

Giving-up diversity (GUDiv):

top-down effects of foraging decisions on local, landscape and regional biodiversity of resources

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JAE conceived and developed the GUDiv concept, designed the empirical study and drafted the first version of the manuscript, MD developed conceptual tables and prediction box, APE collected the empirical data. JAE, CF, MD improved all parts of the manuscript, all authors discussed and improve the final version.

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Giving-up diversity (GUDiv):**top-down effects of foraging decisions on local, landscape and regional biodiversity of resources****Abstract** (150 words)

Foraging by consumers has direct effects on the community of their resource species, and may serve as a biotic filtering mechanism of diversity. Determinants of foraging behaviour may thus have cascading effects on abundance, diversity, and functional trait composition of the resource community. Here we propose giving-up diversity (GUDiv) as a novel concept and simple measure to quantify community effects of foraging at multiple spatial diversity scales. GUDiv provides a framework linking theories of adaptive foraging behaviour with community ecology. In experimental resource landscapes we showcase effects of patch residency of foraging wild rodents on α -GUDiv, β -GUDiv and γ -GUDiv, and on functional trait composition of resources. Using GUDiv allows for prediction-based investigation of cascading indirect predation effects (ecology of fear) across multiple trophic levels, of feedbacks between functional trait composition of resource and consumer communities, and of effects of inter-individual differences among foragers on the diversity of resource communities.

Keywords: biodiversity, cascading effects, giving-up density, foraging behaviour, functional traits, landscape of fear, patch use, optimal foraging

50 Introduction

51 Since all species are part of food webs, foraging decisions of consumers have consequences for
52 lower trophic levels. Habitat choice, space use and selectivity of foragers can modify population
53 dynamics of each of their resource species and, thus, indirectly affect biodiversity on the resource
54 level. Behavioural ecology has developed a strong theoretical background on determinants and
55 consequences of individual foraging decisions - optimal foraging theory - and provided a wealth of
56 experimental tests to understand and predict variation in foraging behaviour of individuals
57 (summarized in Stephens et al. 2007, Stephens & Krebs 1986). In parallel, community ecology
58 developed concepts and theories to explain biodiversity expressed within a species pool, and
59 provides tools to detect diversity patterns and to analyse and predict food web dynamics across
60 trophic levels (e.g. Magurran 1988, Ricklefs & Schluter 1993, Thompson et al. 2012). Further,
61 grouping species according to functional traits helped to explain general patterns in community
62 ecology (McGill et al. 2006). Functional traits of resource species involve attractiveness to
63 consumers, which shapes the adaptive strategy of resources to accommodate both predative
64 pressure and abiotic environmental conditions, with direct consequences on food species diversity
65 and resulting feedbacks between consumer foraging behaviour and their resource species
66 (Hillebrand et al. 2007, Larios et al. 2020). Accordingly, foragers may act as biotic, environmental
67 filtering agents by browsing or seed predation, altering the composition of resource species in a
68 patch relative to a regional species pool (Suzuki et al. 2012, Begley-Miller et al. 2014). Spatial
69 variability in foraging activity may further affect the strength of stochastic community assembly
70 (Germain et al. 2013). Thus, the two research fields - behavioural ecology and community ecology -
71 could complement each other but largely developed in separation. As a consequence, they are
72 currently not fully profiting from theoretical advancements of each other. Here, we propose a novel,
73 conceptual fusion of approaches from both research fields, and a simple measure to investigate the
74 effects of individual foraging behaviour and patch use on the biodiversity of resource species

communities on different spatial and diversity scales. This approach allows quantifying predictable modifications of biodiversity by individual foraging decisions in landscapes of risks and resources across trophic levels, and feedback loops related to functional traits of species in a resource species assemblage.

Based on foraging theory, optimal and selective decisions of foragers for profitable areas (i.e. patches with higher energy return rates than the surrounding matrix) can be expected (e.g. Rosenzweig 1974). Foragers further decide on how much time or effort to devote to the patches they choose to harvest (Charnov 1976), which is based on their mobility, spatial patch layout and profitability of patches. To quantify the use of resources by foraging animals, behavioural ecologists have used a variety of different measures, such as giving-up times in a food patch (Krebs *et al.* 1974; Hubbard & Cook 1978; Townsend & Hildrew 1980), total time spent in a patch (Cowie 1977; Hartling & Plowright 1979), quitting harvest rates (Pyke 1978, 1980; Milinski 1979; Hodges 1981), and giving-up density of resources (Whitham 1977; Hodges and Wolf 1981, Brown 1988). All of these measures focus on foraging decisions from the perspective of the forager and, for simplicity, mainly predict the exploitation of only one, local resource species. Here, we propose a novel integrated measure, giving-up diversity (GUDiv), which quantifies the outcome of a forager's patch use by the diversity of the resource species assemblage after foraging, and thereby directly links behavioural ecology of foraging to community ecology. The method is conceptually based on giving-up density (GUD), which measures the density of food (items or mass) remaining in a depletable food patch after a forager has ceased harvesting the patch (Brown 1988). As a general rule, depletable food patches have diminishing returns because harvesting of discrete food items requires the forager to spend time looking for them or handling them (e.g. extract discrete food items from a substrate by digging). As a consequence, search time per food item increases with each removed item because the density of food items in the patch declines (Brown 1988). With diminishing returns, the patch leaving decision (or patch residency) depends on the alternatives in the surrounding environment, i.e. its mean food level, including neighbouring patches, determining the marginal value of a patch (Charnov 1976).

Applying these general processes to patches containing resource species assemblages in given densities and with diminishing returns, GUDiv allows both (i) to quantify giving-up density of each single resource species – in relation to each other species - and (ii) to quantify the diversity of the resource species assemblage after a forager decides to leave (i.e. “give-up”) a food patch (Box 1-1).

Community ecologists developed a variety of indices to quantify species diversity (e.g. Whittaker 1972, Whittaker et al. 2001) and these indices are applied at different spatial scales (Table 1). The simplest is an assessment of local species diversity (α -diversity). This measure does not directly scale-up to a larger regional scale because of variation among local species assemblages. By pooling data sampled at several locations, a regional species diversity (γ -diversity) can be calculated. Furthermore, differences in species combinations among locations (β -diversity) provide a measure of variability of species diversity across a region (Whittaker 1960, 1972, Whittaker et al. 2001). We propose that top-down effects of a forager on species diversity at lower trophic levels should be assessed similarly at different spatial scales (Figure 1, Table 1), since these scales are differentially affected by the mobility of a forager (Germain et al. 2013, Box 1-2). First, a forager affects the local diversity of a resource species assemblage in a discrete food patch. Second, a forager using several patches across a resource landscape affects species diversity at a regional scale. Thus, the effects of individual foraging decisions can be quantified as giving-up diversity at local and regional scales, i.e. as α -, γ -, and β -GUDiv. Table 1 provides terminology and interpretations of diversity research for behavioural ecology and community ecology.

--- Figure 1 here ---

--- Table 1 here ---

When joining behavioural ecologists' and community ecologists' perspectives on spatial scales, special caution should be given to the scales of 'landscape' and 'region': behavioural ecologists often use the term 'landscape' in the context of 'landscape of fear' (Brown et al. 1999). This landscape of

fear of a forager was famously illustrated by a study on wolves, elk and bison in Yellowstone (Laundre et al. 2001), where fear of predators modified foraging behaviour of their ungulate prey. In this specific example, our human perception of the region coincides with large foraging landscapes used by ungulates, so that the regional scale and the landscape scale were exchangeable. Meanwhile, foraging landscapes as well as landscapes of fear can be perceived by foragers of all mobility scales, and are often much smaller than a landscape perceived by ungulates. A number of small foraging landscapes could, alternatively, be approached as nested within an ecological region. Then foraging landscapes would represent the local samples to describe regional diversity (landscape α -GUDiv, regional γ -GUDiv). Consequently, a landscape β -GUDiv and a regional β -GUDiv can be used to describe variation on different spatial scales, within a foraging landscape among patches, and within a region among landscapes, respectively.

