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

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## **Abstract**

2 Ecology and evolution unfold in spatially structured communities, where dispersal links dynamics across  
scales. Because dispersal is multi-causal, identifying general drivers remains challenging. In a coordi-  
4 nated 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  
6 dispersal. We show that both factors consistently increased emigration rates and use metacommunity  
modelling to highlight consequences on local and regional dynamics.

8 Dispersal is a life-history trait<sup>1</sup> that fundamentally impacts spatial population and community ecol-  
ogy.<sup>2,3</sup> By linking dynamics between local and regional scales via gene flow, dispersal also strongly de-  
10 termines evolutionary change.<sup>4</sup> Dispersal is especially relevant in the context of current global changes<sup>5</sup>:  
increasingly fragmented landscapes, as well as shifting climatic conditions, may force organisms to dis-  
12 perse in order to survive and to maintain metacommunity and foodweb properties.<sup>6</sup> However, dispersal  
is often grossly oversimplified in models,<sup>5</sup> a representation which is at odds with the growing awareness  
14 that dispersal must be considered in sufficient detail for a better understanding of ecology and evolution  
as well as for improving biodiversity forecasts.<sup>5,7</sup>

16 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,<sup>8-10</sup> such as resource  
18 availability,<sup>11,12</sup> intraspecific densities<sup>13,14</sup> or interspecific interactions,<sup>15,16</sup> as illustrated by empirical  
work. Theoretical work has shown that context-dependent dispersal has important consequences in the  
20 context of intraspecific competition,<sup>17,18</sup> predator-prey interactions<sup>19,20</sup> and species coexistence,<sup>21</sup> to  
name but a few examples.

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

28 To investigate this hypothesis as well as to provide a general test of the ubiquity of context-dependent  
dispersal (CDD), we need synthetic datasets covering multiple species. Such datasets should be obtained  
30 using comparable methodology and, most importantly, should include responses to multiple drivers of  
dispersal simultaneously as these may interact, which can lead to non-additive effects.<sup>9,22</sup> Such datasets  
32 have hitherto been largely lacking for dispersal.<sup>5,7</sup> Therefore, we conducted a coordinated distributed  
experiment<sup>23,24</sup> involving 7 laboratories across Europe and 21 species ranging from protozoa to vertebrates  
34 to test for bottom-up and top-down effects on dispersal, more specifically on the emigration phase of  
dispersal,<sup>25</sup> in experimental two-patch systems. By designing the two-patch systems with connections  
36 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  
38 phase is crucial, as it initiates dispersal, is readily controllable by behavioural decisions and therefore  
strongly determines the course of subsequent dispersal phases.<sup>8</sup>

40 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

42 (Fig. 1; Tab. S2). The most parsimonious statistical model suggests that the effects of resource availability  
and predation risk were additive (Tab. S2). While resource limitation led to a clear increase in emigration  
44 across all focal species (on average from approx. 9% to 16% without predation; relative importance of  
resource availability, i.e., sum of AICc weights of models in which the parameter occurs: 1.00), the effect  
46 of predation risk was overall weaker (on average from approx. 9% to 12% without resource limitation;  
relative importance of predation risk: 0.88). The interaction between predation risk and resource avail-  
48 ability suggested by the second ranked model ( $\Delta\text{AICc} = 2.07$ ; AICc weight = 0.23; see Tab. S2) appeared  
to be only of marginal importance, as illustrated by the high overlap of distributions in Fig. 1.

50 In accordance with our results (Fig. 1), we generally expected resource limitation to increase emi-  
gration rates in order to escape from low fitness environments.<sup>9</sup> A post-hoc exploration of emigration  
52 responses for each species, estimated using log odds ratios (Fig. S2, Tabs. S3–S4), confirmed this finding  
overall (the best model only includes the intercept; AICc weight = 0.55), while tentatively suggesting  
54 that the focal species' feeding strategy<sup>26</sup> might have modulated this response (relative parameter im-  
portance: 0.23; second ranked model with  $\Delta\text{AICc} = 2$ ; AICc weight = 0.20). While sit-and-wait and  
56 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  
58 limitation reliably indicates low fitness expectations which should induce emigration. For both other for-  
aging strategies, resources may be too mobile to reliably indicate (future) fitness expectations. However,  
60 we warn readers 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  
62 consensus exists on possible responses to predation risk, which has been suggested to depend on space  
use behaviour of predators and prey.<sup>19</sup> Again, using a post-hoc exploration of emigration responses to  
64 predation, the intercept model ranked first (AICc weight = 0.15, Tabs. S5–S6). However, as suggested  
by the second ranked model ( $\Delta\text{AICc} = 0.15$ ; AICc weight = 0.14) and the averaged model predictions  
66 (Fig. S2), 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 (e.g., a home range)  
68 relative to the predator's space use (Fig. S2, Tab. S5; relative importance of space use: 0.26) and the  
mode of dispersal of the focal species (terrestrial, aquatic or aerial dispersal; which imply characteristi-  
70 cally different dispersal costs;<sup>27</sup> relative importance of dispersal mode: 0.33). Finally, whether predators  
were generalists or specialists may also have impacted emigration responses (relative importance: 0.38),  
72 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  
74 the intercept.

