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When are bacteria really gazelles? Comparing patchy ecologies with dimensionless numbers

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Abstract

From micro to planetary scales, spatial heterogeneity—patchiness—is ubiquitous in ecosystems, defining the environments in which organisms move and interact. However, most large-scale models still use spatially averaged ‘mean fields’ to represent natural populations, while fine-scale spatially explicit models are mostly restricted to particular organisms or systems. In a conceptual paper, Grünbaum (2012, *Interface Focus* 2: 150–155) introduced a heuristic, based on three dimensionless ratios quantifying movement, reproduction and resource consumption, to characterise patchy ecological interactions and identify when mean-field assumptions are justifiable. We calculated these dimensionless numbers for 33 interactions between consumers and their resource patches in terrestrial, aquatic and aerial environments. Consumers ranged in size from bacteria to whales, and patches lasted from minutes to millennia, with separation scales from mm to hundreds of km. No interactions could be accurately represented by naive mean-field models, though 19 (58%) could be partially simplified by averaging out movement, reproductive or consumption dynamics. Clustering interactions by their non-dimensional ratios revealed several unexpected dynamic similarities. For example, bacterial *Pseudoalteromonas* exploit nutrient plumes similarly to Mongolian gazelles grazing on ephemeral steppe vegetation. We argue that dimensional analysis is valuable for characterising ecological patchiness and can link widely different systems into a single quantitative framework.

KEYWORDS

comparative ecology, dimensional analysis, interactions, model systems, patchiness, scale

INTRODUCTION

Most ecosystems are patchy across a range of spatial and temporal scales; consequently, most ecological interactions occur in patchy environments (Hutchinson, 1961; Lawton, 1999; Levin, 1994; Wiens, 1976). In the ocean,

predators search for shifting schools of fish (Benoit-Bird et al., 2013; Weimerskirch et al., 2005). In the forest, grazers move from plant to plant or stand to stand (de Knecht et al., 2007). And at the microscale, bacteria search for organic particles and plumes of dissolved nutrients (Hellweger, 2018; Stocker, 2012; Yawata et al.,

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2020). The uneven distribution of resources means that consumers (i.e., predators, herbivores or detritivores) often experience resources far from their mean density. Patchiness and heterogeneous dynamics have been recognised as critical issues in ecology for decades (Codling & Dumbrell, 2012; Durrett & Levin, 1994) and form the basis of many ecological theories (Chesson, 2000; Davis et al., 2005). However, ecologists still struggle to incorporate them into our mental, mathematical and management models.

Two main challenges have prevented the full integration of patchiness into ecology and management. First, patches are by definition localised in space and time, so incorporating them requires temporally and spatially explicit models. Spatially explicit models are more theoretically complex, computationally expensive and difficult to use than non-spatial models (DeAngelis & Yurek, 2017; Morozov & Poggiale, 2012). Consequently, when making ecological inferences and predictions at landscape, regional or global scales, most researchers still rely on ‘mean-field’ models, assuming that spatially variable quantities can be represented by a single value averaged over coarse-grained grid cells or study areas (Codling & Dumbrell, 2012). Despite their simplicity and wide use, mean-field models are often inadequate descriptions of real ecological dynamics (Priyadarshi et al., 2019). If a mean-field model includes only linear functional relationships, the simplification may be acceptable, but if not, the spatial averaging will run afoul of Jensen’s inequality (Ruel & Ayres, 1999). Mean-field models can be sensitive to functional responses at low population densities, often require arbitrary assumptions of ecological thresholds and can erroneously predict competitive exclusions or extinctions in environments where real populations persist (Grünbaum, 2012; Hutchinson, 1961; Murray, 1989). While mean-field approximations may be appropriate in some situations, they must be justified based on specific hypotheses and scales of ecological processes.

The second challenge arises because ecological patches occur across a vast range of physical scales. Patchiness is present in almost all systems at some scale, and many statistics and metrics exist to quantify it (Fortin, 1999). However, it is less clear how to determine which patches, at which scales, are relevant for which organisms. Moreover, when a patchy process or interaction has been described for one species or system, it is often unclear which, if any, of those conclusions apply more generally. Such studies can remain isolated in their (sub)discipline’s literature as apparent special cases, with no way to identify similar dynamics in other taxa or environments.

One approach capable of addressing both of these challenges is dimensional analysis, as it facilitates comparisons between processes, regardless of scale (Horne & Schneider, 1994; Stephens & Dunbar, 1993; Box 1). In a theoretical paper, Grünbaum (2012) proposed a

BOX 1 Dimensional analysis and dynamic similarity

Dimensional analysis, also called non-dimensionalisation, is a technique for simplifying mathematical representations of physical problems. The key to this method is to reduce the number of parameters required to describe a system by combining the original variables into a smaller number of dimensionless ratios—i.e., ratios where all the physical units cancel out, leaving only a pure number expressing the relative importance of its components. This technique is widely used in the physical sciences, but less so in ecology, at least outside of its mathematical subfield (Nisbet, 2012). Dimensional analysis can provide quantitative insight by identifying the relative importance of different variables. It can also provide qualitative insights by identifying fundamental properties of systems with similar dynamics. Systems are dynamically similar when the relative importance of their attributes is the same—i.e., the ratios between variables are the same. Dynamically similar systems can serve as models for one another, even if their absolute scales differ widely.

A well-known physical example is the Reynolds number (Re), which gives the ratio of inertial to viscous forces within a fluid. Quantitatively, if $Re \gg 1$ a fluid dynamicist can safely drop all frictional terms from their equations, even though some friction is, of course, always present. Qualitatively, flows with Re greater than about 5×10^5 are likely to be turbulent, and thus fundamentally different from the laminar flows prevalent at lower Re . Since Re is unitless, this pattern holds true regardless of the particular fluid and physical scale. Thus, Re is as useful for designing airplanes as it is for describing the biomechanics of plankton (Purcell, 1977).

Well-known examples of dimensionless numbers in ecology include the relationship between growth K and mortality M (Beverton & Holt, 1959; Charnov, 1990; Charnov et al., 1991), the ratio of plankton growth to diffusive losses in the KISS model of plankton patch formation (McGillicuddy & Franks, 2019) and the epidemiological parameter R_0 , giving the number of new cases arising from each infectious carrier of a disease. Finally, the growth parameter r in May’s (1976) logistic map (a simple non-dimensionalised population growth model) provides an ecological analogue of the qualitative transition from laminar to turbulent flow described above. When $r < 1$, a population goes extinct. When it is between 1 and 3, the population approaches a steady state at the carrying capacity. When r is between 3 and ≈ 3.57 , the population oscillates periodically, and when $r > 3.58$, it oscillates chaotically.

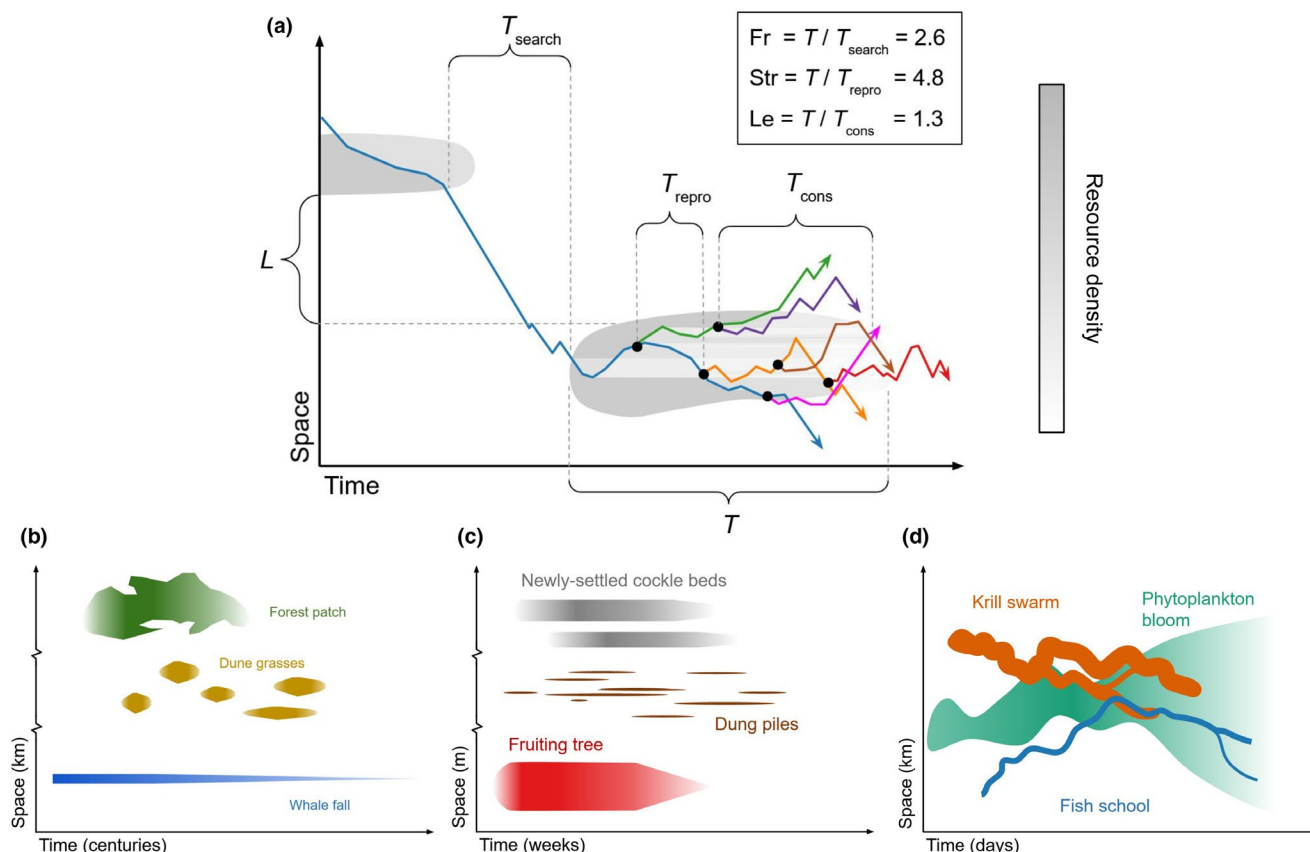


FIGURE 1 Conceptual space-time depictions of patchy consumer-resource interactions. (a) Hypothetical interaction between consumers (solid coloured lines) feeding on resource patches (grey regions). As time (horizontal axis) progresses, consumers move on a simplified one-dimensional spatial domain (vertical axis), seeking resource patches. When they enter a patch, they begin to deplete it, indicated by lightened shading to the right of consumer trajectories (i.e., after their passage). Black dots represent reproduction events, and hence the birth of new consumers. Brackets show patch duration (T) and the separation distance (L), as well as the time for consumers to locate a patch (T_{search}), reproduce (T_{repro}) and consume a patch (T_{cons} , assuming they are at a ‘typical’ density within it). The box in the upper right gives the ratios of the interaction’s time scales as its dimensionless Frost (Fr), Strathmann (Str) and Lessard (Le) numbers. While this schematic shows a single value for each of these quantities, in nature they will of course be variable, so in practice, the three ratios are calculated using ‘characteristic’ order-of-magnitude values for L , T , T_{search} , T_{repro} and T_{cons} . Panels (b), (c) and (d) depict the different physical scales of various resource patches. (b) Forest stands, dune grass patches and whale falls persist for tens or hundreds of years and are spaced at kilometre scales. (c) Trees bear ripe fruit, dung piles remain favourable for dung beetles and newly settled cockles are small enough for crabs to eat for weeks, with separation scales of metres. (d) Phytoplankton blooms persist for days to weeks, while zooplankton and fish aggregations last from hours to days, with separation scales of km