Patch leaving decisions depend on the properties (risk and resources) of a food patch, but also on the properties and accessibility of alternative patches for the forager (Box 1-2). With no restrictions on movement between patches and a complete knowledge of patches and their characteristics, ideal foragers should exploit all patches of a landscape evenly. Under these conditions, they are predicted to continue foraging in a local patch with diminishing returns until the gain rate drops below the landscape's average rate, and only then move to another patch to forage (Charnov 1976). With this behaviour, also GUDiv should be evenly distributed across a landscape leading to high similarity between the average local α -GUDiv and the landscape-wide γ -GUDiv, and consequently low β -GUDiv. Since foragers are typically not omniscient and have to trade-off foraging gain with other fitness enhancing behaviour, they do often not follow the proposed, optimal patch use strategy (Pierce & Ollason 1987). Instead, they might, for example, abandon some patches earlier than others, or restrict movement among patches due to perceived risk while travelling or foraging (e.g. Eccard et al. 2020), which should have direct consequences on all diversity levels. Further, foraging decisions may also depend on the functional traits of species in the resource species assemblage,

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which may also feedback on GUDiv (Larios et al. 2017) so that selective and density-dependent foraging strategies may interact to determine the GUDiv of a patch or a landscape (Fig. 1). In Box 1, we summarize a non-exhaustive set of testable predictions on how variation in a foragers behaviour and in initial diversity and functional trait composition of the resource species assemblage will affect GUDiv at different levels.

--- **Box 1 here** ---

Since GUDs vary with perceived predation risk (Brown 1988), they can be used to map a forager's landscape of fear (e.g. Abu Baker & Brown 2014, Gaynor et al. 2019, Van der Merwe & Brown 2008). If predation risk is unevenly distributed in space a forager will reduce patch residency in unsafe parts of the landscape and thereby creates predictable patterns of patch exploitation across a landscape (Madin et al. 2011, Matassa & Trussell 2011). This spatial variation in foraging effort can have cascading effects on the species diversity of lower trophic levels (e.g. Ripple et al. 2015, Suraci et al 2016). Since foragers adjust local patch residency to perceived predation risk, we predict GUDiv to vary with the level and spatiotemporal distribution of perceived predation risk across a landscape (Box 1-4). Thus, a forager under fear will produce predictable cascading effects on food resource species diversity, which can be mapped via GUDiv (Fig. 1, Box 1-4 and 1-5).

However, predicting the strength and spatiotemporal distribution of these fear effects on patch use requires intimate knowledge about the biology of the forager (e.g. degree of dietary specialisation, abilities to search and find food, movement ability, and mobility). For example, several proxies have been shown to modify cascading effects of fear, such as body size (Cozzoli et al. 2019), population size (Dieckmann et al. 2010) of the forager, and seasonal availability of food (Hefty and Steward 2019). Furthermore, not all foragers may have the same preferences or the same nutritional needs, even within species (Bolnick et al. 2003). Moreover, individual risk-taking behaviour might vary consistently among foragers (Dammhahn & Almeling 2012, Mella et al. 2015, Steinhoff et al. 2020). Individual foragers with different food preferences or risk-taking propensity may enhance diversity

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178 of resource species assemblages by their individualized signatures in diversity, that add to the overall
179 diversity pattern in a landscape (predictions Box 1-5)

180 From the perspective of a species community, i.e. assemblage of resource species, patch residency
181 of the forager changes quantity or density of each resource species, and might thereby alter relative
182 proportions among resource species thus affecting species coexistence or trait distribution (e.g.
183 Larios et al. 2013). Foragers may not extract different food species at random but selectively bias
184 foraging towards more profitable species of larger item size, encounter probability and higher
185 energetic or nutritional content (Wang& Yang 2014, Garb et al. 2010), or shorter handling time
186 (Rosenzweig & Sterner 1970, Zhang & Zhang 2008 (endocarp)). Differences may relate to diet
187 selection of animals which is central to the magnitude of competition among consumer species
188 (McArthur 1968, Rosenzweig & Sterner 1970, Roughgarden 1972).

189 Selection criteria of seed predators are related to functional traits of each resource species (McGill
190 et al. 2006) since they directly affect a species dispersal ability, energy allocation, reproductive
191 strategies, and mortality rates, and, thus, fitness. The functional trait approach allows to deduct
192 general principles in community ecology (McGill et al. 2006) and, in the context here, general effects
193 of foraging decisions of foragers with similar food selection. Resource species with similar traits and
194 similar attractiveness to foragers should be exchangeable. Thus, patch residency in combination with
195 selectivity of a forager will determine the functional trait distribution within an assemblage of
196 resource species remaining in a patch. Accordingly, dynamic feedbacks are expected between the
197 changes in trait composition during the foraging process and the relative selectivity of the forager
198 (Fig. 1, Box 1-3). Individual foragers, even of the same species, may differ in their selectivity due to
199 individual foraging strategies or differences in state (individual niche specialisation: Bolnick et al.
200 2003, Araujo et al. 2011). Therefore, knowledge on food selectivity of foragers may be helpful to
201 predict functional trait distribution and remaining diversity patterns (see predictions Box 1-6 and 1-

7), and *vice versa*, the combination of functional traits available in an assemblage of resource species may feedback on the feeding behaviour and selectivity of the forager.

A test case for GUDiv: seed predation experiment with free-ranging rodents

To test and illustrate the GUDiv approach, we run a foraging experiment offering mixed-seed food patches to free-ranging rodents as seed consumers, testing predictions of Box 1 (predictions 1, 2, 3, 4 and 7). Many rodents shape plant diversity by consuming seeds, i.e. are “seed predators”. To avoid confusion between trophic levels in food webs, we will refer to them as “foragers” here and reserve the term “predator” for animals preying on the foragers.

We created resource landscapes with nine experimental food patches, each containing sand and a mix of seeds from 8 different plant species such as sunflower or sesame, varying in functional traits of seeds (Table 2) such as seed size, mass, nutritional value, or presence of husks. Food items were mixed with two litres of sand of 0.1 - 0.5 mm grain size and filled in 30 cm x 30 cm plastic trays, covered with Perspex corrugated plastic as rain protection. After exposure of food patches to foragers overnight, we sifted the remaining seeds from the sand and counted them by species to obtain seed-specific giving-up density (GUD, items per liter of sand). Based on the local seed counts we calculated unspecific GUD, the local giving up diversity (α -GUDiv), as well as γ -GUDiv and β -GUDiv on the landscape level. Diversities were reported as true diversity (Hill 1973) reporting number of effective species (nES) based on the Shannon-Weiner (SW) entropy ($nES = \exp(SW)$), which considers both species richness and equitability in a sample. nES possesses a uniform set of mathematical properties, important for further calculations of β -GUDiv from α -GUDiv and γ -GUDiv. (Jost 2006, Keylock 2006). Camera traps (WildBlick 3.0c RL, triggered with an infrared sensor to obtain three photos in a sequence every 90 seconds) at each tray allowed to identify foragers species and to quantify the time spent in each patch (i.e. patch residency).

