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Bottom-up and top-down control of dispersal across major organismal groups

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Ecology and evolution unfold in spatially structured communities, where dispersal links dynamics across scales. Because dispersal is multicausal, identifying general drivers remains challenging. In a coordinated distributed experiment spanning organisms from protozoa to vertebrates, we tested whether two fundamental determinants of local dynamics, top-down and bottom-up control, generally explain active dispersal. We show that both factors consistently increased emigration rates and use metacommunity modelling to highlight consequences on local and regional dynamics.

Dispersal is a life-history trait[1] that fundamentally impacts spatial population and community ecology[2,3]. By linking dynamics between local and regional scales via gene flow, dispersal also strongly determines evolutionary change[4]. Dispersal is especially relevant in the context of current global changes[5]: increasingly fragmented landscapes, as well as shifting climatic conditions, may force organisms to disperse to survive and maintain metacommunity and food web properties[6]. However, dispersal is often grossly oversimplified in models[5], a representation at odds with the growing awareness that dispersal must be considered in sufficient detail for a better understanding of ecology and evolution as well as for improving biodiversity forecasts[5,7].

Understanding the causes and consequences of dispersal is challenging because dispersal is a highly plastic trait that depends on multiple factors at both the intra- and interspecific level[8–10], such as resource availability[11,12], intraspecific densities[13,14] or interspecific interactions[15,16], as illustrated by empirical work. Theoretical work has shown that context-dependent dispersal has important consequences in the context of intraspecific competition[17,18], predator–prey interactions[19,20] and species coexistence[21], to name but a few examples.

The challenge is to uncover fundamental proximate drivers of dispersal, which are relevant to population and community dynamics, while simultaneously maintaining generality and tractability. We argue that dispersal is best understood and investigated within the relevant community setting where it is probably a function of the fundamental ecological forces that determine local population dynamics, including bottom-up (resource availability) and top-down (predation risk) impacts that regulate the demography of focal species.

To investigate this hypothesis, and to provide a general test of the ubiquity of context-dependent dispersal (CDD), we need synthetic data sets covering multiple species. Such data sets should be obtained using comparable methodology and, most importantly, should include responses to multiple drivers of dispersal simultaneously since these may interact, which can lead to non-additive effects[9,22]. Such data sets have hitherto been largely lacking for dispersal[5,7]. Therefore, we conducted a coordinated distributed experiment[23,24] involving 7 laboratories across Europe and 21 species ranging from protozoa to vertebrates to test for bottom-up and top-down effects on dispersal, more specifically on the emigration phase of dispersal[25], in experimental two-patch systems. By designing the two-patch systems with connections between them to be 'hostile matrices', incompatible with sustained population survival, we test emigration decisions rather than routine movement (see Supplementary Information for details). The emigration phase is crucial because it initiates dispersal, is readily controllable by behavioural decisions and therefore strongly determines the course of subsequent dispersal phases[8].

We found that resource availability and predation risk, that is, the perceived presence of a predator based on chemical, visual and/or auditory cues, impacted emigration decisions across all study species (Fig. 1 and Supplementary Table 2). The most parsimonious statistical model suggests that the effects of resource availability and predation risk were additive (Supplementary Table 2). While resource limitation led to a clear increase in emigration across all focal species (on average from approximately 9 to 16% without predation; relative importance of resource availability, that is, sum of Akaike information criterion corrected (AICc) weights of models in which the parameter occurs: 1.00), the effect of predation risk was overall weaker (on average from approximately 9 to 12% without resource limitation; relative importance of predation risk: 0.88). The interaction between predation risk and resource availability suggested by the second-ranked model (ΔAICc = 2.07; AICc