dimensional analysis of interactions between consumers and their resource patches. In this framework, the resource landscape is simplified as a collection of discrete patches which are separated by a characteristic distance, persist for a characteristic time span and contain a characteristic density of resources. Consumers are distinguished by their typical movement rates, generation times and consumption rates (Figure 1). From these parameters, three dimensionless ratios can be calculated: the Frost, Strathmann and Lessard numbers.

The Frost number, Fr , is the ratio of patch duration T to the time required for consumers to locate a patch, T_{search} , and captures the importance of consumer movement to patch occupancy. When $Fr \gg 1$, consumers locate patches easily and spend most of their time inside them. When $Fr \ll 1$, consumers spend most of their time searching for patches. The Strathmann number, Str , is

the ratio of patch duration to the consumer’s generation time, T_{repro} , and expresses the importance of reproduction for patch occupancy. When $Str \gg 1$, multiple generations of consumers can reproduce inside a patch, allowing for population growth within the patch. When $Str \ll 1$, consumers must visit many patches per generation. Finally, the Lessard number, Le , is the ratio of a patch’s undisturbed duration to the time, T_{cons} , required for consumers to deplete it when they are present at a typical density. It characterises the impact consumers have on the persistence of resource patches: when $Le \gg 1$, they tend to quickly deplete patches, while when $Le \ll 1$, they have little impact on the abundance of resources. These three ratios quantify the importance of movement, reproduction and resource depletion to the consumer-resource interaction, independent of the absolute scales and rates involved.

The most practical application of these ratios is to determine which consumer-resource interactions can be approximated using a mean-field model. If Fr , Str and Le are 'small' (i.e., $\ll 1$), then consumer movement, reproduction and consumption operate on time scales much longer than those of individual resource patches. Consumers encounter patches randomly and integrate over many patches in time, justifying the mean-field assumption. If any of the ratios are *not* 'small,' then the interaction is 'functionally patchy,' and must be treated as such. For instance, if $Fr \gg 1$, consumers will spend most of their time inside patches, experiencing local resource densities well above the average value. In circumstances like these, naive mean-field assumptions underestimate the resources available to the consumers and may predict extinction when real populations persist (Benoit-Bird et al., 2013; Lasker, 1975). Very large values of a ratio ($\gg 1$) indicate that consumer movement, reproduction and consumption operate on time scales much shorter than those of individual resource patches and may suggest their own opportunities for simplification leveraging this difference in timescales. The case of commensurate timescales (ratios ~ 1) is the most challenging and may require the explicit modelling of patch and consumer dynamics.

Grünbaum (2012) also proposed several conjectures for patchy interactions. For instance, consumer populations will struggle to persist if they cannot locate patches easily, reproduce within patches or both. This leads to the prediction that all interactions should have at least one of Fr or $Str > 1$. Relatedly, if either movement or reproduction is difficult or costly for a consumer species, evolution should select for movement or reproductive rates that are 'just fast enough' to raise Fr or Str above the critical value of ≈ 1 .

Despite their conceptual power and potential utility, to our knowledge, these dimensionless ratios have never been empirically calculated. This was the objective of our study. We conducted a literature review and meta-analysis of patchy consumer-resource interactions across a wide range of taxa, scales and ecosystems. We obtained values for consumer rates and the spatio-temporal scales of their resource patches and used these to calculate Frost, Strathmann and Lessard numbers for each interaction. Using these ratios, we determined which interactions were functionally patchy and which could be approximated using mean-field assumptions, and evaluated several of Grünbaum's conjectures. Finally, we identified consumer-resource interactions that were dynamically similar—that is, close together in Fr - Str - Le space. This approach identified commonalities which might otherwise be obscured by differences in taxon, environment or spatiotemporal scale, shifting the focus from individual species towards generalised interactions between consumers, resources and their environments. The ultimate goal of such an analysis is to enable more parsimonious

models and a deeper, more general understanding of patch dynamics in ecology.

MATERIALS AND METHODS

We took a meta-study approach to calculate Grünbaum's dimensionless ratios for consumers feeding on patchy resources. For this analysis, a 'patch' was defined as a spatially and temporally bounded region, within which a resource is dense enough for profitable exploitation by a consumer (Charnov, 1976; Wiens, 1976; Figure 1). Some researchers have used 'patchiness' as a loose synonym for 'heterogeneity,' including spatial gradients (e.g., Arditi & Dacorogna, 1988), but we required patches to contain a local maximum of the resource's density. We restricted our analysis to trophic interactions, where exploitation of the resource involved an energy transfer to the consumer. For example, a hydrothermal vent is a resource patch for chemosynthetic organisms because they use the vent fluids as a source of chemical energy. In contrast, a lake is not a resource patch for a fish—rather, it is a habitat.

To calculate values for Fr , Str and Le , we searched the literature for data on specific consumer-resource pairs. Pairs were selected to reflect a diversity of systems, based on author expertise and availability of necessary data. Literature searches were performed using Google Scholar and Web of Science for the parameters of interest (Table 1). Search terms included 'speed', 'turning interval', 'movement', 'growth rate', 'reproduction', 'consumption rate', 'foraging' and 'patch'. We took values directly from published sources when possible, though some values were estimated based on published ranges or the interpretation of published figures. In the rare cases where data were not available, parameters were estimated either via the authors' expertise or consultation with experts. All raw values used for the analysis, with their sources, are tabulated in Table S1. While our selection of consumer-resource interactions cannot be considered random or unbiased, we made conscious efforts to represent marine, freshwater and terrestrial environments; microbial, invertebrate and vertebrate taxa; employing carnivorous, herbivorous and detrital feeding strategies and patches which were stationary, passively moving and actively moving.

These 'characteristic' rates, scales and densities for consumers and resource patches were necessarily broad-brush descriptions; selecting a single value based on the available literature was often challenging and somewhat arbitrary. Fortunately, for their intended use as descriptive heuristics, the dimensionless numbers did not require precision greater than 1–2 significant digits. With better data and domain knowledge, it would be possible to calculate them more precisely, but was beyond the scope of this paper. In practice, the dimensionless ratios varied across many

TABLE 1 Parameters and rates obtained from the literature to develop data-derived Frost, Strathmann and Lessard numbers (Grünbaum, 2012). The physical dimensions of each quantity are denoted as **T** (time), **L** (length), **N** (number of individuals) and **M** (biomass), with the subscripts 'R' and 'C' indicating 'resource' or 'consumer.' In each ratio, T represents the typical patch duration, T_{search} is the time required for a consumer to locate a patch, T_{repro} is the consumer's generation time and T_{cons} is the time required for consumers to deplete a patch. All of these durations are 'characteristic time scales,' accurate to an order of magnitude but not necessarily more so. (Adapted from Table 1 in Grünbaum, 2012.)

Parameter	Description	Dimension
Consumer level	s	L T^{-1}
	τ	T
	g	T
	η	$\text{N}_R \text{N}_C^{-1} \text{T}^{-1}$, or $\text{M}_R \text{M}_C^{-1} \text{T}^{-1}$
Resource patch level	T	T
	L	L
	R	$\text{N}_R \text{L}^{-2}$ or $\text{M}_R \text{L}^{-2}$
	C	$\text{N}_C \text{L}^{-2}$ or $\text{M}_C \text{L}^{-2}$
Timescales	T	T
	$T_{\text{search}} = L/s^2\tau$	T
	$T_{\text{search}} = L/s$	T
	$T_{\text{repro}} = g$	T
	$T_{\text{cons}} = R/\eta C$	T
Ratio	$Fr = T/T_{\text{search}}$	—
	$Str = T/T_{\text{repro}}$	—
	$Le = T/T_{\text{cons}}$	—

orders of magnitude (see Results and Discussion), so greater precision would not have qualitatively changed the results.

To allow for comparisons, we converted all rates and quantities to base SI units (seconds, metres and grams) and checked for dimensional consistency with the Julia package Unitful.jl (Keller, 2021). Values for Fr , Str and Le were then calculated for each consumer-resource pair (Box 2). We calculated two Frost numbers for each consumer: one based on an assumption of diffusive (i.e., random walk) movement and one on directed-line (i.e., ballistic) movement. These two movement types are unrealistically simple, but define reasonable bounds for the range of more complex movement types used by real organisms.

To determine when systems are functionally patchy and to visualise the potential impact of that patchiness on consumer-resource dynamics, we developed four-quadrant diagrams similar to those in Grünbaum (2012). These diagrams provide a graphical assessment of patch dynamics and the importance of consumer movement (Fr), reproduction (Str) and patch consumption rate (Le) to trophic interactions. These three ratios can be visualised as a point in three dimensions; for readability, we display the ratios on logarithmic axes and examine this 3-D point cloud projected on only two axes at a time. These figures also let us compare our results with predictions from Grünbaum (2012). We also calculated the Pearson product-moment correlation between each pair of dimensionless numbers.