226 We hypothesised that unspecific GUD and local α -GUDiv decrease with increasing patch residency
227 (Box 1-1). We assumed that food items are not removed at random but by functional trait, and more
228 profitable food species are removed at higher rates (Box 1-3). We predicted that such foraging
229 patterns will create non-linear dynamics of local diversity with residency of the foragers. We
230 compared the empirical diversity dynamics with dynamics emerging from hypothetical “random”
231 and “fully selective” seed removal. At regular removal of food species (result of a random process if
232 numbers of items are sufficiently large), diversity should remain high until very few seed items are
233 left, while a fully selective food removal in a successive depletion of species by species would result
234 in a linear reduction of diversity (Figure 2A). Further, we assumed that other functional traits of
235 seeds may further affect seed mortality (i.e. seed specific removal rates and consequently diversity
236 patterns), such as husks and size. Since husks need to be removed before consumption, a forager’s
237 handling time could potentially be prolonged for coated seeds and seed mortality reduced; on the
238 other hand larger seeds may be more easy to detect, collect, and store for later consumption, and a
239 husk that protects from insect damage may thus increase mortality of the seed species caused by
240 larger, mobile foragers (Box 1-7).

241 By experimentally providing a default local species pool - identical across all patches - to foragers,
242 landscape wide γ -GUDiv describes a pattern of species loss due to foraging. We hypothesised, that γ -
243 GUDiv will decrease with the absolute time a forager spends in the landscape (landscape residency,
244 cumulated from 9 patch residencies). We predicted, that β -GUDiv will be lower if patch residencies
245 are distributed uniformly over the landscape, while a heterogeneous distribution would produce
246 higher β -GUDiv (Box 1-2 and 4). Evenness of the distribution of patch residency over the landscape
247 as quantified by calculation the coefficient of variation ($CV = \text{landscape mean} / \text{landscape variance}$) for
248 each landscape, the smaller the value, the more even the distribution.

249 During autumn 2017, patch grids were placed at four sites in old fields with high vegetation (> 50 cm,
250 site A and B) or low vegetation (ca. 10 cm, two sites), originally aimed to measure the effect of plant

cover (perceived predation risk for forager) on seed diversity (Box 1-2 and 1-4). After two days of pre-baiting to attract foragers, we found that only locations A and B were visited, and that the majority of visitors were Norway rats (*Rattus norvegicus*) foraging at night. Therefore we recovered the foraging landscape from the previous night during daytime and prepared a fresh resource landscape for the next nights. With one grid set of cam traps available we used A and B alternatingly over 9 nights.

Data is provided as supplemental material (ESM (*doi specifications will follow during the editing process, if the manuscript will be accepted*)). Statistical analyses were done in R (R Core Team 2016), using the packages *lme4* (Bates 2010) and *car* (Fox and Weisberg 2019). For easier comprehension, we report linear slopes, and indicate where we modelled non-linear relationships. To obtain estimates of species-specific removal rates, we ran mixed-effects models of species-specific GUD and patch residency for each food species in each food patch, using the Patch ID as random factor, specified as random intercept, to control for spatiotemporal dependencies of food items within the same patch.

Unspecific GUD, α -GUDiv and selectivity of foragers in local food patches

A total of 20 food patches were visited, each for a patch residency of 0.5 to 34 min (mean \pm SD: 16 ± 9 min). Unspecific GUD was 48.7 ± 16.5 (29 - 79) food items per litre of substrate. GUD decreased with patch residency (-1.7 ± 0.2 food items per litre removed per min, Spearman's $\rho = 0.92$, $p < 0.001$). α -GUDiv ranged from 8.0 to 4.9 effective species, and also decreased with patch residency (-0.07 ± 0.01 nES / liter / min, Spearman's $\rho = 0.90$, $p < 0.001$). The more food items rats removed overall, the lower was α -GUDiv (-0.04 nES / food item / litre; $R^2 = 0.80$, $p < 0.001$, Figure 2A; i.e. - 1 nES removed per 25 removed seeds / l (there were only 10 seeds / l of each species). The observed pattern of species loss resulting from foraging by Norway rats was, thus, slower than expected for a fully selective forager removing one food species after the other but faster than expected if the

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276 forager was removing food items at random (Fig. 1A). Meanwhile, in only one sample rats were able
277 to completely deplete a single food species (Fig. 2B) and nES stayed above five in all but one patch,
278 although up to two thirds of food items were removed.

279 Harvest rates differed among food species (Fig. 2B, LMM: interaction food species and patch
280 residency, $\chi^2 = 94.7$, $df = 7$, $p < 0.001$, Appendix Table 1). Sunflower, safflower, and hemp formed a
281 group of very profitable food species with seeds of large size and high caloric content (*post-hoc tests*,
282 Table 2), which were harvested at the highest rates (-0.34 to -0.27 food items / min / litre), although
283 these food species should have longer handling time because of their husks. Millet, flax and canary
284 formed a group of small to medium food species with harvest rates ranging between -0.16 to -0.19
285 food items / min / litre. Sesame had the lowest harvest rate (-0.03 food items / min / litre) and was
286 harvested in only six out of 20 food patches (Fig. 2B). Wheat, with high caloric value but no husk,
287 was harvested less than the most profitable, husked sunflower seed, but more than the least
288 profitable small, husked seeds (Table 2, Fig. 2B). Food species-specific harvest rates were best
289 explained by average seed mass, rather than caloric value or seed length (separate models due to
290 low sample size of 8 species, Table 2).

291 - Figure 2 here -

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294 .Landscape-wide GUDiv

295 In five out of nine experimental resource landscapes, Norway rats had foraged for a landscape
296 residency between 4 and 90 minutes. They visited two to six food patches per landscape. To increase
297 sample size and prolong the gradient of landscape residencies for a meaningful analysis of
298 landscape-wide GUDiv patterns, we re-shuffled the data empirically obtained from patches
299 (residencies and see species specific GUDs, Figure 2B) into 12 additional, simulated foraging

landscapes (Table 3) including two landscapes combining the 9 longest and the 9 shortest original patch residencies (208 and 78 minutes landscape residency, respectively), 5 landscapes with random combination of visited patches, and 5 random combinations of visited and non-visited patches. Thus, we analysed food species diversity in a total of 17 foraging landscapes (Table 3).

Giving-up diversities of seeds decreased with landscape residency (mean α -GUDiv ($\beta = -0.40 \pm 0.03$ nES per hour, $R^2 = 0.89$, $p < 0.001$; γ -GUDiv ($\beta = -0.27 \pm 0.04$ nES per hour, $R^2 = 0.75$, $p < 0.001$, Fig. 3B) and the number of patches visited, i.e. the mobility of rats (number of trays foraged: mean α -GUDiv: $\beta = -0.1 \pm 0.03$ nES per hour, $R^2 = 0.57$, $p < 0.001$; γ -GUDiv: $\beta = -0.07 \pm 0.02$ nES per hour, $R^2 = 0.46$, $p < 0.001$). Residency distribution became more even (inverse CV of distribution of patch residency by Norway rats) if the foragers were more mobile, i.e. visited more patches ($R^2 = 0.86$ (linear), $p < 0.001$) and if foragers stayed longer in the landscape (CV and landscape residency, $R^2 = 0.70$ (linear), $p < 0.001$, Fig. 3A).

- **Figure 3 here** -

The longer Norway rats had foraged in a landscape higher was the variation in diversity across the landscape (β -GUDiv; linear model: by landscape residency: $\beta \pm SE = 0.020 \pm 0.007$, $R^2 = 0.32$, $p = 0.009$, Fig. 3C). However, non-linear models explained more variation in the data; e.g. when assuming a saturation of β -GUDiv over landscape residency (logistic model: 0.020 ± 0.005 , $R^2 = 0.56$, $p < 0.001$) or for assuming a peak at intermediate (70 – 170 min) patch residency (polynomial model: $R^2 = 0.66$, $p < 0.001$, Fig. 3, estimates in Appendix). A landscapes with only few foraged patches showed an uneven distribution of patch residency (higher CV) but a low β -GUDiv, because many patches remained unvisited and were thus very similar to each other, while longer landscape

residencies and visitation of many patches created a higher beta diversity and a higher evenness among residencies (i.e. lower CV value, β -GUDiv by CV: -0.02 ± 0.009 , $R^2 = 0.22$, $p = 0.039$)).