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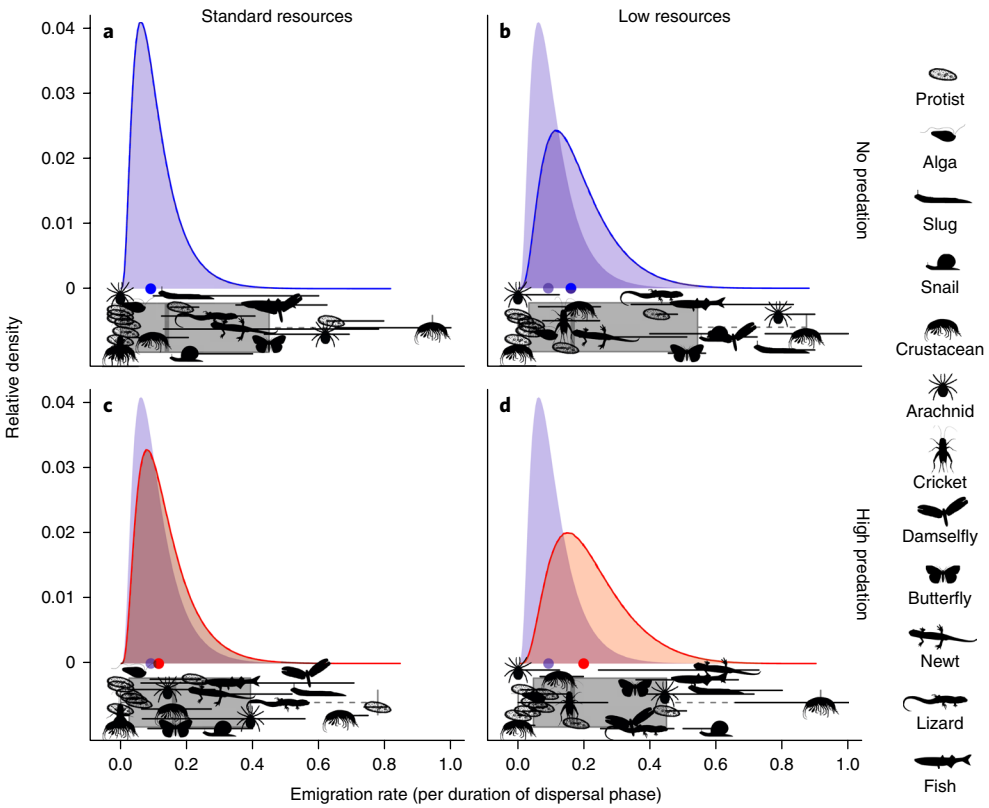


Fig. 1 | Effect of bottom-up resource limitation and top-down predation risk on emigration across 21 species, ranging from protists to vertebrates. **a**–**d**, AICc-based model selection on binomial generalized linear mixed models suggest an additive effect of predation risk and resource limitation (see Supplementary Table 2; intercept (resource availability (RA) low, predation risk (PRED) no: −1.65 ± 0.69; RA standard: −0.64 ± 0.11; PRED yes 0.26 ± 0.11)). We show posterior predictive distributions (continuous lines and coloured shaded areas; the dots represent the medians of the distributions) of the most parsimonious, that is, additive model (lighter shades indicate resource limitation (**b**,**d**); blue: without predator cues (**a**,**b**); red: with predator cues (**c**,**d**)). For pairwise differences between the posterior distributions, see Supplementary Fig. 1. For comparison, all panels include the distribution of the reference scenario. **a**, Standard resources and no predation (dark blue). Additionally, we plotted the posterior predictive distributions of the model including the interaction between resource limitation and predation risk (dashed lines), which completely overlaps with the prediction of the additive model. Below the model predictions, we show the observed median emigration rates (black animal symbol) and quartiles (corresponding black error line) per study species, as well as box plots across all species (grey; showing the median and quartiles, the whiskers extend beyond the quartiles by 1.5 times the interquartile range).

weight = 0.23; see Supplementary Table 2) appeared to be only of marginal importance, as illustrated by the high overlap of distributions in Fig. 1.

In accordance with our results (Fig. 1b), we generally expected resource limitation to increase emigration rates to escape from low-fitness environments[9]. A post hoc exploration of emigration responses for each species, estimated using log OR, where OR is odds ratios (Supplementary Fig. 2a and Supplementary Tables 3 and 4), confirmed this finding overall (the best model only includes the intercept; AICc weight = 0.55), while tentatively suggesting that the focal species' feeding strategy[26] might have modulated this response (relative parameter importance: 0.23; second-ranked model with ΔAICc = 2; AICc weight = 0.20). While sit-and-wait and active capture foragers tended to respond less, grazers clearly responded more to resource limitation by increased emigration. We hypothesize that, if grazers rely on resources of limited mobility, local resource limitation reliably indicates low fitness expectations that should induce emigration. For both of the other foraging strategies, resources may be too mobile to reliably indicate (future) fitness expectations. However, we warn readers not to draw firm conclusions on this specific point. The strength of the effect is relatively weak and species are not evenly distributed across feeding strategies. By contrast, in the literature, little consensus exists on possible responses to predation risk, which has been suggested to depend on space use behaviour of predators and prey[19]. Again, using a post hoc exploration of emigration responses to predation, the intercept model ranked first (AICc weight = 0.15; Supplementary Tables 5 and 6). However, as suggested by the second-ranked model (ΔAICc = 0.15; AICc weight = 0.14) and the averaged model predictions (Supplementary Fig. 2b), the direction of the effect of predation indeed depended somewhat on the relative space use of the focal species, that is, the extent of space routinely used by the focal species (for example, a home range) relative to the predator's space use (Supplementary Fig. 2b and Supplementary Table 5; relative importance of space use: 0.26) and the mode of dispersal of the focal species (terrestrial, aquatic or aerial dispersal, which imply characteristically different dispersal costs;[27] relative importance of dispersal mode: 0.33). Finally, whether predators were generalists or specialists may also have impacted emigration responses (relative importance: 0.38), with specialist predators tentatively leading to higher emigration rates. However, these effects have to be interpreted cautiously, as the analysis is post hoc and the first ranking model consistently included only the intercept.