To determine which consumer-resource pairs were dynamically similar, we performed a cluster analysis based on the Euclidean distance between the $\log_{10}$ Fr , Str and Le ratios for each consumer-resource pair with complete agglomeration. The dendrogram was partitioned into five discrete clusters using a k-medoids algorithm (Reynolds et al., 2006; Schubert & Rousseeuw, 2019) within the ComplexHeatmap R package (Gu et al., 2016). This number of clusters was chosen based on the 'elbow method' (Thorndike, 1953, Figure S2) and our subjective assessment of the level of clustering that generated biologically meaningful groups. Within each cluster, we examined each interaction's ecosystem, consumer type, patch mobility and consumer/resource size ratio, to explore whether these characteristics were associated with particular types of consumer-resource dynamics. All data and associated code for this project are available at <https://doi.org/10.5281/zenodo.6338651>.

RESULTS AND DISCUSSION

We analysed a total of 33 interactions between consumers and their resource patches. Of these, 12 took place in terrestrial environments, 18 in marine environments and 3 in freshwater (Table S1). The consumers ranged in average body size from 0.5 μm to 22 m and in mass from 10 picograms to 200 tonnes. They included representatives of multiple trophic strategies (11 herbivores, 17 carnivores and 5 detritivores) and body plans

BOX 2 Calculating Frost, Strathmann and Lessard numbers: a tutorial

In theory, the Frost, Strathmann and Lessard numbers are all easy to calculate: they are the ratio of an undisturbed patch's duration, T , to the time a consumer spends searching for a patch (T_{search}), the consumer's generation time (T_{repro}) and the time required for consumers to deplete the patch (T_{cons}), respectively (Table 1). In practice, using real biological information, they require a bit more calculation and interpretation. As a concrete example, consider interaction 19, between common terns, *Sterna hirundo*, and their forage fish prey. Terns are small, shallow-diving seabirds which feed on schools of small fishes forced to the surface by under-water predators (Safina & Burger, 1985) or physical flows (Urmy & Warren, 2018).

Quantifying resource patches

The first step is to characterise the patchy resource landscape. This requires estimating the characteristic duration of surface fish schools T , the typical distance between them L and the density of resources within them, R (Table 1). Based on hydroacoustic surveys and observations of tern feeding aggregations (Safina & Burger, 1985; Urmy, 2020; Urmy & Warren, 2018), we set the characteristic patch scales at $T = 6$ h, $L = 5$ km and $R = 100$ fish m^{-2} .

Quantifying consumer rates

The second step is to find appropriate rates for consumer movement, reproduction and consumption. We estimated T_{search} based on both directed (straight line) and diffusive (random walk) movement types. For directed movement, $T_{\text{search}} = L / s$, where s is the consumer's speed (approximately 11 m s^{-1} for terns, Urmy & Warren, 2017). For diffusive movement, T_{search} can be calculated as $L^2 / (s^2 \tau)$, where τ is the time interval between turns in the assumed random walk, estimated at roughly 10 s for the terns. Plugging in these quantities yielded a directed search time of 460 s (just under 8 min) and a diffusive search time of 21,000 s (almost 6 h). Terns reach reproductive maturity in about 4 years (Di Costanzo 1980), so this is their reproductive timescale T_{repro} . Finally, typical densities C of terns over a patch of fish are approximately $0.05 \text{ birds m}^{-2}$ (Urmy & Warren, 2018), and their individual consumption rate η is on the order of $40 \text{ fish bird}^{-1} \text{ day}^{-1}$. From these numbers, we can calculate $T_{\text{cons}} = R / C \eta = 4.3 \times 10^6 \text{ s}$ (over 3 years).

Calculating the ratios and other considerations

With the relevant patch and consumer timescales defined, it is easy to calculate the three non-dimensional ratios, and we obtain values of $\text{Fr}_{\text{diff}} = 1.1$, $\text{Fr}_{\text{dir}} = 48$, $\text{Str} = 1.7 \times 10^{-4}$ and $\text{Le} = 5.0 \times 10^{-3}$. It is critical to convert all quantities to the same units before calculating the ratios; otherwise, they will not actually be dimensionless. Care must be taken to check each calculation for dimensional consistency and compatibility of units. Finally, it is important to remember that these ratios are only a heuristic characterisation of patchy dynamics. Depending on the consumer and resource, good measurements of all rates may or may not be available, and where they are not, rough estimates and order-of-magnitude educated guesses may be used and still provide useful insights.

(2 microbes, 13 invertebrates and 18 vertebrates). In most cases, resource patches were composed of more than one organism; these covered a similarly large range of body sizes (Figure 2a). The resource patches lasted anywhere from 5 min (groups of seals swimming from their haul-out to deep water) to 1500 years (whale falls being buried by sediment) and were separated by distances ranging from 4 cm (nutrient patches from lysing phytoplankton) to 55 km (schools of zooplankton and fish in the open ocean) (Figure 2b). When the consumers' search, reproduction and patch depletion times were normalised by the durations of their resource patches, the resulting Frost, Strathmann and Lessard numbers ranged across more than 10 orders of magnitude (Table 2, Figure 3). Despite the huge diversity of biology and range of scales considered, the dimensional analysis framework allowed us to identify

a number of generalities, trends and similarities across all the interactions.

All interactions were functionally patchy

Every consumer-resource interaction considered here was functionally patchy with respect to movement, population growth or consumption. All interactions had at least one of the three dimensionless ratios ≥ 1 , and in 23 out of the 33 pairs, at least one of the ratios was >10 (Table 3). Seven of the 33 consumer-resource interactions (21%) had all three numbers >1 , indicating that patch dynamics had a significant influence on all of these aspects of consumer-resource ecology. Given these findings, a model using a simple mean-field assumption would not be justifiable for any of these interactions.

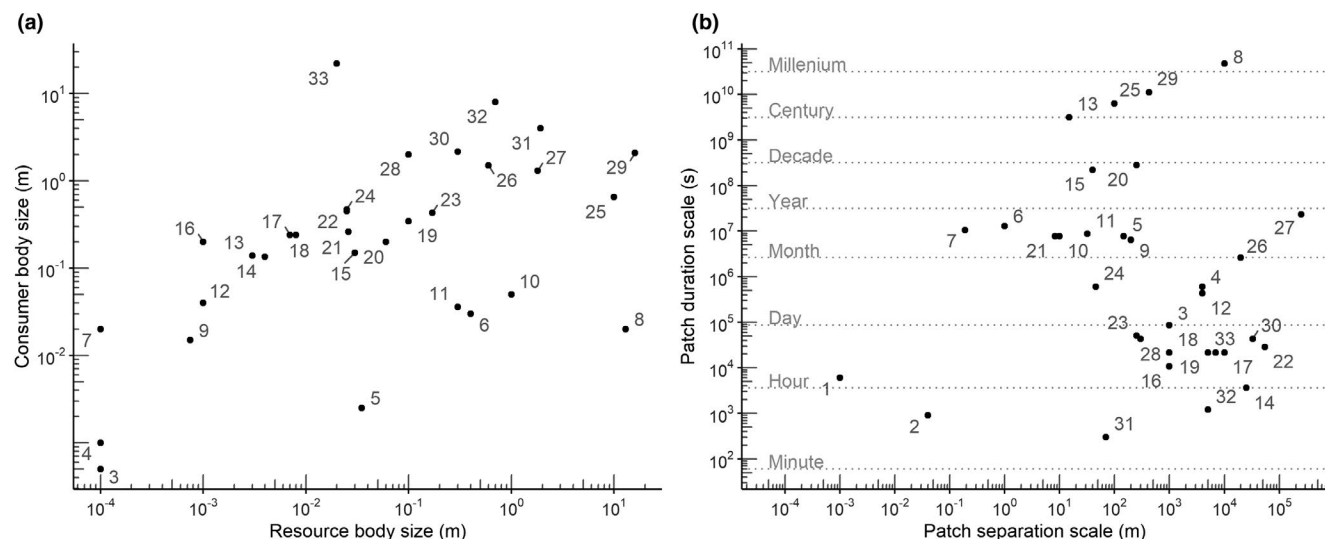


FIGURE 2 The sizes of consumer and resource organisms, and the spatio-temporal scales of resource patches, spanned many orders of magnitude. (a) Body size of consumer organisms (vertical axis) plotted against the size of an individual resource item (horizontal axis). Numbered labels refer to the interaction IDs in Table 3, each containing a consumer organism and a corresponding resource. (Note that the two bacterial interactions are excluded, since ‘organism size’ is poorly defined for a dissolved nutrient resource.) (b) Resource patches spanned approximately eight orders of magnitude in their spatial and temporal scales. Each point represents the resource patch within an interaction, labelled as in (a). The horizontal axis represents the typical distance scale separating patches in space, ranging from ~ 1 mm (microscale nutrient plumes, interaction 1) to ~ 250 km (caribou herds, interaction 27). The vertical axis represents the patches’ typical duration, ranging from ~ 5 min (seal groups, interaction 31) to $\sim 1,500$ years (whale falls, 8)

Given our deliberate selection of systems with patchy resources, this result is perhaps not surprising and precludes generalising this result to all consumer-resource interactions. The fact that every interaction surveyed was functionally patchy raises questions: what would a non-patchy interaction look like, and how common are they? A trivial answer is one where the resource landscape is homogeneous in time and space. Such interactions may exist, but since these dimensionless ratios require identifying and quantifying patches (their duration timescale, separation distance, etc.), they are undefined in truly homogeneous landscapes. A less-trivial answer is an interaction in which resources are patchy, but the scales of the interaction make them effectively homogeneous from the perspective of the consumer, enabling a mean-field simplification (for a contrived hypothetical example, refer to Box S1). While the frequency of such ‘literally patchy but functionally homogeneous’ interactions in nature is unknown, it does not appear to be high. Our results are thus a warning to ecologists dealing with foraging movements, consumption, predation or trophic transfer rates: if a system looks like it might have patchy dynamics, do not assume they can be ignored.