For completeness and future comparisons, regional diversity after one night of rat foraging, based on the landscapes as local samples were: mean α -GUDiv = 7.29 nES, γ -GUDiv = 7.87 nES and β -GUDiv = 1.04 nES.

Discussion

Here we introduced GUDiv as a novel concept and simple measure to quantify cascading effects of foraging behaviour of a consumer on the diversity of resource species communities on local, landscape and regional scale (predictions Box 1). GUDiv can be used as a tool to connect patterns of foraging behaviour to resource diversity of different spatial scales (Table 1). A study on wild Norway rats foraging in artificial seed communities provided first illustrative evidence for predictions on how variation in their foraging behaviour has cascading effects on biodiversity of their resources; and on feedbacks between functional trait composition of the resource species assemblage and foraging behaviour (Box 1). Specifically, we showed that (i) longer patch residency decreased local α -GUDiv, (ii) landscape residency affected diversities on all spatial levels (Box 1-1 diversity effects of foraging behaviour), (iii) higher mobility among patches affected diversity on all spatial levels (Box 1-2); (iv) rats were not foraging in high-risk landscapes, which therefore remained untouched, and maintained their high α - and γ -diversity and a low β -diversity (Box 1-4 cascading effects of perceived predation risk on forager), and (v) rats foraged selectively and preferred heavier seeds over lighter ones (Box 1-3 on selectivity and 1-7 on functional traits). Diversity measures on a regional scale based on the landscape as sample sites showed, that through overnight foraging of Norway rats hardly any resource species were lost.

Local resource diversity and functional traits of food species

The time a forager spent in a patch reduced local GUDiv of the resource species community in a patch. For each resource species, removal functions followed typical patterns of diminishing returns, albeit with species-specific slopes (Fig. 2B). A qualitative comparison of empirical patterns with two extreme foraging tactics (completely random and completely selective) revealed that foragers did not deplete single most preferred species before using the next preferred species. Indeed, functional depletion of species-based diversity ranged between selective and random foraging (Fig. 1A). *Post-hoc* grouping of removal rates per food species exposed similarities and differences in attractiveness among the eight food species provided as perceived by the foragers, corroborating the importance of functional traits over seed identity (McGill et al. 2006). Variation in attractiveness may relate to handling time (e.g. Rosenzweig & Sterner 1970, Zhang & Zhang 2008), encounter probability, and caloric value (e.g. Garb et al. 2010, Wang & Yang 2014) and is a strong determinant of diet selection of animals, which in turn has a fundamental impact on competition among consumer species (McArthur 1968, Rosenzweig & Sterner 1970, Roughgarden 1972).

From the resource species perspective, differences in attractiveness to foragers ought to be a key functional trait for its survival probability. In the dynamic process of foraging, a consumer is predicted to respond to the functional trait's average of resources in a patch but also to relative trait differences between resource species within a patch. Thus, the combination of functional traits of resource species and the relative proportions thereof will result in predictable, frequency dependent patterns of resource species community dynamics as a result of foraging. Plant ecologists are well aware of the importance of consumers (e.g. seed predators) for altering species coexistence, community structure and invasion patterns (Larios et al. 2017). The GUDiv approach offers a chance to entangle the relative importance of specific functional traits and will, thus, help trait-based generalizations of community patterns (McGill et al. 2006) by experimentally offering resource communities with defined combinations and relative proportions of functional traits in foraging landscapes (Box 1).

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In our experiment, rodents removed food species with heavier seeds at a higher rate from the local patch than the lighter seeds, and *post-hoc* grouping of removal rates (Figure 2B, Table 2) indicated that there were five partly overlapping categories of attractiveness of seeds for Norway rats. The smallest, apparently least attractive seed species (sesame, Fig. 2B) was consumed only after the most attractive group (sunflower, safflower, hemp) had largely been removed. This most attractive group was unified by a combination of large seed size and presence of husk, and were preferred over other seeds despite the (assumed) increased handling time for de-husking (Zhang & Zhang 2008). The husk, on the other hand, may have increased the encounter probability of the seed by further enhancing item size (Garb et al. 2000).

Meanwhile, traits affecting seed predation (e.g. seed size) are viewed in how they influence immediate consumption rates and thus whether and how they act as a biotic, environmental filter on plant diversity (e.g. Larios et al. 2013). However, the same traits (or other non-independent traits – such as seed size or carbohydrate content) might simultaneously affect growth patterns or competitive abilities in various other life stages of the food species and thereby counteract trait effects on seed predation. We suggest rigorous experimentation to entangle importance of food species' functional traits along plant life history stages to understand plant diversity and trait-based community assemblages.

Biodiversity and cascading effects

The longer foragers used a landscape, the more even they distributed their foraging effort across patches. This pattern indicates that rodents in our case study were not switching among patches, as predicted by optimal foraging theory, but rather depleted one patch to unacceptably low returns before moving on to the next patch. Reasons for such a subsequent foraging pattern may include, for example, travelling costs among patches (Charnov 1976) or food hoarding and transporting it back to

a central place (Kacelnik 1984), incomplete knowledge of food density at other patches (e.g. Hefty and Steward 2019), a Bayesian approach to predation risk with a preference for known, safe patches relative to yet unknown (Welton et al. 2003), or an underestimation of missed opportunity costs by the foragers (e.g. Eccard & Liesenjohann 2008, but see also Pierce and Ollason 1987). Foraging landscapes are a shaped product of cascading effects of forager behaviours, so that the movement restrictions of foragers by fear of predation (landscape of fear) may result in higher GUDiverse landscapes. Difference in landscape-wide GUDiv cannot directly reveal causes for movement restrictions of foragers, as for example perceived predation risk, heterogeneity of cover or of surrounding resource levels. Meanwhile, causes (or determinants) of uneven distribution of foraging effort should be of interest for community ecologists because they affect the landscape-wide diversity dynamics of food species (see Box 1). Therefore, rigid experimentation is required to investigate the driving forces behind cascading effects of foraging behaviour on resource level biodiversity.

In the case study, rodents did not deplete the same food species everywhere, so that the difference among local depletion patterns created landscape wide γ -GUDivs that were higher than the mean local α -GUDivs. Foragers may thus produce heterogeneity in diversity across a landscape and increased β -diversity, without differences in predation risk conceivable to us. Our data suggest further that β -GUDiv may follow a hump shape, with highest values at intermediate patch residencies, which is when not all patches were yet visited. Thus, a reason not to visit all patches, such as risk distribution in a landscape, proves to be important for overall diversity in a landscape.

Understanding foraging behaviour and its effects on resource diversity may also be of importance related to anthropogenic disturbances (Speziale et al. 2008, Bleicher & Rosenzweig 2018), such as in cases of urbanized landscapes, where there is an active anthropogenic effort to repel some pest foragers (Krijger et al 2017, Mahlaba et al 2017), or with conservation measures, such as the reintroduction of species (Ripple & Beschta 2004, Kujiper et al 2013) or the manipulation of fear in

consumers which may affect biodiversity in their resource species assemblage (e.g. Suraci et al. 2016). Further, with climate change affecting the distribution of food resources it may shape the GUDiv of foragers generating a bottom-up effect on the predator and forager's diversity (Riginos 2014).

Conclusions

GUDiv is a tri-trophic approach (predator, consumer, resources) to biodiversity of food species assemblages measured on the lowest trophic level; and may offer a theoretical and experimental tool to connect foraging behaviour as a process to patterns in community ecology. With a non-optimal, uneven use of food within a foraging landscape the complexity and dynamics of resource species assemblages may increase. Factors modifying resource exploitation patterns of consumers are well studied in behavioural ecology and include heterogeneity of predation risk, the avoidance of places perceived as dangerous or intra-specific territoriality. GUDiv can be used to experimentally to rigorously test predicted effects of variation among foragers in efficiency of foraging, food preferences, or perception of risk, and of changes in the consumer community on biodiversity of resource species (Box 1). Further, functional traits of resource species may affect emerging diversity patterns. Thus, using the GUDiv approach proposed here allows both theoretical and experimental insights into cascading effects, behavioural patterns, and interaction with trait-based ecology and their effects on biodiversity of assemblages of resource species.