Shifting our focus from causes of dispersal to its consequences, we illustrate the potential impact of CDD in metacommunities using a simple food chain model that includes a basal resource, a focal consumer and a top predator in analogy to the experiment (Fig. 2; for a sensitivity analysis, see Supplementary Tables 13, 14

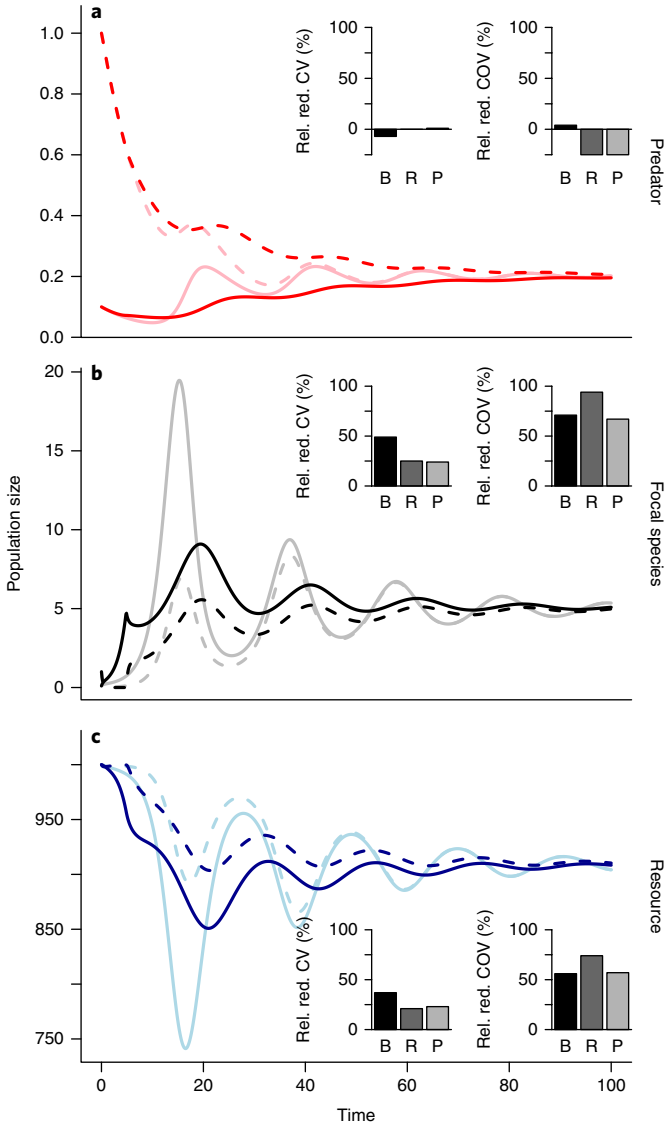


Fig. 2 | Consequences of CDD for local and regional metacommunity dynamics. We show the dynamics of all three trophic levels. **a**, Top predator in red, *P*. **b**, Focal species in black, *N*. **c**, Resources in blue, *R*. All three are shown in both patches (patch 1: solid lines; patch 2: dashed lines). While the random dispersal (RD) (light colours) and CDD (dark colours) scenarios are characterized by the same model parameters, we compare the specific scenarios in which the RD and CDD parameters minimize the focal species' population dynamics coefficient of variation (CV), that is, the most locally stable communities (see ref. [28]). The insets show the reduction (Rel. red.) in the CVs of dynamics within patches, respectively covariance (COV) between patches, under the CDD relative to the RD scenario, as well as the differences between scenarios assuming CDD with respect to resources and predators (B), only resources (R) and only predators (P). The strong local effects are due to emigration being simultaneously resource- and predator-dependent. If CDD is only resource- or predator-dependent, local population fluctuations are reduced to a smaller degree, while the reduction in synchrony may be stronger. The RD emigration rate that minimized the focal species CV was $m_N = 0.35$. The corresponding CDD thresholds were $T_R = 956.94$ and $T_P = 0.12$. Parameter values (see Methods): $\omega = 0.5$; $R_0 = 1{,}000$; $e_N = 0.1$; $a_N = 0.01$; $d_N = 0.1$; $e_P = 0.005$; $a_P = 4$; $d_P = 0.1$.