Even though patch dynamics could not be ignored entirely in any of the consumer-resource pairs, the majority (19 out of 33 interactions or 58%) had at least one dimensionless ratio < 0.1 , indicating that at least one of the processes (movement, reproduction or consumption) could potentially be simplified using a mean-field approximation. Additionally, ratios with values $\gg 1$ may also suggest useful simplifications, including alternative ways

to formulate mean-field models. As a concrete example, consider interaction 19, between common terns *Sterna hirundo* and forage fishes. This interaction is characterised by a Fr_{dir} of 48, indicating that the terns’ rapid flight allows them to spend more time over fish patches than over empty water. When modelling trophic transfer between fishes and terns, estimates of energy flow based on the mean prey density (e.g., measured by a fishery survey) would be biased low. While this naive formulation of a mean-field model is clearly unsuitable, a more reasonable (if slightly more complex) one could be parameterised based on the mean fish and tern densities *within* schools, perhaps with second-order effects to account for the proportion of the landscape in patches, search times and other foraging dynamics. At the same time, terns visit many patches per generation ($Str = 1.7 \times 10^{-4}$), so if a parameterised energy transfer function was developed, averaging it over days, weeks or even an entire breeding season would be justifiable. Finally, the low Lessard number ($Le = 0.005$) indicates that terns rarely deplete patches, so models of this interaction can treat the density and distribution of their prey as endogenous variables (cf. Urmy, 2021).

Analogous simplifications for low and high values of each non-dimensional number can be identified for most of the consumer-resource interactions (Table 3). In general, low values of the Frost number indicate that spatial mean-field models may be appropriate, while high values mean they are not. As always, spatial mean-field models are highly dependent on scale; interactions with a high Frost number may be modelled based on mean densities inside

TABLE 2 Rates and dimensionless ratios for all consumer-resource pairs. Parameters are defined in Table 1. Consumer and resource quantities are presented in their original units from the primary literature, which vary from interaction to interaction. For instance, the 'currency' of an interaction could be expressed in individuals or biomass, densities could be areal or volumetric, etc. However, when plugged into the equations in Table 1, the quantities within each row are dimensionally consistent. Abbreviations: m = metres, g = grams, s = seconds, min = minutes, h = hours, d = days, mo = months, y = years, ha = hectares, c = consumer individuals, r = resource individuals, mol = molecules, pch = patch, diff = diffusive, dir = directed. For a more detailed presentation of this information with literature citations, refer to Table S1

ID	Consumer-resource pair	Consumer level				Resource patch level			
		s	τ	g	η	C	T (s)	L (m)	R
1	<i>Vibrio</i> –Nutrients	0.01 mm s ⁻¹	4 s	5 h	2.0×10^4 mol c ⁻¹ s ⁻¹	5290 c mm ⁻³	6000	0.001	3.0×10^{20} mol mL ⁻¹
2	<i>Pseudoalteromonas</i> – Nutrients	8.7×10^{-5} m s ⁻¹	0.25 s	3 h		1.0×10^4 c mL ⁻¹	900	0.04	5.7×10^{-4} mol L ⁻¹
3	Bosmina–Diatoms	0.8 mm s ⁻¹	6.7 s	12.5 h	168 r c ⁻¹ d ⁻¹	252 c m ⁻³	8.6×10^4	1000	21 r mL ⁻¹
4	Copepods– Phytoplankton layers	1.42 mm s ⁻¹	1.25 s	20 d	4.0×10^4 r c ⁻¹ d ⁻¹	2.0×10^4 c m ⁻³	6.1×10^5	4000	1000 r mL ⁻¹
5	Fruit flies–Marula fruit	30 cm s ⁻¹	1 s	15 d	2×10^{-6} g c ⁻¹ d ⁻¹	1.0×10^4 c pch ⁻¹	7.8×10^6	146	14 kg pch ⁻¹
6	Caterpillar–Kale plants	0.2 cm s ⁻¹	6 min	32 d	0.41 g c ⁻¹ min ⁻¹	100 c pch ⁻¹	1.3×10^7	1	100 g pch ⁻¹
7	Caddisfly–Periphyton	50 cm min ⁻¹	15 s	1 y	3.3×10^{-7} g c ⁻¹ h ⁻¹	70 c m ⁻²	1.1×10^7	0.19	1.2×10^{-5} g cm ⁻²
8	Bone worms–Whale falls	10 cm s ⁻¹	22.2 h	2 mo		10 c cm ⁻²	4.7×10^{10}	1.0×10^4	
9	Green crabs–Cockles	0.54 cm s ⁻¹	3.2 s	3 y	6.5 r c ⁻¹ d ⁻¹	25 c m ⁻²	6.5×10^6	200	1×10^4 r m ⁻²
10	Desert locust–Vegetation	10 km h ⁻¹	2 s	60 d	2 g c ⁻¹ d ⁻¹	6.0×10^7 c km ⁻²	1.6×10^7	10	1000 kg ha ⁻¹
11	Dung beetle–Dung	0.05 m s ⁻¹	8 s	6 mo	0.91 g c ⁻¹ min ⁻¹	1 c pch ⁻¹	8.7×10^6	32	5620 g pch ⁻¹
12	Ctenophores–Copepods	0.7 cm s ⁻¹	10 s	7.75 d	10 r c ⁻¹ h ⁻¹	50 c m ⁻³	4.3×10^5	4000	2×10^4 r m ⁻³
13	Beach mouse–Dune seeds	11.4 km h ⁻¹	1 s	26 d	14 r c ⁻¹ d ⁻¹	8 c ha ⁻¹	3.2×10^9	15	270 r m ⁻²
14	Chimney swifts–Aerial plankton	11.3 m s ⁻¹	2 s	2 y	415 r c ⁻¹ h	3.8×10^{-6} c m ⁻³	3600	2.5×10^4	0.001 r m ⁻³
15	Northern sea stars–Mussels	5 cm min ⁻¹	10 min	2 y	2 r c ⁻¹ d ⁻¹	5.5 c m ⁻²	2.2×10^8	40	3000 r m ⁻²
16	Trout–Zooplankton	30 cm s ⁻¹	7 s	4 y	0.02 g c ⁻¹ s ⁻¹	3.5×10^{-3} c m ⁻³	1.1×10^4	1000	50 g m ⁻³
17	Red knots–Cockles	20 m s ⁻¹	40 s	2 y	0.4 mg c ⁻¹ s ⁻¹	1×10^{-4} c m ⁻²	2.2×10^4	1.0×10^4	2 g m ⁻²
18	Red knots–Clams	20 m s ⁻¹	40 s	2 y	0.4 mg c ⁻¹ s ⁻¹	1×10^{-4} c m ⁻²	2.2×10^4	1000	1 g m ⁻²
19	Terns–Forage fishes	11 m s ⁻¹	10 s	4 y	40 r c ⁻¹ d ⁻¹	0.05 c m ⁻²	2.2×10^4	5000	100 r m ⁻²
20	Pisaster sea star–Mussels	1.67 m h ⁻¹	10 min	6 y	80 r c ⁻¹ y ⁻¹	16.5 c m ⁻²	2.9×10^8	250	250 r m ⁻²
21	Eastern grey squirrel–Acorn	50 cm s ⁻¹	10 s	1.25 y	6.1×10^{-3} r c ⁻¹ s ⁻¹	0.03 c pch ⁻¹	7.8×10^6	8.3	1000 r pch ⁻¹
22	Murres–Zooplankton/ fish	20.9 m s ⁻¹	1 min	4 y	700 r c ⁻¹ d ⁻¹	26 c km ⁻²	2.9×10^4	5.5×10^4	75 r m ⁻²
23	Penguin–Fish school	1.1 m s ⁻¹	1 min	2.5 y	192 g c ⁻¹ d ⁻¹	4 c pch ⁻¹	5.0×10^4	250	243 kg pch ⁻¹
24	Spider monkeys–Fruit trees	4.8 m min ⁻¹	5 min	6.5 y			6.0×10^5	45.8	
25	Beaver–Maple tree	28 m min ⁻¹	1 min	5.4 y	6.7×10^{-3} r c ⁻¹ s ⁻¹	2.6 c km ⁻²	6.3×10^9	50	0.18 r m ⁻²
26	Mongolian gazelle–Vegetation	8.2 km d ⁻¹	1 d	2 y	5 g c ⁻¹ min ⁻¹	281 c km ⁻²	2.6×10^6	2.0×10^4	20 g m ⁻²
27	Wolf–Caribou	8.7 km h ⁻¹	1 h	22 mo	0.045 r c ⁻¹ d ⁻¹	9 c pch ⁻¹	2.3×10^7	2.5×10^5	1000 r pch ⁻¹
28	Fur seals–Pollock	3.5 m s ⁻¹	1 min	4 y	3 kg c ⁻¹ d ⁻¹	2 c pch ⁻¹	4.3×10^4	300	3 kg pch ⁻¹
29	Elk–Forest patch	759 m h ⁻¹	3 min	5.7 y	989 g c ⁻¹ d ⁻¹	0.625 c km ⁻²	1.1×10^{10}	427	245 g m ⁻²
30	Tuna–Herring	1.63 m s ⁻¹	1.8 min	14 y	24.6 r c ⁻¹ d ⁻¹	0.54 c m ⁻²	4.3×10^4	3.3×10^4	10 r m ⁻²
31	White sharks–Seals	1.34 m s ⁻¹	30 s	12.3 y	0.25 r c ⁻¹ d ⁻¹	1 c pch ⁻¹	300	70	8 r pch ⁻¹
32	Killer whale–Chinook salmon	1.6 m s ⁻¹	1 min	24 y	7 r c ⁻¹ min ⁻¹	1.2×10^{-6} c m ⁻³	1200	500	0.05 n m ⁻³
33	Blue whale–Krill	3.7 km h ⁻¹	400 s	10 y	105 kg c ⁻¹ min ⁻¹	0.02 c km ⁻²	2.2×10^4	7000	1 kg m ⁻²