441 **Literature**

- 442 Abdulwahab, U.A., Osinubi, S.T. & Abalaka, J. (2019). Risk of predation: a critical force driving
443 habitat quality perception and foraging behavior of granivorous birds in a Nigerian forest
444 reserve. *Avian Res*, 10, 33.
- 445 Abu Baker, M.A. & Brown, J.S. (2014). Foraging in space and time structure an African small
446 mammal community. *Oecologia*, 175, 521–535.
- 447 Araújo, M.S., Bolnick, D.I. & Layman, C.A. (2011). The ecological causes of individual specialisation.
448 *Ecology Letters*, 14, 948–958.
- 449 Baselga, A. (2007). Disentangling distance decay of similarity from richness gradients: response to
450 Soininen et al. 2007. *Ecography*, 30, 838–841.
- 451 Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global*
452 *Ecology and Biogeography*, 19, 134–143.
- 453 Begley-Miller, D.R., Hipp, A.L., Brown, B.H., Hahn, M. & Rooney, T.P. (2014). White-tailed deer are a
454 biotic filter during community assembly, reducing species and phylogenetic diversity. *AoB*
455 *PLANTS*, 6.
- 456 Bleicher, S.S. & Rosenzweig, M.L. (2017). Too much of a good thing? A landscape-of-fear analysis for
457 collared peccaries (*Pecari tajacu*) reveals hikers act as a greater deterrent than thorny or bitter
458 food. *Can. J. Zool.*, 96, 317–324.
- 459 Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., *et al.* (2003). The
460 ecology of individuals: incidence and implications of individual specialization. *The American*
461 *Naturalist*, 161, 1–28.
- 462 Brown, J.S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition.
463 *Behav Ecol Sociobiol*, 22, 37–47.
- 464 Brown, J.S., Laundré, J.W. & Gurung, M. (1999). The Ecology of Fear: Optimal Foraging, Game
465 Theory, and Trophic Interactions. *J Mammal*, 80, 385–399.
- 466 Charnov, E.L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*,
467 9, 129–136.
- 468 Cowie, R.J. (1977). Optimal foraging in great tits (*Parus major*). *Nature*, 268, 137–139.
- 469 Cozzoli, F., Gjoni, V. & Basset, A. (2019). Size dependency of patch departure behavior: evidence
470 from granivorous rodents. *Ecology*, 100, e02800.
- 471 Dammhahn, M. & Almeling, L. (2012). Is risk taking during foraging a personality trait? A field test
472 for cross-context consistency in boldness. *Animal Behaviour*, 84, 1131–1139.
- 473 Eccard, J.A. & Liesenjohann, T. (2008). Foraging Decisions in Risk-Uniform Landscapes. *PLOS ONE*, 3,
474 e3438.

- Eccard, J.A. & Liesenjohann, T. (2014). The Importance of Predation Risk and Missed Opportunity Costs for Context-Dependent Foraging Patterns. *PLOS ONE*, 9, e94107.
- Eccard, J.A., Liesenjohann, T. & Dammhahn, M. (2020). Among-individual differences in foraging modulate resource exploitation under perceived predation risk. *Oecologia*, 194, 621–634.
- Fischer, C. & Türke, M. (2016). Seed preferences by rodents in the agri-environment and implications for biological weed control. *Ecology and Evolution*, 6, 5796–5807.
- Garb, J., Kotler, B.P. & Brown, J.S. (2000). Foraging and community consequences of seed size for coexisting Negev Desert granivores. *Oikos*, 88, 291–300.
- Gaynor, K.M., Brown, J.S., Middleton, A.D., Power, M.E. & Brashares, J.S. (2019). Landscapes of Fear: Spatial Patterns of Risk Perception and Response. *Trends in Ecology & Evolution*, 34, 355–368.
- Germain, R.M., Johnson, L., Schneider, S., Cottenie, K., Gillis, E.A. & MacDougall, A.S. (2013). Spatial Variability in Plant Predation Determines the Strength of Stochastic Community Assembly. *The American Naturalist*, 182, 169–179.
- Hartling, L.K. & Plowright, R.C. (1979). Foraging by bumble bees on patches of artificial flowers: a laboratory study. *Can. J. Zool.*, 57, 1866–1870.
- Hill, M.O. (1973). Diversity and Evenness: A Unifying Notation and Its Consequences. *Ecology*, 54, 427–432.
- Hodges, C.M. & Wolf, L.L. (1981). Optimal foraging in bumblebees: Why is nectar left behind in flowers? *Behav Ecol Sociobiol*, 9, 41–44.
- Hubbard, S.F. & Cook, R.M. (1978). Optimal Foraging by Parasitoid Wasps. *Journal of Animal Ecology*, 47, 593–604.
- Jost, L. (2006). Entropy and diversity. *Oikos*, 113, 363–375.
- Kacelnik, A. (1984). Central Place Foraging in Starlings (*Sturnus vulgaris*). I. Patch Residence Time. *Journal of Animal Ecology*, 53, 283–299.
- Keylock, C.J. (2005). Simpson diversity and the Shannon–Wiener index as special cases of a generalized entropy. *Oikos*, 109, 203–207.
- Krebs, J.R., Ryan, J.C. & Charnov, E.L. (1974). Hunting by expectation or optimal foraging? A study of patch use by chickadees. *Animal Behaviour*, 22, 953–IN3.
- Krijger, I.M., Belmain, S.R., Singleton, G.R., Koerkamp, P.W.G. & Meerburg, B.G. (2017). The need to implement the landscape of fear within rodent pest management strategies. *Pest Management Science*, 73, 2397–2402.
- Kuijper, D.P.J., Kleine, C. de, Churski, M., Hooft, P. van, Bubnicki, J. & Jędrzejewska, B. (2013). Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography*, 36, 1263–1275.

- Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001). Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Can. J. Zool.*, 79, 1401–1409.
- MacArthur, R.H. (1968). The theory of the niche. *Population biology and evolution*, 159–176.
- Madin, E.M.P., Madin, J.S. & Booth, D.J. (2011). Landscape of fear visible from space. *Scientific Reports*, 1, 14.
- Magurran, A.E. (1988). Ecological diversity and its measurement. Princeton university press, Princeton.
- Mahlaba, T.A.M., Monadjem, A., McCleery, R. & Belmain, S.R. (2017). Domestic cats and dogs create a landscape of fear for pest rodents around rural homesteads. *PLOS ONE*, 12, e0171593.
- Matassa, C.M. & Trussell, G.C. (2011). Landscape of fear influences the relative importance of consumptive and nonconsumptive predator effects. *Ecology*, 92, 2258–2266.
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178–185.
- Mella, V.S., Ward, A.J., Banks, P.B. & McArthur, C. (2015). Personality affects the foraging response of a mammalian herbivore to the dual costs of food and fear. *Oecologia*, 177, 293–303.
- van der Merwe, M. & Brown, J.S. (2008). Mapping the Landscape of Fear of the Cape Ground Squirrel (*Xerus inauris*). *J Mammal*, 89, 1162–1169.
- Pierce, G.J. & Ollason, J.G. (1987). Eight Reasons Why Optimal Foraging Theory Is a Complete Waste of Time. *Oikos*, 49, 111–118.
- R Core Team. (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Ricklefs, R.E. & Schluter, D. (1993). Species diversity in ecological communities: historical and geographical perspectives. *University of Chicago Press Chicago*, 414.
- Riginos, C. (2015). Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology*, 84, 124–133.
- Ripple, W.J. & Beschta, R.L. (2004). Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? *BioScience*, 54, 755–766.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., et al. (2014). Status and Ecological Effects of the World's Largest Carnivores. *Science*, 343.
- Rosenzweig, M.L. (1974). On the evolution of habitat selection. In: *Proceedings of the first international congress of ecology*. Center for Agricultural Publishing and Documentation, p. 404.