Shifting our focus from causes of dispersal to its consequences, we illustrate the potential impact of

76 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 Tabs. S13 – S14  
78 and Figs. S3 – S5). Simultaneous resource- and predator-dependent emigration as found experimentally  
greatly reduced local fluctuations of population dynamics through time. At a regional metacommunity  
80 level, CDD dramatically reduced covariance between patch dynamics. Both of these effects are directly  
relevant to local and regional metacommunity stability,<sup>28</sup> as stability increases with smaller intrinsic fluc-  
82 tuations 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 which highlights the importance of  
84 dispersal for driving species network dynamics.<sup>6</sup> These results suggest that CDD could, via its stabilizing  
effect, reduce stochastic extinction risk in metacommunities, at least for lower and intermediate trophic  
86 levels.

Given the general challenges of forecasting ecological dynamics,<sup>5,29</sup> the absence of a strong interaction  
88 between bottom-up and top-down emigration modulators (Fig. 1) has the advantage of making the  
prediction of ecological metacommunity dynamics potentially easier.<sup>30</sup> This finding, along with the  
90 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  
92 process is more complex than emigration<sup>31</sup> and future work should integrate all three phases of dispersal.<sup>32</sup>

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

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

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## 198 **Author contributions**

Detailed authors contributions can be found summarized in the Supplementary Information and in more  
200 detail at the beginning of each specific Supplementary methods section.

## **Competing interests statement**

202 The authors declare no competing interests.

# Material and methods

## Study organisms

We used 21 focal study species (*Armadillidium vulgare*, *Chilomonas* sp., *Colpidium* sp., *Cornu aspersum*, *Cryptomonas* sp., *Deroceras reticulatum*, *Dexiostoma* sp., *Dikerogammarus villosus*, *Gammarus fossarum*, *Lissotriton helveticus*, *Paramecium caudatum*, *Phoxinus phoxinus*, *Pieris brassicae*, *Pirata latitans*, *Platycnemis pennipes*, *Pteronemobius heydenii*, *Tetrahymena ellioti*, *Tetrahymena pyriformis*, *Tetrahymena thermophila*, *Tetranychus urticae*, *Zootoca vivipara*), including aquatic, terrestrial and aerially dispersing taxa of protists, algae, arthropods, molluscs and vertebrates. 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 setup 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) in order for experimental populations to reflect naturally occurring densities and living conditions. Experimental conditions therefore ranged from connected microcosms<sup>33</sup> to semi-natural connected mesocosms (the Metatron<sup>34</sup>).

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,<sup>22,25,35</sup> 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). Predation risk (PRED) was represented by the presence (yes PRED) or absence of cues (no PRED) belonging to a natural and relevant (i.e., 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 in order 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 which took approximately one quarter of the time of the subsequent dispersal

phase. During the acclimation phase no dispersal was possible. The absolute time of the acclimation  
236 and dispersal phases were adapted depending on the focal species (see Supplementary Information). All  
treatments were replicated 5 times, with the exception of few species where replication was lower (2  
238 replicates for *Pieris brassicae* and *Platycnemis pennipes* respectively; 4 replicates for *Zootoca vivipara*)  
or higher due to experimental constraints (for details see Tab. S1). For some species, the experimental  
240 design included a block, which always included replicates of all treatments and was accounted for in  
the statistical analysis (see below). The coordinated distributed experiment on the 21 focal species was  
242 carried out in 7 different laboratories across Europe (see Tab. S1).

## Data collection

244 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  
246 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<sup>36</sup> or by direct observation. Using data from  
248 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  
250 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  
252 for understanding the modulators of resource and predator impacts on emigration (see Tab. S1). All data  
is available at Dryad (<http://dx.doi.org/xxxxx>).

## 254 Statistical analysis

All statistical analyses were performed using the R Language and Environment for Statistical Computing  
256 (version 3.4.4) and occurred in two steps. We analysed overall treatment effects on all species together  
using generalized linear mixed effects models (GLMM) on proportion counts of residents and dispersers  
258 (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  
260 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  
262 Tab. S1). We further included the laboratory in which the experiment was performed as a random effect  
in order to account for potential experimenter effects. Overdispersion was accounted for by additionally  
264 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

266 model using AICc.<sup>37</sup> 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  
268 occurs.

In an exploratory, post-hoc analysis, species-specific models were used to extract log odds ratios.  
270 Subsequently, these log odds ratios were used to determine species-specific modulators of the global CDD  
response. Model structure for obtaining log odds ratios (logORs) of both bottom-up (resource availability)  
272 and top-down (predation risk) effects was analogous to the global analysis described above. However, the  
only potential random effect at the species level was ‘block’. In case the specific experiment did not include  
274 a block we used a GLM and potential overdispersion was accounted for by using a ‘quasibinomial’ error  
structure. We only modelled an additive effect of resource availability and predation risk, as the global  
276 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 the  
278 Supplementary Information Tab. S7–S12. For the subsequent analyses, one protist species (*Chilomonas*  
sp.) was excluded, as the logOR and the associated errors were meaningless due to zero emigration in  
280 the reference treatment (standard resources, no predation).