Timescales				Dimensionless ratios			
T_{search} (diff, s)	T_{search} (dir, s)	T_{repro} (s)	T_{cons} (s)	Fr (diff)	Fr (dir)	Str	Le
2.5×10^3	100	1.8×10^4	2.8×10^9	2.4	60.0	3.3×10^{-1}	2.1×10^{-6}
8.5×10^5	460	1.1×10^4	900	1.1×10^{-3}	2.0	8.3×10^{-2}	1.0
2.3×10^{11}	1.3×10^6	4.5×10^4	4.3×10^7	3.7×10^{-7}	6.9×10^{-2}	1.9	2.0×10^{-3}
6.4×10^{12}	2.8×10^6	1.7×10^6	1.1×10^5	9.5×10^{-8}	2.2×10^{-1}	3.5×10^{-1}	5.6
2.4×10^5	490	1.3×10^6	6.1×10^{10}	33	1.6×10^4	6.0	1.3×10^{-4}
690	500	2.8×10^6	150	1.9×10^4	2.6×10^4	4.7	8.8×10^4
35	23	3.2×10^7	1.9×10^7	3.0×10^5	4.6×10^5	3.3×10^{-1}	5.5×10^{-1}
1.3×10^5	1.0×10^5	5.2×10^6	3.2×10^8	3.8×10^5	4.7×10^5	9.1×10^3	150
4.3×10^8	3.7×10^4	9.5×10^7	5.3×10^6	1.5×10^{-2}	170	6.9×10^{-2}	1.2
6.5	3.6	5.2×10^6	7.2×10^4	2.4×10^6	4.3×10^6	3.0	220
5.1×10^4	640	1.6×10^7	3.7×10^5	170	1.4×10^4	5.6×10^{-1}	24.0
3.3×10^{10}	5.7×10^5	6.7×10^5	1.4×10^5	1.3×10^{-5}	7.6×10^{-1}	6.5×10^{-1}	3.0
22	4.7	2.3×10^6	2.1×10^9	1.4×10^8	6.7×10^8	1.4×10^3	1.5
2.5×10^6	2.2×10^3	6.3×10^7	2.3×10^3	1.5×10^{-3}	1.6	5.7×10^{-5}	1.6
3.8×10^6	4.8×10^4	6.3×10^7	3.2×10^7	57.5	4.6×10^3	3.5	7.0
1.6×10^6	3.3×10^3	1.3×10^8	7.1×10^5	6.8×10^{-3}	3.2	8.6×10^{-5}	1.5×10^{-2}
6.3×10^3	500	6.3×10^7	5.0×10^7	3.5	43	3.4×10^{-4}	4.3×10^{-4}
63	50	6.3×10^7	2.5×10^7	35	430	3.4×10^{-4}	8.6×10^{-4}
2.1×10^4	455	1.3×10^8	4.3×10^6	1.1	48	1.7×10^{-4}	5.0×10^{-3}
4.8×10^8	5.4×10^5	1.9×10^8	6.0×10^6	0.59	530	1.5	48
28	17	3.9×10^7	2.5×10^4	2.8×10^5	4.7×10^5	0.2	310
1.2×10^5	2.6×10^3	1.3×10^8	3.6×10^8	2.5×10^{-1}	11	2.3×10^{-4}	8.1×10^{-5}
860	230	7.9×10^7	2.7×10^7	59	220	6.4×10^{-4}	1.9×10^{-3}
1.1×10^3	700	2.0×10^8	810	550	860	3.0×10^{-3}	750
190	70	1.7×10^8	3.8×10^7	3.3×10^7	9.0×10^7	37.0	170
5.1×10^5	2.1×10^5	6.3×10^7	8.5×10^5	5.0	12	4.1×10^{-2}	3.0
3.0×10^6	6.1×10^5	5.7×10^7	2.1×10^8	7.9	39	4.1×10^{-1}	1.1×10^{-1}
120	86	1.3×10^8	4.3×10^4	350	500	3.4×10^{-4}	1.0
2.3×10^4	2.0×10^3	1.8×10^8	3.4×10^{10}	4.9×10^5	5.5×10^6	62.0	3.3×10^{-1}
3.8×10^6	2.0×10^4	4.4×10^8	6.5×10^4	1.1×10^{-2}	2.1	9.8×10^{-5}	6.6×10^{-1}
91	52	3.9×10^8	2.8×10^6	3.3	5.7	7.7×10^{-07}	1.1×10^{-4}
1.6×10^3	310	7.6×10^8	3.6×10^5	7.4×10^{-1}	3.8	1.6×10^{-6}	3.4×10^{-3}
1.2×10^5	6.8×10^3	3.2×10^8	2.7×10^7	1.9×10^{-1}	3.2	6.9×10^{-5}	7.9×10^{-4}

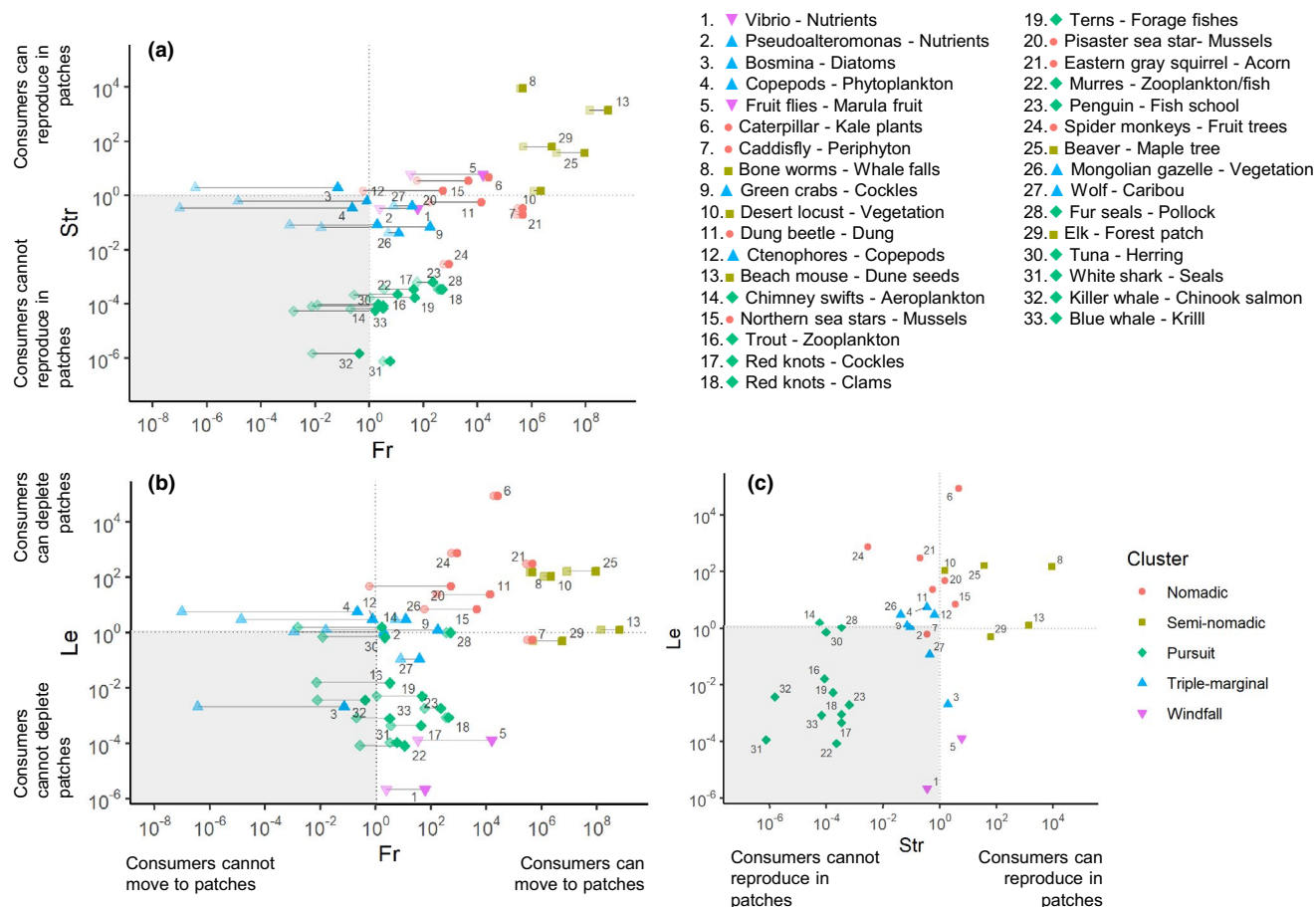


FIGURE 3 All consumer-resource interactions plotted on logarithmic axes in dimensionless Frost-Strathmann (a), Frost-Lessard (b) or Strathmann-Lessard (c) space, showing the relative importance of movement (Fr), reproduction (Str) and depletion (Le) in driving patch dynamics. In (a) and (b), two points, connected by a line, are plotted for each consumer-resource pair: the lighter point is the Frost number assuming diffusive (i.e. random walk) movement, while the filled point is the Frost number for directed movement. The horizontal and vertical grey lines show the critical values, where Fr, Str and Le equal 1. The shaded regions on each plot indicate interactions which are not functionally patchy with respect to each pair of dimensionless ratios. For interactions in these regions, the mean-field simplification may be (partially) justifiable. Point shapes and colours represent clusters of similar interactions identified via a k-medoids analysis; see Figure 4 and text for details

TABLE 3 Guidance for modelling approaches based on dimensionless ratios

	Ratio $\ll 1$	Ratio ~ 1	Ratio $\gg 1$
Fr	Consumers spend most time outside patches. Encounter and trophic transfer rates $\propto$ average densities of consumer and resource <i>over entire region</i> . Mean-field assumption may be ok	Movement and foraging behaviours must be modelled or parameterised explicitly	Consumers spend most of their time inside patches. Mean-field model, for example, encounter and trophic transfer rates $\propto$ average densities of consumer and resource <i>within patches</i> may be appropriate. (By definition, these rates will be higher than the overall spatial average)
Str	Consumers visit many patches per generation. Temporal averaging ok	Multitrophic population dynamics à la 2-species Lotka-Volterra, must be modelled or parameterised explicitly	Multiple generations reproduce within each patch. If $Le \ll 1$, approaches metapopulation dynamics and can be simplified as such
Le	Consumers have negligible effect on duration or density of resource patches, which appear and disappear independently of consumers. Feedbacks between consumer and resource density can be ignored	Consumers may deplete resource patches. Effects of movement, reproduction, dispersal and/or death must be modelled or parameterised to account for persistence of populations. If $Le \gg 1$, resource patches deplete quickly	

patches. Similarly, low values of the Strathmann number suggest that temporal averaging may be acceptable. With $Str \gg 1$, many generations of consumers can reproduce in each patch, and the appropriateness of mean-field models depends on the impact of those generations (i.e., Le). If the consumers do not deplete the patches (i.e., $Le \ll 1$), the interaction is essentially a traditional metapopulation (Hanski, 1998) and can be simplified as such. On the other hand, if $Le > 1$, there will be a more complex balance between patch appearance, colonisation and depletion, similar to the susceptible-infected-recovered dynamics familiar from epidemiological models (Kermack et al., 1927). If any of the ratios are ~ 1 , simple approximations will overlook crucial aspects of the system. In these cases, the relevant dynamic processes must be modelled or parameterised explicitly. It may also be possible, in these cases, to develop a situation-specific adjustment factor to mean-field model predictions that is some function of Fr , Str and Le .