and Supplementary Figs. 3–5). Simultaneous resource- and predator-dependent emigration as found experimentally greatly reduced local fluctuations of population dynamics through time. At a regional metacommunity level, CDD dramatically reduced covariance between patch dynamics. Both of these effects are directly relevant to local and regional metacommunity stability[28], since stability increases with smaller intrinsic fluctuations and less synchronous patch dynamics. Interestingly, CDD in the focal species did not only affect its own dynamics, but had cascading effects on the other trophic levels; this highlights the importance of dispersal for driving species network dynamics[6]. These results suggest that CDD could, via its stabilizing effect, reduce stochastic extinction risk in metacommunities, at least for lower and intermediate trophic levels.

Given the general challenges of forecasting ecological dynamics[5,29], the absence of a strong interaction between bottom-up and top-down emigration modulators (Fig. 1) has the advantage of making the prediction of ecological metacommunity dynamics potentially easier[30]. This finding, along with the general and predictable responses of emigration to bottom-up and top-down influences, is encouraging for projecting the dynamics of spatially structured communities into the future. Of course, the dispersal process is more complex than emigration[31] and future work should integrate all three phases of dispersal[32].

Our insights could only be gained using our coordinated distributed experimental approach[23,24] with well-defined and unified experimental protocols that allow us to achieve generality beyond a meta-analysis. Here, we strongly advocate the widespread use of such large collaborative efforts because they represent a unique possibility to collect high-quality mechanistic data urgently needed for biodiversity forecasting[5].

In conclusion, our work provides clear insights into the generality of the resource- and predation-dependency of the first dispersal phase, emigration. We highlight the potential for far-reaching consequences of the multicausal nature of dispersal, as well as its cascading effects on regional metacommunity dynamics.

Methods

Study organisms. We used 21 focal study species: *Armadillidium vulgare* (woodlouse; predator licence: 09-2016-02 and 2012-10 DREAL); *Chilomonas* sp.; *Colpidium* sp.; *Cornu aspersum* (garden snail); *Cryptomonas* sp.; *Deroceras reticulatum* (grey field slug); *Dexiostoma* sp.; *Dikerogammarus villosus* (killer shrimp); *Gammarus fossarum*; *Lissotriton helveticus* (palmate newt; licence: 09-2016-02); *Paramecium caudatum*; *Phoxinus phoxinus* (Eurasian minnow; licence: E-2016-130); *Pieris brassicae* (large white butterfly; licence: 09-2016-02); *Pirata latitans* (pirate wolf spider; licence: 2012-10 DREAL); *Platycnemis pennipes* (white-legged damselfly; licence: 09-2016-02); *Pteronemobius heydenii* (Marsh-cricket; licence: 09-2016-02 and 2012-10 DREAL); *Tetrahymena elliotti*; *T. pyriformis*; *T. thermophila*; *Tetranychus urticae* (two-spotted spider mite); *Zootoca vivipara* (common lizard; licence: 2012-10 DREAL). Species included aquatic, terrestrial and aerially dispersing taxa of protists, algae, arthropods, molluscs and vertebrates. The resources and predators of these focal species were chosen based on known natural co-occurrences to allow for the possibility of a common evolutionary history (see Supplementary Information for details).

Experimental set-up and treatments. Experiments across all study species followed the same general experimental procedure. We used experimental two-patch systems adapted to each study species (for example, species-specific patch sizes, corridor size and positions) for experimental populations to reflect naturally occurring densities and living conditions. Therefore, experimental conditions ranged from connected microcosms[33] to semi-natural connected mesocosms (the Metatron[34]).

Importantly, all experimental metacommunities were characterized by the presence of a 'hostile matrix' connecting the patches, which ensured that inter-patch relocation was indeed dispersal[22,25,35], that is, a change of habitat with potential consequences for gene flow, and not routine foraging movement (see the Supplementary Information for details).