- Rosenzweig, M.L. & Sterner, P.W. (1970). Population Ecology of Desert Rodent Communities: Body Size and Seed-Husking as Bases for Heteromyid Coexistence. *Ecology*, 51, 217–224.
- Roughgarden, J. (1972). Evolution of Niche Width. *The American Naturalist*, 106, 683–718.
- Roughgarden, J. (1974). Niche Width: Biogeographic Patterns Among Anolis Lizard Populations. *The American Naturalist*, 108, 429–442.
- Speziale, K.L., Lambertucci, S.A. & Olsson, O. (2008). Disturbance from roads negatively affects Andean condor habitat use. *Biological Conservation*, 141, 1765–1772.
- Steinhoff, P.O.M., Warfen, B., Voigt, S., Uhl, G. & Dammhahn, M. (2020). Individual differences in risk-taking affect foraging across different landscapes of fear. *Oikos*, n/a.
- Stephens, D.W., Brown, J.S. & Ydenberg, R.C. (Eds.). (2007). *Foraging: behavior and ecology*. University of Chicago Press, Chicago.
- Stephens, D.W. & Krebs, J.R. (1986). *Foraging Theory*. Princeton University Press.
- Suraci, J.P., Clinchy, M., Dill, L.M., Roberts, D. & Zanette, L.Y. (2016). Fear of large carnivores causes a trophic cascade. *Nature Communications*, 7, 10698.
- Suzuki, M., Miyashita, T., Kabaya, H., Ochiai, K., Asada, M. & Kikvidze, Z. (2013). Deer herbivory as an important driver of divergence of ground vegetation communities in temperate forests. *Oikos*, 122, 104–110.
- Thompson, R.M., Brose, U., Dunne, J.A., Hall, R.O., Hladysz, S., Kitching, R.L., *et al.* (2012). Food webs: reconciling the structure and function of biodiversity. *Trends in Ecology & Evolution*, 27, 689–697.
- Townsend, C.R. & Hildrew, A.G. (1980). Foraging in a patchy environment by a predatory net-spinning caddis larva: a test of optimal foraging theory. *Oecologia*, 47, 219–221.
- Tuomisto, H. (2010a). A consistent terminology for quantifying species diversity? Yes, it does exist. *Oecologia*, 164, 853–860.
- Tuomisto, H. (2010b). A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, 33, 2–22.
- Ulrich, W., Almeida-Neto, M. & Gotelli, N.J. (2009). A consumer's guide to nestedness analysis. *Oikos*, 118, 3–17.
- Ulrich, W. & Gotelli, N.J. (2007). Null Model Analysis of Species Nestedness Patterns. *Ecology*, 88, 1824–1831.
- Wang, B. & Yang, X. (2014). Teasing Apart the Effects of Seed Size and Energy Content on Rodent Scatter-Hoarding Behavior. *PLOS ONE*, 9, e111389.
- Welton, N.J., McNamara, J.M. & Houston, A.I. (2003). Assessing predation risk: optimal behaviour and rules of thumb. *Theoretical Population Biology*, 64, 417–430.

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577 Whitham, T.G. (1977). Coevolution of Foraging in Bombus and Nectar Dispensing in Chilopsis: A Last
578 Dreg Theory. *Science*, 197, 593–596.

579 Whittaker, R.H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological*
580 *Monographs*, 30, 279–338.

581 Whittaker, R.H. (1972). Evolution and Measurement of Species Diversity. *TAXON*, 21, 213–251.

582 Whittaker, R.J., Willis, K.J. & Field, R. (2001). Scale and species richness: towards a general,
583 hierarchical theory of species diversity. *Journal of Biogeography*, 28, 453–470.

584 Zhang, H. & Zhang, Z. (2008). Endocarp thickness affects seed removal speed by small rodents in a
585 warm-temperate broad-leafed deciduous forest, China. *Acta Oecologica*, 34, 285–293.

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587 **Tables:**

588 **Table 1:** Joining the behavioural ecologists' and the community ecologists' perspectives on terms,
589 scales, and interpretations of species diversity research

	Behavioural Ecology	Community Ecology
Temporal scale of observation	Short term result of foraging process	Long term patterns of species composition
Local scale	A discrete food patch	Single sample of a local species assemblage (sampling site)
Landscape scale	<u>Foraging landscape</u> : A set of food patches after being used by a set of defined foraging agents, such as an individual, a group, a population or a community. Its spatial scale depends on movement/mobility of the defined forager(s). <u>Resource landscape</u> : Distribution of resources before the (experimental) foraging process. <u>Landscape of fear</u> ⁵ : Spatial distribution of perceived predation risk of a forager; predators are involved in shaping foraging decisions of the forager.	
Regional scale	May contain one or many foraging landscapes	A set of species/communities unified by defined similarities in e.g. geography, land use, geology etc.
α -Diversity	α -GUDiv is the diversity of the assemblage of resource species within a local food patch as a result of foraging by a forager/foragers, i.e. consumer(s); it represents a marginal diversity affected by marginal patch residency.	Species diversity of a local assemblage (sampling site), sometimes generalised by the combination of functional traits of the species.
γ -Diversity	γ -GUDiv is the diversity of the cumulated assemblages of resource species left in a foraging landscape. Can also be calculated on a larger regional scale combining several foraging landscapes.	Species diversity at a given region based on the cumulative data of species presence from the defined set of sampling sites.
β -Diversity	β -GUDiv is the variability in diversity among assemblages of resource species left in food patches of a foraging landscape. Can also be calculated on a regional scale, i.e. diversity across	Variability in species diversity among local assemblages in a region.

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	foraging landscapes.	
Species pool	Initial set of resource species available to the forager, provided experimentally or present in nature ⁵ .	Regional species pool, into which assemblages can be nested, e.g. due to isolation or due to differences in land use ^{1,2} , or an environmental (e.g. latitudinal) gradient with spatial or temporal species turnover ^{3,4} .

590 ¹Sedalgo 2008; ²Ulrich et al. 2008; ³Baselga 2010; ⁴Ulrich et al. 2010, ⁵Germain et al. 2014, ⁶Brown 1999

591 **Table 2:** Experimental assemblage of resource species, provided to Norway rats (*Rattus norvegicus*)
592 as foragers, consisted of seeds of eight plant species differing in functional traits (weight, length,
593 caloric value based on USDA (United States Department of Agriculture) or package information, and
594 presence/absence of husks). Species are ordered according to attractiveness (based on removal
595 rates) to wild Norway rats foraging in 20 patches with equal shares of seeds provided. Empirical
596 species-specific removal rates are expressed here as linear slopes for comprehension, but see
597 exponential slopes in Fig. 2B and effect size and errors in Table 2). Shown are adjusted R²-values of
598 single regression models of removal rates (link function) by functional trait variable, significance
599 levels as **p < 0.01, ***p < 0.001; *post-hoc* grouping of removal rates refers to the residency time by
600 resource species interaction in a linear mixed-effects model (GUD of each resource species nested
601 within patches, Table LMM Appendix).