Dimensionless ratios such as Fr , Str and Le provide a simple way to check whether complex models are required. Crucially, they also provide a means to develop those models in a more general way. Models expressed in terms of dimensionless ratios benefit from a reduced parameter space and often express a problem in its simplest possible form (Stephens & Dunbar, 1993). Additionally, the specific units attached to the variables become irrelevant, clarifying the essential dynamics of the system. Connections between dynamically similar systems can also be identified independent of their absolute size or scale.

Assessing Grünbaum's conjectures for organisms in patchy environments

Most interactions fell in the upper right three quadrants in Fr - Str space (Figure 3a), indicating that consumers would be able to find and exploit patches through movement, reproduction or both. For most consumers, the Frost number increased dramatically when directed rather than diffusive movement was assumed. Nine consumers would only be able to occupy patches if they used directed movement: if they relied on random search behaviour, their theoretical search time would be longer than a patch's typical duration. Figure S1 gives an alternate visualisation of critical Frost numbers following the scheme of Grünbaum's (2012) Figure 1a; this presentation suggests all but one consumer (killer whales feeding on salmon, interaction 32) would be able to access their patches. Overall, most consumers had $Fr > 1$, suggesting they would spend more time inside patches than in between them. While testing this prediction is beyond the scope of this paper, it is interesting to note that $Fr \gg 1$ implies a consumer movement pattern of many small steps within patches, interspersed with a few long ones in between them. Such patterns are frequently observed in animal telemetry and sometimes attributed

to 'Lévy flight' foraging behaviour (Viswanathan et al., 1999). Our results raise the possibility that many of these putative Lévy flights are simply high-Frost number interactions where the resource landscape was not measured (cf. Benhamou, 2007).

Three consumers (ctenophores feeding on copepods, interaction 12, copepods consuming phytoplankton thin layers, interaction 4 and killer whales feeding on salmon, interaction 32) fell just inside the lower left quadrant, suggesting they would struggle to locate and exploit their respective resources. Only one consumer (the water flea *Bosmina*, feeding on phytoplankton) fell in the upper left quadrant, indicating a primary reliance on explosive reproduction to maintain populations within patches—though it is possible that other consumers with similar reproductive strategies, e.g. insects or microbes, might also fall within this quadrant. Finally, most of the large marine predators exploited patches too ephemeral to allow reproduction within them.

Across all interactions, the directed Frost and Strathmann numbers were positively correlated ($r = 0.68$, $p < 0.001$). Rather than a trade-off between movement- and reproduction-based strategies, this pattern suggests that patch duration controls these numbers—i.e., longer-lasting patches enable easier movement between and reproduction within them. A variety of other ecological processes might also lead to this pattern, and to differences between the potential rates expressed by Fr and Str and the true rates realised in nature. Predator evasion, for instance, might select for increased consumer speed as well as decreased foraging time. While faster movement implies a higher Frost number, and therefore more time spent in patches, predation risk could counteract this tendency if consumers also try to minimise their time in (potentially risky) resource patches. Interference competition or territoriality, which gives the first consumer in a patch significant advantages, may also select for lower search times.

As shown in Frost-Lessard space (Figure 3b), roughly half the consumers (15 out of 33 or 45%) had $Le > 1$ and were thus theoretically capable of depleting their resource patches. Of these patch-depleting consumers, all but two also had $Fr > 1$, suggesting they were able to effectively move between patches (Figure 3b). There was a positive correlation between Fr and Le in log-log space ($r = 0.44$, $p = 0.01$), with relatively faster-moving consumers also tending to consume their resource patches faster. Competition (intraspecific or interspecific) may also play some role in generating this pattern. Only two consumer-resource pairs (copepods-phytoplankton thin layers and ctenophores-copepods) fell in the upper left quadrant of Figure 3b, where depletion of patches is possible, but movement between them is not.

Across all consumer-resource pairs, there was also a positive correlation between the Strathmann and Lessard numbers ($r = 0.49$, $p = 0.004$), indicating that the capacity for rapid population growth within a patch

was associated with the ability to totally consume the resource (Figure 3c). However, consumer-resource pairs were present in all quadrants, so this tendency was far from a rule. Eight consumers fell in the upper left quadrant ($Str < 1$, $Le > 1$), indicating they could deplete patches without being able to reproduce within them. Only three consumers—*Bosmina*, fruit flies and elk—were capable of reproducing in a patch but incapable of depleting it, placing them in the lower right quadrant with $Str < 1$ and $Le < 1$.

Consumer populations should only persist if they can locate patches easily, reproduce within patches or both, leading Grünbaum (2012) to predict that consumers must have either Fr or $Str > 1$. In our analysis, this prediction was borne out for 30 out of 33 interactions. The exceptions included two planktonic consumers feeding on planktonic resources (copepods-phytoplankton thin layers, with $Fr_{dir} = 0.2$ and $Str = 0.35$ and ctenophores-copepods, with $Fr_{dir} = 0.76$ and $Str = 0.65$) and one large pelagic predator feeding on nektonic prey (killer whale-chinook salmon, with $Fr_{dir} = 0.38$ and $Str = 1.6 \times 10^{-6}$). According to the logic of the dimensionless ratios, populations of these consumers should not be able to persist in nature—though this prediction is belied by the fact that all three do persist, with ctenophores and copepods being two of the most widespread and abundant animal groups in the ocean.

There are several possible explanations for this discrepancy. One is mismeasurement of the relevant patch scales or generation times: since both Frost and Strathmann numbers were within an order of magnitude of 1, only relatively small errors would be required to move them from above to below the critical value. Another explanation is our use of generation times, rather than intrinsic rates of population growth, to estimate the Strathmann number. Both copepods and ctenophores can produce more than one offspring per generation, so their potential for explosive growth in patches is higher than predicted by the generation time alone. The intrinsic rate of increase would be a more appropriate basis for calculating the Strathmann number and should be used in future studies. However, because values for it were not available in the literature for many of the consumers considered here, we used generation time instead. Estimating T_{search} based on different assumptions could also lead to different values. For instance, ctenophores are primarily ambush predators, so their effective search rate could depend more on water and prey movements than their own swimming speed. Pelagic copepods, meanwhile, perform diel vertical migration, trading off access to food and predation risk (Hays, 2003). Since their habitat has strong, consistent vertical stratification, their search for food is likely more efficient than the assumption of randomly distributed patches would indicate. Likewise, killer whales use memory, biosonar and social communication to potentially increase their foraging efficiency. It is also worth noting that salmon-eating resident killer

whales are vulnerable to human disturbances to their prey availability and foraging behaviour (Williams et al., 2006), a vulnerability that may be particularly acute for a predator whose specialist foraging interaction has $Fr \sim 1$.

The randomness or predictability of patches is a critical question. For instance, the average path travelled by a consumer from a random starting point to the first patch encountered will likely be longer than the average separation between patches, leading to a lower Fr and less-efficient search than the simple calculation would suggest. Alternatively, if patches' locations or densities are predictable, consumers may be able to exploit them more efficiently. In addition, while we selected a single 'characteristic' value for each of the time and space scales used in our calculations, these values are not fixed quantities, but variables that can take on a range of values. Since the expected value of a ratio is not equal to the ratio of the expected values of its terms (i.e., $E[a/b] \neq E[a] / E[b]$), dimensionless ratios based on average values might not be representative. While beyond the scope of this paper, this effect is worth considering, especially when the ratios are close to the critical value of 1.

This non-dimensional framework reveals the importance of understanding a consumer's movement ecology. Some consumers appear to need directed search behaviour in order to effectively exploit patches: white sharks, killer whales, chimney swifts, trout, common terns, common murrelets, green crabs and the marine bacterium *Pseudoalteromonas* would all have difficulty accessing their resources using only diffusive search. All but one of these (the green crab) feeds on mobile prey in aquatic or aerial pelagic environments, suggesting that this may be a general tendency for pelagic predators, whether they are pursuing prey through air or water. While we did not estimate costs of movement for consumers, the fact that none of these predators' Frost numbers were $\gg 1$ is consistent with Grünbaum's conjecture that species will evolve movement abilities 'good enough' to exploit their prey, but not greater. At the opposite extreme, the only consumer-resource interaction to rely on a purely reproductive strategy for patch exploitation ($Fr < 1$, $Str > 1$, the upper left quadrant in Fr - Str space) was *Bosmina*-diatoms. Whether or not this is a viable strategy in non-planktonic interactions would be an interesting topic for future research.

Dynamic similarities across scales and systems

A number of dynamic similarities were revealed when interactions were clustered according to their dimensionless ratios. We identified five groups of dynamically similar consumer-resource interactions (Figure 4). These groups should not be overinterpreted, since the selection of consumer-resource pairs and the number of clusters

