain a realistic equilibrium diversity of metacommunities (Hubbell 2001, Latimer et al. 2005).

In addition to environmental heterogeneity and speciation, there might be other mechanisms that foster biodiversity within metacommunities, such as competition–colonization tradeoffs (Amarasekare 2003), non-hierarchical competition networks with intransitivities (Allesina and Levine 2011), and/or temporal variability (Chesson 1985, Roxburgh et al. 2004). Importantly, all these mechanisms are not mutually exclusive, but may act in concert as drivers of biodiversity. Our primary point is that regardless of which specific mechanism or set of mechanisms maintain metacommunity diversity, these are likely to be necessary for the maintenance of diversity independent of CNDD due to local interactions.

Conclusions

Theory on coexistence within local communities, which has stressed the importance of fitness and stabilizing niche differences among species (Chesson 2000, Adler et al. 2007) has developed rather independently from metacommunity theory, which focuses on spatial heterogeneity and dispersal (Leibold et al. 2004, Leibold and Chase 2017). The focus on CNDD as demographic fingerprint of stabilizing mechanism is clearly rooted in local-scale and non-spatial coexistence theory. However, studies that suggested CNDD as an important process for diversity maintenance tended to neglect the influence of metacommunity-level processes such as dispersal and immigration. Our study is a step towards a deeper integration of local diversity maintenance mechanisms indicated by CNDD with metacommunity-level mechanisms such as dispersal and source–sink dynamics.

Our results are consistent with the idea that local-scale CNDD can allow coexistence, but we also show how these effects can be diluted and potentially overwhelmed by larger scale metacommunity processes and/or interspecific variation in CNDD. Therefore, we conclude that CNDD potentially drives local patterns of species distributions, but it is unlikely to be a major determinant of biodiversity maintenance at larger spatio–temporal scales. Of course, it would be an interesting next step to examine this prediction in a framework that explicitly describes the dynamics of the metacommunity, including additional mechanisms for diversity maintenance such as species-sorting along environmental gradients, mass effects and/or speciation–extinction dynamics. Our analysis highlights that we need better empirical knowledge on potential tradeoffs that involve CNDD. Overall, our study shows the importance of considering interacting processes at different spatial and temporal scales for understanding species coexistence and biodiversity maintenance.

Data availability statement

This study is based on a simulation model and does not make use of any empirical data. The model source code is publicly available at: <https://github.com/FelixMay/confettiRbasic>.

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Author contributions – FM, TW, AH and JMC conceived the study. FM implemented the model, conducted the simulations and analysed the simulation results. FM wrote the first manuscript draft and all authors significantly contributed to revisions.

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Supplementary material (available online as Appendix oik-06785 at <www.oikosjournal.org/appendix/oik-06785>). Appendix 1.