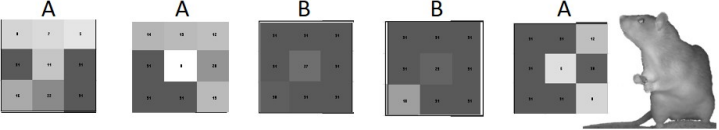
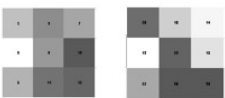
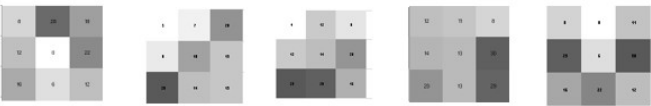
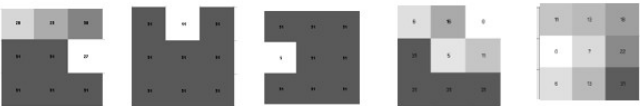
Seed species		Husked	Mass (mg)	Length (mm)	Caloric value (J)	Removal rate (seeds/min/l)	Post-hoc grouping for removal rates
Sunflower	<i>Helianthus annuus</i>	Yes	58.5	10	1100	-0.34	a
Safflower	<i>Carthamus tinctorius</i>	Yes	37.6	7	760	-0.29	ab
Hemp	<i>Cannabis sativa</i>	Yes	14.4	4	230	-0.27	ab
Wheat	<i>Triticum aestivum</i>	No	40.0	7	540	-0.25	b
Millet	<i>Pennisetum glaucum</i>	No	5.9	2	100	-0.19	bcd
Flax	<i>Helianthus annuus</i>	Yes	6.8	5	160	-0.17	cd
Canary gras	<i>Helianthus annuus</i>	Yes	7.6	5	80	-0.16	d
Sesame	<i>Helianthus annuus</i>	No	2.6	3	90	-0.03	e
Regression by removal rate, n = species (transformation)			0.81** (log)	0.44 *	0.77** (log)		

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603 **Table 3:** Foraging landscapes created by Norway rats overnight in experimental landscapes with 9
604 food patches containing 8 seed species with 20 seeds each. Rats exploited a total of 20 patches in 5
605 landscapes (first line) offered at two sites, and we obtained giving-up density (GUD) data for each
606 seed species within each patch. The empirical patch data were reshuffled on patch level to obtain
607 additional landscape-wide giving-up diversity (GUDiv) data

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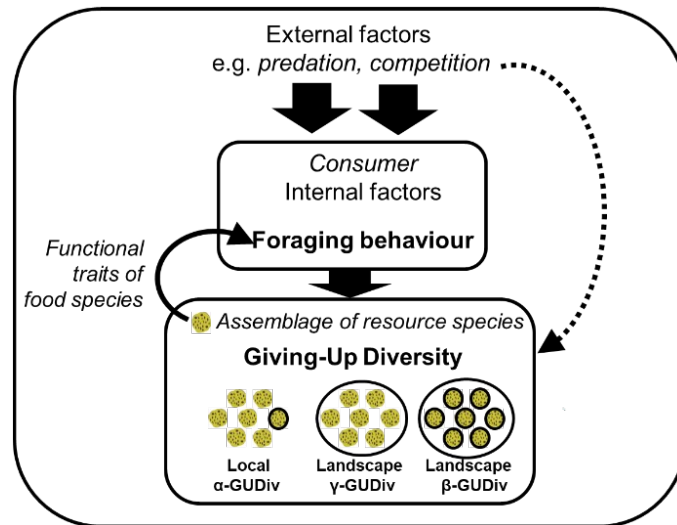
Empirical data of patch residencies (lighter patches indicate longer residencies) A and B refer to site	
Reshuffling of empirical data:	
Extreme residency: 9 patches combining either longest or shortest patch residencies	
Random residency: Random combination of all-visited patches	
Random visits: random combination of visited and unvisited patches	

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611 **Figures**



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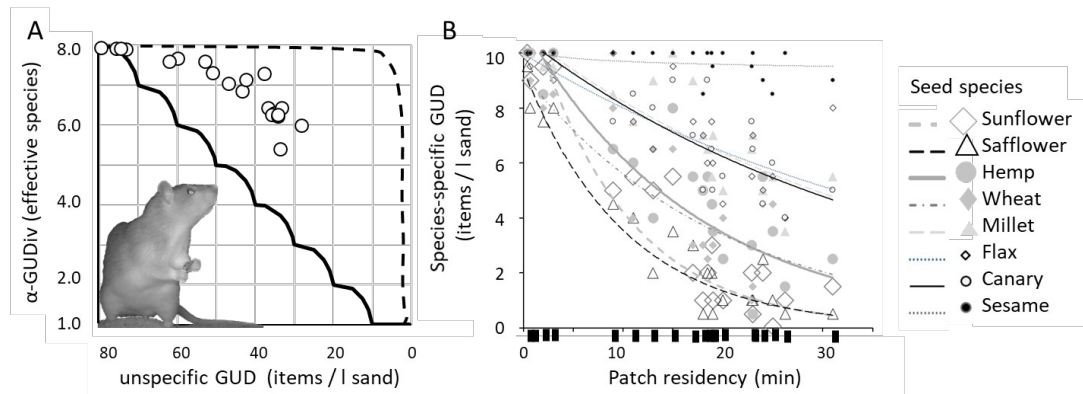
613 **Figure 1:** Foraging decisions of a consumer indirectly affect diversity and functional trait
614 distribution of an assemblage of resource species in a food patch, which can be measured as
615 Giving-Up diversity, i.e. the diversity at which the consumer quits foraging on different spatial
616 and diversity scales. Black arrows: direct effects, dotted arrows: indirect effects, solid line:
617 feedback loop. Internal factors include state, selectivity and perceived predation risk, i.e. the
618 landscape of fear (Brown et al. 1999), and may differ among individual foragers. The distribution
619 of functional traits within the resource assemblage may directly feedback on foraging behaviour.

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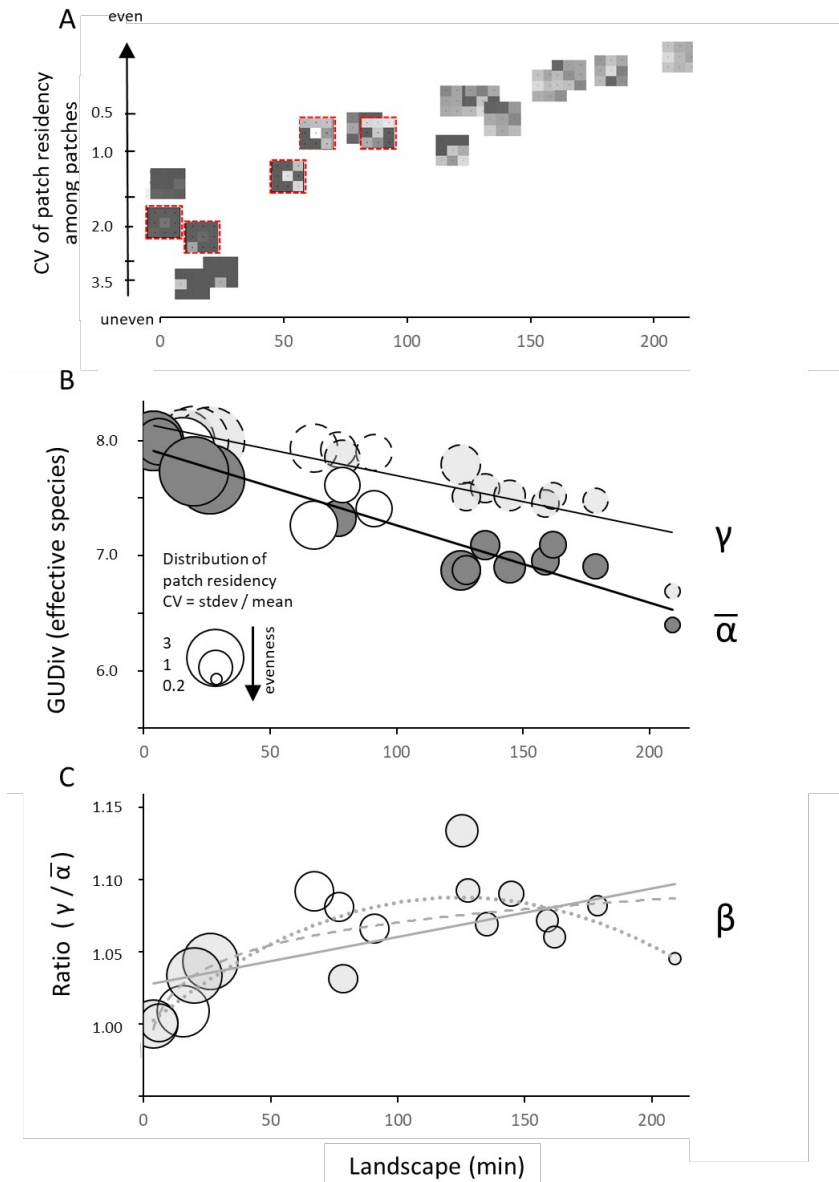