We applied a full factorial design crossing two levels of resource availability (RA) and predation risk (PRED). Resources were ad libitum ('standard' condition; standard RA) or seriously limiting (low RA). PRED was represented by the presence (PRED yes) or absence of cues (PRED no) belonging to a natural and relevant (that is, shared evolutionary history) predator of the focal species. Predator cues could be chemical, visual and auditory, depending on the biology of the focal species. We manipulated predator cues instead of the physical presence

of predators to avoid concurrent effects on population dynamics. The treatments were always applied to one patch ('origin') that was initially populated by similar densities of individuals of the focal species for each treatment. The second patch ('target') always had reference conditions (standard resources, no predator cues) and was initially empty.

After placing a population of individuals in the 'origin' patch, treatments were applied at the beginning of an acclimation phase that took approximately one quarter of the time of the subsequent dispersal phase. During the acclimation phase no dispersal was possible. The absolute times of the acclimation and dispersal phases were adapted depending on the focal species (see Supplementary Information). All treatments were replicated five times, with the exception of a few species where replication was lower (two replicates for *P. brassicae* and *P. pennipes* respectively; four replicates for *Z. vivipara*) or higher (six replicates for *A. vulgare*, *L. helveticus*, *P. phoxinus*, *P. latitans* and the protists, except *T. thermophila*; nine and ten replicates for *D. villosus* and *G. fossarum*, respectively; eight replicates for *P. heydenii*) due to experimental constraints (for details, see Supplementary Table 1). For some species, the experimental design included a block, which always included replicates of all treatments and was accounted for in the statistical analysis (see later in the text). The coordinated distributed experiment on the 21 focal species was carried out in 7 different laboratories across Europe (see Supplementary Table 1).

Data collection. Data on dispersal, more specifically emigration, that is, the number of residents (individuals in the patch of origin at the end of the experiment) and dispersers (individuals that had left their patch of origin and were in the target patch at the end of the experiment) after the dispersal phase in each replicate, were either collected using video recording and analysis[36] or by direct observation. Using data from further analyses or literature surveys (specified in the Supplementary Information), we collected species-specific information for the focal species, resources and predators including: movement; space use; feeding strategy; body size; predator specialization; and focal species escape strategies. The latter information was either used directly or in relevant focal species to predator ratios as potential explanatory variables for understanding the modulators of resource and predator impacts on emigration (see Supplementary Table 1).

Statistical analysis. All statistical analyses were performed using the R language and environment for statistical computing (version 3.4.4) and occurred in two steps. We analysed overall treatment effects on all species together using generalized linear mixed models on proportion counts of residents and dispersers (aggregate binomial regression; binomial error structure with logit link function; 'glmer' function of the lme4 package using the 'bobyqa' optimizer). As random effects, we included experimental block within species within taxon. We used taxon as a random effect to account for potential phylogenetic non-independence and included the levels 'protists', 'algae', 'arthropods', 'molluscs' and 'vertebrates' (see Supplementary Table 1). We further included the laboratory in which the experiment was performed as a random effect to account for potential experimenter effects. Overdispersion was accounted for by additionally including an observation level random effect. Model selection was performed on all models from the full model, which included an interaction between resource availability and predation risk, to the intercept model using AICc[37]. Besides identifying the most parsimonious model, we also provide information on relative variable importance, which is the sum of AICc weights of models in which the variable of interest occurs.

In an exploratory, post hoc analysis, species-specific models were used to extract log OR. Subsequently, these log OR were used to determine species-specific modulators of the global CDD response. Model structure for obtaining log OR of both bottom-up (resource availability) and top-down (predation risk) effects was analogous to the global analysis described earlier. However, the only potential random effect at the species level was 'block'. In case the specific experiment did not include a block, we used a generalized linear model; potential overdispersion was accounted for by using a 'quasibinomial' error structure. We only modelled an additive effect of resource availability and predation risk, since the global analysis suggested the absence of an interaction (see results). We nevertheless provide the analysis of the species-level effects based on models including the interaction between the two explanatory variables in Supplementary Tables 7–12. For the subsequent analyses, one protist species (*Chilomonas* sp.) was excluded since the log OR and the associated errors were meaningless due to zero emigration in the reference treatment (standard resources, no predation).