The statistical analysis of the species level logORs and potential explanatory variables was executed  
282 in a meta-analysis framework in order to account for the uncertainty associated with each species specific  
logOR (‘rma.mv’ function of the ‘metafor’ package). Again, ‘taxon’ and ‘laboratory’ were included as  
284 random effects. Model selection using AICc was performed on the additive models including all possible  
combinations of explanatory variables, which can be found in Tab. S1). Specifically, we used ‘focal species  
286 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’, ‘rel. space use’,  
288 ‘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 Tab. S1.  
290 We included ‘focal species ID’ to test whether the responses were truly species specific, that is, varied  
idiosyncratically between species, or were more readily explained by other explanatory variables. For  
292 visualization, model predictions were averaged using AICc model weights as proportions.<sup>38</sup>

## A simple two-patch food-chain model with CDD

294 To illustrate the consequences of context-dependent, more precisely resource- and predation-dependent  
emigration, we explored the dynamics of a simple, two-patch food-chain model that captures the essence  
296 of our experimental setting. The basal resource ( $R$ ) is abiotic and flows in and out of the system at a  
given rate ( $\omega$ ). The focal species ( $N$ ) feeds upon this resource and is itself subject to predation by a top  
298 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 is able to disperse (emigration rate  $m_N$ ; see the  
 300 Supplementary Information Fig. S4 – S5 for an exploration of the consequences of predator dispersal).  
 The dynamics of this food chain in patch  $i$  are given by:

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

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

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

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

We compared the dynamics of this two-patch food-chain model with random dispersal (RD) and  
 306 context-dependent dispersal (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 & Gyllenberg.<sup>39</sup>  
 308 The probability to disperse in the latter scenario will be zero if resources are above a threshold resource  
 density and one if they are below. Simultaneously, the emigration rate will be zero if predators are below a  
 310 threshold predator density and one if they are above. In summary, we assume negative resource-dependent  
 emigration and positive predator-dependent emigration, as we found experimentally.

312 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  
 314 species population dynamics coefficient of variation (CV), as a proxy for local population stability.<sup>28</sup>  
 Alternatively, we compare RD and CDD scenarios that have the same emigration rates as measured at  
 316 the end of the analysed time series (see Fig. S3). In analogy to Wang & Loreau,<sup>28</sup> we use temporal  
 coefficients of variation within local communities as well as covariances between communities as proxies  
 318 for (meta)community stability.

The results we report here should be understood as an illustration of potential consequences of CDD.  
 320 Although based on a sound mathematical framework (Eqs. 1a–c) and accompanied by a sensitivity anal-  
 ysis (Tabs. S13–S14 and Figs. S3 – S5), the results are a snapshot of possible dynamics as a full analysis  
 322 of the model is beyond the scope of this manuscript.

## Figure legends

Figure 1: Effect of bottom-up resource limitation and top-down predation risk on emigration across 21 species, ranging from protists to vertebrates. AICc-based model selection on binomial GLMMs suggest an additive effect of predation risk and resource limitation (see Tab. S2; Intercept (RA low, PRED no):  $-1.65 \pm 0.69$ ; RA std.:  $-0.64 \pm 0.11$ ; PRED yes  $0.26 \pm 0.11$ ). We show posterior predictive distributions (continuous lines and coloured shaded areas; dots represent medians of the distributions) of the most parsimonious, that is additive, model (lighter shades indicate resource limitation; blue: without predator cues; red: with predator cues). For pairwise differences between the posterior distributions see Fig. S1. For comparison all panels include the distribution of the reference scenario (standard resources and no predation; dark blue) and we additionally 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 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).

Figure 2: Consequences of CDD for local and regional metacommunity dynamics. We show the dynamics of all three trophic levels (resources in blue,  $R$ ; focal species in black,  $N$ ; top predator in red,  $P$ ) in both patches (patch 1: solid lines, patch 2: dashed lines). While the random dispersal (RD; light colours) and context-dependent dispersal (CDD; dark colours) scenarios are characterized by the same model parameters, we compare the specific scenarios in which the RD, respectively CDD, parameters minimize the focal species' population dynamics CV, that is, the most locally stable communities sensu Wang & Loreau.<sup>28</sup> The insets show the reduction (Rel. red.) in coefficients of variation (CV) of dynamics within patches, respectively covariance (COV) between patches, under 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:  $\omega = 0.5$ ,  $R_0 = 1000$ ,  $e_N = 0.1$ ,  $a_N = 0.01$ ,  $d_N = 0.1$ ,  $e_P = 0.005$ ,  $a_P = 4$ ,  $d_P = 0.1$ .