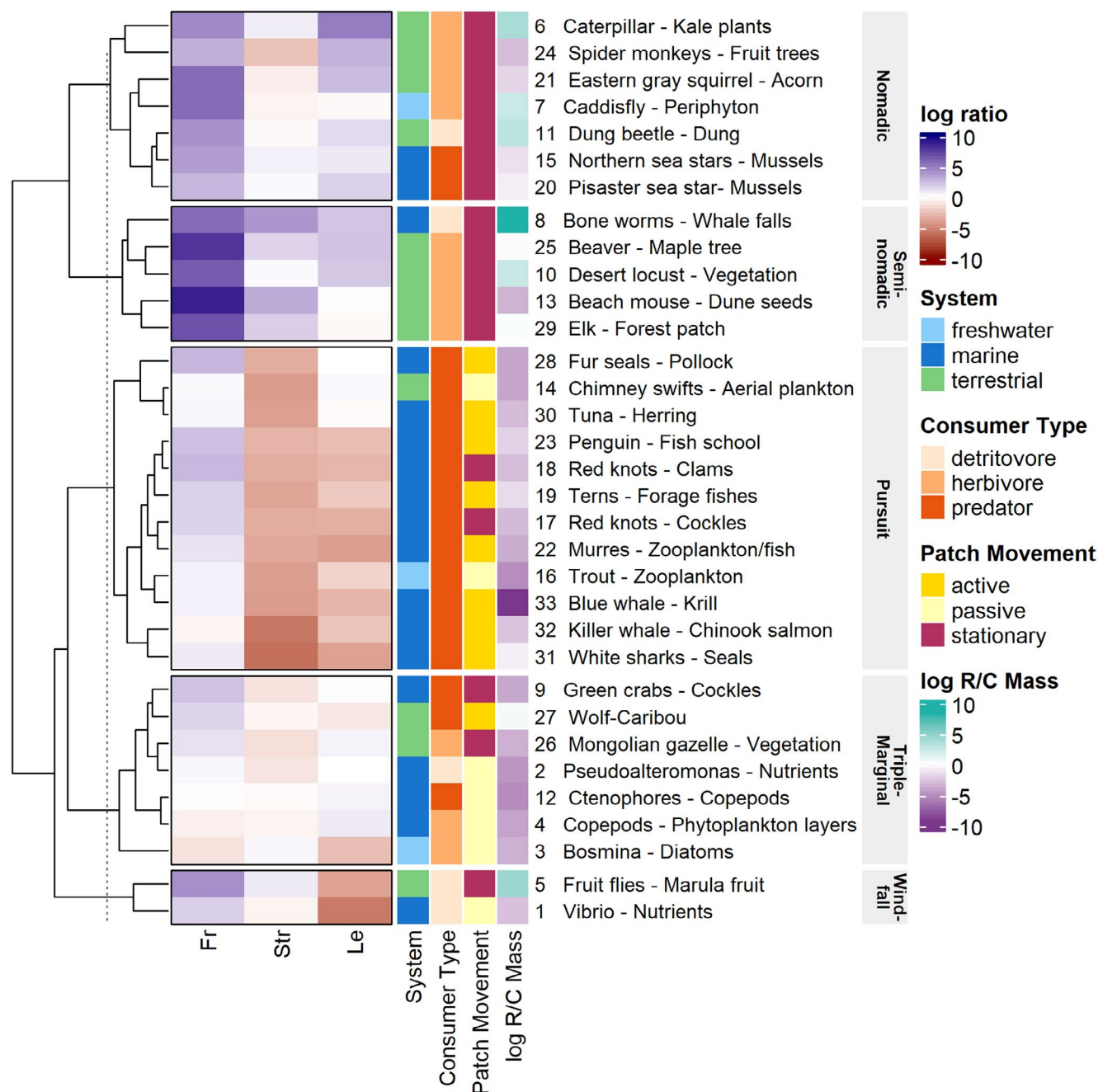


FIGURE 4 Clustering based on the log-transformed directed Frost, Strathmann and Lessard numbers identified five groups of dynamically similar consumer-resource interactions. The three left columns in the heatmap (red–blue colour scale) show the logarithmic values of Fr, Str and Le for each interaction. The four right columns display the ecosystem in which the interaction takes place, the consumer and patch types and the log-ratio of body mass between resource (R) and consumer (C). These latter four variables are shown for additional context but did not influence the clustering, which was driven entirely by Fr, Str and Le. Each cluster is labelled with a descriptive name; see text for details

were both chosen semisubjectively. The clusters could, thus, potentially shift with the addition of more data. Still, these clusters provide a useful perspective on generalities in patch dynamics and hint at some of the reasons for their similarities and differences.

The first cluster was defined by $Fr > 1$, $Str \sim 1$ and $Le > 1$, indicating consumers could move relatively easily between patches and sometimes reproduce within them, but usually depleted them first. We termed these

interactions nomadic, since these dynamics require constant movement by the consumers. We termed the second cluster semi-nomadic, since it shared similar features with nomadic interactions, though with faster movement and reproduction relative to patch duration ($Fr \gg 1$, $Str > 1$) and a slightly lower chance of depletion ($Le \sim 1$).

Both of these clusters were grouped together in the same branch of the dendrogram, and their broadly similar patch dynamics can be seen as falling on a continuum,

with stationary resources exploited by mostly herbivorous consumers. Consumers within the semi-nomadic cluster had, on average, higher Frost and Strathmann numbers, indicating they could locate and reproduce within patches more easily than the nomads. The nomadic cluster included three benthic aquatic and four terrestrial interactions, while all interactions in the semi-nomadic cluster were terrestrial except for *Osedax* bone worms on whale falls. Taken together, these two clusters encompass interactions where consumers travel easily between patches, moving from one to the next as they deplete their stationary resources. This depletion could happen relatively quickly (e.g., a quarter of an hour for a troupe of spider monkeys to eat the fruit off a tree) or over multiple generations (e.g., the decade or so for a population of bone worms to decompose a whale skeleton). The main difference between nomadic and semi-nomadic clusters was thus the length of residency the consumers had within their stationary resource patches and the 'ease' of patch exploitation.

For the semi-nomadic interactions, the Frost and Strathmann numbers were apparently higher than necessary to exploit resource patches. This could imply that for these interactions, simple patch/no patch characterisations are inappropriate (although this is difficult to believe in the case of whale falls) or that movement and reproduction are not costly for consumers at the patch scale. *Osedax* bone worms move between patches as planktonic larvae, and so movement costs are likely low. For the terrestrial herbivores, non-random patch distribution and behaviours such as learning and spatial memory may increase access to patches. Alternatively, these high numbers may indicate that resource exploitation is mediated by additional factors such as predation and competition.

The third cluster included 12 interactions. All were driven by movement ($Fr > 1$), with very slow reproductive dynamics ($Str \ll 1$) and marginal to very weak depletion ($Le \sim 1$ to $Le \ll 1$). Based on their movement-dominated dynamics, we termed these interactions pursuit-type. While these consumers still moved relatively rapidly between resource patches, their Frost numbers were lower than those of the nomadic interactions ($3 < Fr < 500$). Pursuit-type consumers thus spent relatively more time searching for patches, perhaps because most of their resources actively moved, in contrast to the stationary patches in the nomadic and semi-nomadic interactions. The pursuit-type Strathmann and Lessard numbers were also uniformly < 1 , meaning that patches were relatively shorter lived and usually disappeared on their own before being fully exploited. Whereas the nomadic and semi-nomadic consumers could theoretically reproduce within patches, and would be forced to move only after depleting their resources, the pursuit-type consumers could never reproduce within patches. Instead, they relocated due to the patches' inherent ephemerality.

Pursuit-type interactions exclusively involved carnivorous species preying on smaller-bodied animals. With the

exception of chimney swifts—aeroplankton, all took place in aquatic environments, and, except for red knots feeding on clams and cockles, all prey were mobile and suspended in a fluid medium. The separation of the pursuit-type and (semi-) nomadic groups highlights the dynamical differences between consumer-resource interactions in fluid environments and those in benthic or terrestrial environments where prey are attached to surfaces (Carr et al., 2003; Steele, 1991; Strathmann, 1990). For instance, the marine tuna-herring and terrestrial chimney swift-aeroplankton interactions were more similar to each other than either was to sea stars (a non-pelagic marine predator) or wolves (a non-aerial terrestrial predator). It is ironic that tuna, because of their voracity and pack hunting, have often been called the 'wolves of the sea'—when in fact, they are better compared to an insectivorous bird, and wolves pursuing caribou are closer (at least in terms of patch dynamics) to crabs feeding on cockles (Figure 4).

The fourth cluster included seven interactions, representing a varied collection of consumers, resources and environments: microscopic and macroscopic; marine and terrestrial; and carnivorous, herbivorous and detritivorous. Their commonality was having all three dimensionless numbers close to the critical value of one—i.e., the timescales at which consumers moved between, reproduced within and depleted patches were all similar to the patches' durations. Consequently, these interactions were unlikely to satisfy any mean-field assumption. Because movement, reproduction and consumption processes were all marginal in these interactions, we called them triple-marginal.

For these consumers, small differences in reproductive or movement efficiency would mean the difference between effective and unsuccessful exploitation of patches. For instance, assuming diffusive movement, five of the consumers in this group would not be able to locate their resource patches, and based on the numbers we found, two consumers would be unable to locate patches even with directed movement. Several of the triple-marginal interactions did have large differences between the directed and diffusive Frost numbers, so if these consumers moved in a random walk rather than directed fashion (as assumed for clustering), a spatial mean-field assumption might be justifiable. The triple-marginal cluster included four of the five planktonic consumers in our dataset (*Bosmina*, Copepods, Ctenophores and *Pseudoalteromonas*), suggesting a hypothesis that planktonic consumers across a range of sizes may face similar challenges in gaining and maintaining access to resource patches. However, this cluster also included several non-planktonic interactions, including benthic and terrestrial predator-prey pairs and one terrestrial grazer.

The fifth cluster included only two interactions (fruit flies-marula trees and *Vibrio*-nutrients). Both had $Fr > 1$, $Str \sim 1$ and $Le \ll 1$, indicating that the consumers could move between patches and possibly reproduce within them, but would not significantly deplete their resources. Because these interactions involved consumers exploiting

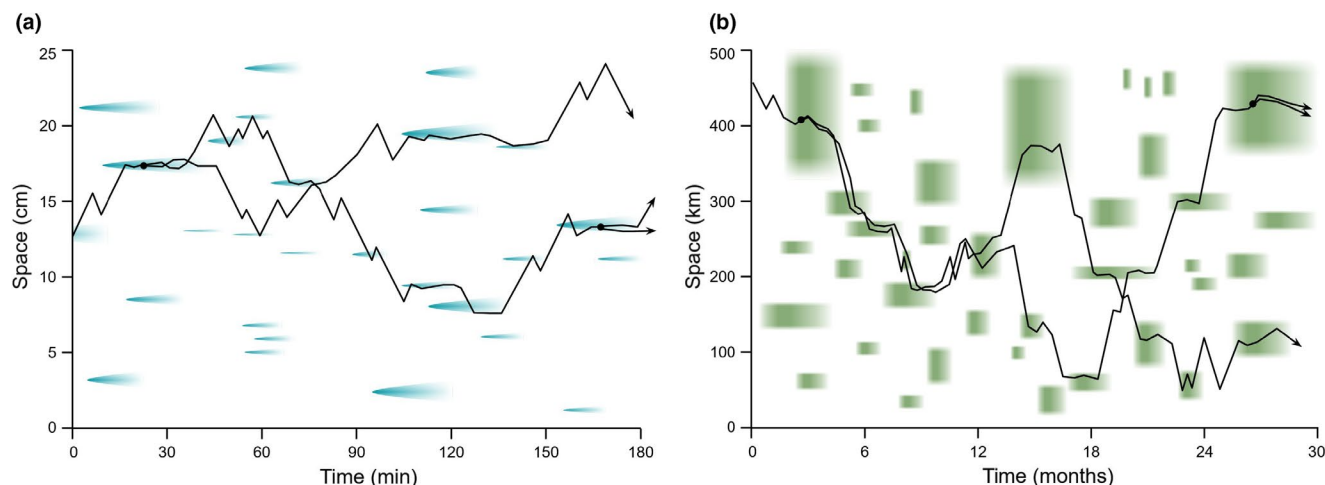


FIGURE 5 Patch exploitation by the marine bacterium *Pseudoalteromonas haloplanktis* and the Mongolian gazelle *Procapra gutturosa* are dynamically similar, despite temporal scales that differ by a factor of $\sim 10^3$ and spatial scales that differ by a factor of $\sim 10^6$. (a) Conceptual space-time diagram showing several bacteria (black lines) foraging for nutrient plumes from sinking phytoplankton cells (blue patches) in a simplified one-dimensional seascape. Black dots mark cell divisions, and hence the birth of new bacteria. (b) Similar diagram showing hypothetical paths of several gazelles browsing on patches of steppe vegetation which bloom following localised rains. As in a), black dots mark births of new organisms. The spatial and temporal scales of the patches are approximately accurate for each system, as are the speeds and generation times of the organisms. Note that for simplicity, only a few trajectories are plotted; in reality, the density of both organisms within their patches would be significantly higher