The statistical analysis of the species-level log OR and potential explanatory variables was executed in a meta-analysis framework to account for the uncertainty associated with each species-specific log OR ('rma.mv' function of the 'metafor' package). Again, 'taxon' and 'laboratory' were included as random effects. Model selection using AICc was performed on the additive models including all possible combinations of explanatory variables, which can be found in Supplementary Table 1. Specifically, we used 'focal species ID', 'relevant taxon', 'dispersal mode', 'focal species feeding strategy' and 'log(focal body size)' for the effect of resource limitation and 'focal species ID', 'relevant taxon', 'dispersal mode', 'relative space use', 'predator mobility', 'predator feeding strategy', 'predator specialization', 'escape strategy', 'log(focal body size)' and 'log body size ratio' for the effect of predation. For further information, see Supplementary Table 1. We included 'focal species ID' to test whether the responses were truly species-specific, that is, they varied idiosyncratically between species, or were more readily explained by other explanatory variables. For visualization, model predictions were averaged using AICc model weights as proportions[38].

A simple two-patch food chain model with CDD. To illustrate the consequences of context-dependent, or more precisely resource- and predation-dependent emigration, we explored the dynamics of a simple, two-patch food chain model that captures the essence of our experimental setting. The basal resource (R) is abiotic and flows in and out of the system at a given rate (ω). The focal species (N) feeds on this resource and is itself subject to predation by a top predator (P). For simplicity, we assume that both consumers follow a linear, that is type I, functional response (feeding rate a) and that only the focal species can disperse (emigration rate m_N; see Supplementary Figs. 4 and 5 for an exploration of the consequences of predator dispersal). The dynamics of this food chain in patch i are given by

$$\frac{dP_i}{dt} = e_P a_P N_i P_i - d_P P_i \quad (1a)$$

$$\frac{dN_i}{dt} = e_N a_N R_i N_i - d_N N_i - a_P P_i N_i + m_N (N_j - N_i) \quad (1b)$$

$$\frac{dR_i}{dt} = \omega R_0 - \omega R_i - a_N N_i R_i \quad (1c)$$

where e is the assimilation coefficient, d is the death rate and R_0 is the resource concentration flowing into the system. The subscripts either indicate the patch (i, j) or whether the consumer parameters describe the focal species (N) or top predator (P).

We compared the dynamics of this two-patch food chain model with RD and CDD. In the earlier scenario, m_N is an unconditional rate. For CDD, we assume that the emigration reaction norm is a step function as derived by Metz and Gyllenberg[39]. The probability to disperse in the latter scenario will be 0 if resources are above a threshold resource density and 1 if they are below it. Simultaneously, the emigration rate will be 0 if predators are below a threshold predator density and 1 if they are above it. In summary, we assume negative resource-dependent emigration and positive predator-dependent emigration, as we found experimentally.

While the RD and CDD scenarios we contrast are characterized by the same model parameters, we compare the specific scenarios in which the RD and CDD parameters, respectively, minimize the focal species population dynamics CV as a proxy for local population stability[28]. Alternatively, we compare RD and CDD scenarios that have the same emigration rates as measured at the end of the analysed time series (see Supplementary Fig. 3). In analogy to Wang and Loreau[28], we use temporal CVs within local communities as well as covariances between communities as proxies for (meta)community stability.

The results we report here should be understood as an illustration of the potential consequences of CDD. Although based on a sound mathematical framework (equations (1a–c)) and accompanied by a sensitivity analysis (Supplementary Tables 13 and 14, and Supplementary Figs. 3–5), the results are a snapshot of possible dynamics because a full analysis of the model is beyond the scope of this work.

Data availability

The data set and computer code generated and analysed during the current study are available in the Zenodo repository, https://doi.org/10.5281/zenodo.1344579.

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Author contributions

All authors commented on the drafts and have read and approved the final manuscript. More details on individual contributions can be found in the Supplementary Information at the beginning of each specific Supplementary methods section. F.A., D.B., A.C., J.C., M.D., F.D.L., E.A.F., D.L., S.J., E.L., S.M., Fr.P. and N.S. designed the research. This research was designed during a meeting of the dispNet group (https://dispnet.github.io/) organized at UCL by N.S. and D.B. F.A., A.A., S.B., D.B., J.C., M.D., F.D.L., J.D.R., L.D.G., E.A.F., D.L., S.J., O.K., E.L., C.J.L., L.M., F.M., S.M., Fe.P., Fr.P., N.S., L.T., A.V. and L.W. performed the experiments. More information can be found in the Supplementary Information. J.C. and E.A.F. analysed the experimental data. E.A.F. designed and analysed the model and drafted the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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