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624 **Figure 2A** Local α -GUDiv (Giving-up diversity) in experimental food patches with 160 food items
625 of eight species (20 items each) mixed in 2 litre of sand, exploited by Norway rats (*Rattus*
626 *norvegicus*) **A**) Number of effective species (Hill number, Hill 1973) in relation to the (unspecific)
627 food density left in the patch (Giving-up density GUD, expressed as items per litre). Lines:
628 Predictions for GUDiv for two extreme foraging strategies: equal removal of food species
629 (broken line); selective removal of one food species after the other (solid line), inset: Norway rat
630 handling a sunflower seed caught on camera trap. **2B** Species-specific GUDs for 8 seed species in
631 mixed seed patches exploited by wild Norway rats by patch residency. Exponential exploitation
632 patterns are typical for diminishing returns. Patch residency values are displayed as rug-plot with
633 marks along the x-axis. Symbol sizes relate to seed size.

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Figure. 3: Foraging landscapes created by Norway rats (*Rattus norvegicus*) in experimental landscapes with 9 food patches with 20 food items of 8 food species per patch (see Table 3). Empirical data (dashed frame (A) and white circles (B and C) and simulated landscapes from re-shuffled empirical patch data (no frame in A and coloured circles in B and C). (A) Evenness of landscapes (inverse coefficient of variation among patch residencies) by landscape residency (cumulated over patches of a landscape). Each symbol represents a landscape composed of 9 patches, lighter patch colours indicate longer patch residencies. (B) Giving-up diversities (GUDiv) of food species assemblages in foraging landscapes exploited by Norway rat foragers. Shown are the mean local scale diversity (mean α -GUDiv) and the landscape-wide diversity (γ -GUDiv); (C)

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645 Between patch variation in giving-up diversity (β -GUDiv). Circle size refers to CV in landscape
646 residency of a landscape (the larger circle size the more uneven distribution)

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648 ---Text Box 1----

649 **Box 1: Non-exhaustive list of testable predictions on A) how variation in foraging behaviour of**
650 **consumers have cascading effects on biodiversity of resource species and on B) feedbacks between**
651 **functional trait composition of the resources species assemblage and foraging behaviour of the**
652 **consumer.**

653 A) Variation in foraging behaviour of consumers affect giving-up density of single food species (GUD)
654 and giving-up diversity (GUDiv) of the remaining assemblage of resource species on different diversity
655 levels (α -GUDiv, γ -GUDiv and β -GUDiv).

656 Potential factors modifying foraging behaviour of the consumer and resulting GUD and GUDivs:

- 657 1. **Patch residency:** With increasing residency in a food patch both GUD and α -GUDiv decrease.
- 658 2. **Mobility among patches:** With increasing mobility (i.e. patch change frequency) patches are
659 homogenised resulting in low β -GUDiv. Further, if foragers are selective, single food species
660 may disappear across a region, i.e. both α -GUDiv and γ -GUDiv may decrease.
- 661 3. **Selectivity:** The higher the selectivity of a forager for certain functional traits (e.g.
662 profitability, energy content, nutrient content, or handling time), the faster local resource
663 species diversity (i.e. α -GUDiv) decreases with patch residency. Local depletion of preferred
664 resources will motivate faster patch changes, resulting in higher variation between patches
665 (increased β -GUDiv) at medium time scales when not all patches have been visited by the
666 forager, but lower β -GUDiv at long time scales, i.e. when foragers homogenised α -GUDiv
667 among patches.
- 668 4. **Perceived predation risk ("fear"):**
 - 669 a. **Risk-heterogeneous landscapes:** Landscapes of fear that restrict foraging to areas
670 perceived as safe by the forager may create diversity patterns reflecting the
671 heterogeneous distribution of risk in a landscape. With foraging effort unevenly
672 distributed across a landscape, local diversity of resource species assemblages (i.e. α -
673 GUDiv) should differ among patches, while resource species are conserved across the
674 landscape at dangerous locations. Thus, landscape-wide γ -GUDiv is predicted to be
675 higher than mean local α -GUDiv and β -GUDiv of the landscape should be high.
 - 676 b. **Risk uniform landscapes:**
 - 677 i. At uniformly distributed low risk, optimal foragers deplete local food
678 patches evenly, resulting in low α -GUDiv. Due to long patch residencies and
679 safe travel among patches, α -GUDiv is homogenised among patches,

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680 *resulting in low mean α -GUDiv and similar low landscape wide γ -GUDiv;*
681 *correspondingly among-patch variation in biodiversity (β -GUDiv) is also low.*

682 *ii. At uniformly distributed high risk, local depletion rates can be very uneven*
683 *(Eccard and Liesenjohann 2008, 2014) since foragers behave sub-optimally*
684 *and deplete single locations to low levels, due to incomplete information or*
685 *due to avoiding risky travelling among locations. This behaviour ought to*
686 *result in high variation in α -GUDiv, but should maintain high landscape wide*
687 *γ -GUDiv and high β -GUDiv.*

688 **5. Fear and selectivity:** *Selectivity decreases local α -GUDiv, while fear prevents homogenisation*
689 *of landscape-wide mean α -GUDiv. Thus, high selectivity and great fear produce the highest*
690 *variability among patches (high β -GUDiv).*

691 **6. Inter-individual differences among foragers:**

692 *a. In selectivity: Among-individual variation in selectivity should result in a mosaic of*
693 *assemblages with similar local α -GUDiv, but high variation among local assemblages*
694 *resulting in higher γ -GUDiv and higher β -GUDiv (compared to a landscape where all*
695 *foragers behave similarly).*

696 *b. In fear: Among-individual variation in fear should result in great differences in*
697 *distribution of foraging effort. Fearful foragers deplete single, safe patches resulting*
698 *in heterogeneous patterns and, thus, low α -GUDiv, high γ -GUDiv and high β -GUDiv,*
699 *while fearless forgers should produce more homogeneous foraging landscapes (low*
700 *α -GUDiv, low γ -GUDiv and low β -GUDiv).*

701 **B) Dynamic feedbacks between resource trait combinations and forager's behaviour on GUDiv:**

702 **7. Higher diversity of functional traits** *in the assemblage of resource species should result in*
703 *faster/stronger decrease in local α -GUDiv. Diversity patterns at the regional level (γ -level) will*
704 *depend on whether all foragers select the same food species.*

705 **8. Absolute and relative abundance of resource species:**

706 *a. When patches are similar, foragers may specialise on the most abundant food and*
707 *increase landscape-wide γ -GUDiv and β -GUDiv and thereby facilitate an increase*
708 *when rare effects (Garb et al. 2000).*

709 *b. If patches are dissimilar, flexible foragers may homogenise landscape-wide species*
710 *pool (decreasing γ -GUDiv and β -GUDiv).*

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