resources which appeared suddenly and were more abundant than they could exploit (and because the fruit flies were literally consuming fallen fruit), we named them windfall interactions. These interactions were similar to the pursuit interactions, in that movement between patches was possible while depletion was not ($Fr > 1$, $Le \ll 1$). However, the windfall interactions had $Str \sim 1$, indicating that one generation of offspring could be produced within a nutrient plume or a marula fruit before it diffused away or rotted, respectively. In these cases, resource patches were both rich and moderately ephemeral, with a duration on the same order of magnitude as its consumer's generation time. The small size of this cluster compared to the others is notable. While our selection of interactions cannot be assumed to be representative, the relative frequency of different types of consumer-resource interactions would be an interesting direction for future research.

Are bacteria really gazelles? Dynamic similarities and biological differences

Conceptualising patchy consumer-resource dynamics in terms of dimensionless ratios can unite disparate ecological interactions into a common framework and identify hidden similarities between them. However, these comparisons may at first appear quite abstract. To help make this style of thinking more concrete, we present a case study on one of the most surprising dynamic similarities we found, which gives this paper its title: the similarity between Interaction 2, bacteria exploiting dissolved nutrients, and Interaction 26, gazelles grazing on the Mongolian steppe (Table 2, Figure 5).

Pseudoalteromonas haloplanktis is a cold-water planktonic bacterium which, in this interaction, seeks out a plume of nutrients left behind by a dead, sinking phytoplankton cell. Such plumes are typically separated by several cm and disperse via diffusion over about 15 min. Laboratory tracking has shown that *P. haloplanktis* can swim incredibly fast for its body size, moving up nutrient gradients at speeds of up to 0.4 mm/s (Barbara & Mitchell, 2003), implying a directed Frost number of 2.0. Their doubling time of ~ 3 h (Piette et al., 2010) is fast by human standards, but 12 times longer than the duration of an individual nutrient plume (implying $Str = 0.083$), meaning that a bacterium dividing in a plume cannot expect its daughter cells to inherit the resource patch. Still, the relatively high density of bacteria that can aggregate in such a nutrient plume means that they can absorb the nutrients at about the same rate as diffusion carries them away, leading to a Lessard number approximately equal to one.

The Mongolian gazelle, *Procapra gutturosa*, differs in several respects from *P. haloplanktis*. To name a few, it is terrestrial, reproduces sexually and possesses a body made of multiple eukaryotic cells that is 2.8 quadrillion times the mass of *P. haloplanktis*. Nevertheless, the foraging dynamics of gazelles are quantitatively similar, with (directed) $Fr = 12.3$, $Str = 0.04$ and $Le = 3.0$, all on the same order of magnitude as the corresponding numbers for the bacterium. An examination of the gazelles' natural history provides an explanation for this similarity: Herds of gazelles travel nearly constantly across the steppe, tracking patches of productive pasture that appear following rains. These patches last on the order of 30 days, long enough for herds to locate them, but

an order of magnitude shorter than the gazelles' 2-year generation time. Still, the size and density of the herds (281 gazelles km^{-2} , Olson et al., 2009) mean that they actively graze down their pastures.

The bacterium and the gazelle's interactions were closer to each other in logarithmic Fr-Str-Le space than to any others considered here. Both consumers are fast for their size and highly mobile relative to their resources, and would be expected to spend the majority of their time inside patches. While these patches are long-lasting enough to enable easy discovery, they disappear too quickly to host population growth, meaning that each consumer must visit 10–20 patches per generation. At typical consumer densities, each patch is a finite resource, being depleted faster than it would be in the absence of the consumers. Figure 5 shows the conceptual space-time arrangement of patches and consumer trajectories for both these interactions. The dynamic similarity between them is intuitively obvious when comparing the two panels: if one ignores the axis labels and stylised patch shapes, the distribution of patches and the consumers' space-time trajectories are difficult to tell apart.

Of course, this is a deliberately simplified picture of these interactions' dynamics. In many respects, bacteria are *not* gazelles. Nutrient plumes are small compared to the spaces separating them, while patches of steppe vegetation vary widely in size and connectivity (Mueller et al., 2008). The consumers' sensory capabilities and foraging behaviours also differ significantly. While *Pseudoalteromonas* can perform chemotaxis, gazelles use multiple senses, memory and social information to locate food. Bacterial division occurs whenever cellular development and nutrient assimilation permit, while gazelles have a seasonal reproductive cycle. Finally, the bacteria move in a three-dimensional environment, whereas the gazelles are restricted to the (approximately) flat surface of the earth. Nevertheless, dimensional analysis suggests that some of these differences in biology will be less important than dynamic similarities between the arrangement of patches in space and time and the ways consumers travel between and exploit them over the course of their lives. Outside this dimensionless scaling framework, such a surprising dynamic similarity would not be apparent.

Significance, perspective and future directions

As it is the case for most dimensionless ratios, Fr, Str and Le are based on a simplified caricature of the real world and do not capture all dynamical similarities (or differences) that can exist between systems (e.g., density dependence, functional responses, other species interactions, or responses to environmental drivers; Rogers & Munch, 2020). Further, each set of numbers characterises an interaction, not a taxon. Most consumers do

not consume just one resource, and most resources are not exploited by only one consumer. The same consumer could have different values for Fr, Str and Le when feeding on a different resource, or even the same resource in a different place or time. Just as the dimensionless ratios can identify dynamic similarities across species, they can also identify dynamic differences within a single species as it grows, changes behaviour or encounters different resource and environmental conditions. Of course, resources are heterogeneous at a range of spatiotemporal scales and patches can be nested inside each other. It is thus important to think critically about which of these scales are relevant for the consumers and the ecological questions at hand when calculating these dimensionless ratios. Examining the sensitivity of Fr, Str and Le to patch scales in hierarchical resource landscapes would be a worthwhile direction for future investigation. Ultimately, though, it is important to remember that these ratios are not intended to be more precise than an order of magnitude; they are tools for reasoning about the relative magnitudes of different rates, not precisely modelling dynamics.

We believe dimensionless ratios are widely useful. Although the ratios explored here were derived from specific details about individual consumers and resources, clear groupings emerged that reflected similarities in life history (herbivorous vs. predatory consumers and mobile vs. stationary resources) and environment ('pelagic' vs. 'benthic' systems). These separations hint at fundamental trade-offs long discussed in ecology and evolution (Hutchinson, 1961; Menge & Sutherland, 1987; Strathmann, 1990). The dimensionless ratio approach is similar to the use of functional traits within community ecology (e.g., McGill et al., 2006), where the diversity of organism traits is reduced to their functional similarities in a comparative framework. Dimensionless descriptions highlight how species interact with each other and their environment and provide an opportunity for ecologists studying dynamically similar systems to learn from each other. They may also suggest experimentally tractable systems that can be used as 'scale models' of dynamically similar interactions occurring at intractable spatial and temporal scales.

While our selection of consumer-resource pairs was extensive, it was not random or representative. For instance, our author group has little expertise with insects, so they are underrepresented in this paper. Additionally, we did not consider plants or fungi as consumers, even though they move between generations via seed or spore dispersal and can actively seek resource patches by extending roots or mycorrhizae. Finally, it was surprisingly difficult to find values for basic rates (speeds, reproductive and consumption rates, patch sizes, densities, etc.) in the literature, even for well-studied species. Most values we did find were published in older papers. While funders, publishers and researchers may not consider

measuring and reporting basic natural history information as ‘high-impact’ or career-advancing ecology, their value to future researchers is hard to overstate (Greene, 2005).

Understanding when patchiness matters and when it may be ignored is a constant challenge to ecological modellers. The Frost, Strathmann and Lessard numbers can serve as diagnostic tools to assist model development by identifying when mean-field approaches will work for a given system. For theoreticians seeking to understand patchy consumer-resource dynamics (e.g., Hein & Martin, 2019), empirical information on the Fr-Str-Le space occupied by real organisms can aid in model formulation and the placement of realistic parameter bounds. The broad utility of these values is analogous to the Reynolds number in fluid dynamics: it is not the only number one needs to design an airplane, or predict the weather, but neither is possible without it. To model and understand ecological patchiness, we ought to start from a common framework. The Frost, Strathmann and Lessard numbers, proposed by Grünbaum (2012) and quantified here, may provide such a starting point from which to develop a deeper, more general understanding of patch dynamics in ecology.

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AUTHOR CONTRIBUTIONS

SSU conceived the study. All authors discussed the study's design, reviewed literature and curated data. ANC, SSU and TLR analysed the data. ANC and SSU drafted the manuscript with input from all authors. ANC, CCS, JSS, SSU and TLR contributed to figures and tables. All authors revised and edited the manuscript.

PEER REVIEW

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OPEN RESEARCH BADGES



This article has earned Open Data Design badge. Data design and analysis plan are available at: <https://doi.org/10.5281/zenodo.6338651>.

DATA AVAILABILITY STATEMENT

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