BACKGROUND AND RATIONALE: The idea that habitat structure is a fundamental mediator of trophic interactions is practically as old as ecology[1]. Today, changes to habitat structure are ubiquitous: from the fragmentation and simplification of forests[2] and reefs[3] to the spread of agricultural and urban landscapes[4,5]. Habitat is the fundamental niche dimension[6], but we currently lack a strong theoretical basis for understanding if and how habitat structure mediates interactions[7,8], which remain the proximal driver of extinctions in a rapidly changing world[9]. Four related issues have contributed to the persistence of poor knowledge vis-à-vis habitat structure and interactions. This fellowship seeks to address each: (1) ***Imprecise measures of habitat structure***. Qualitative descriptors are frequently used for habitat structure (e.g. 'simple' versus 'complex'[10]) preventing objective comparisons among studies. Other metrics such as fractal geometry are quantitative but imprecise with respect to describing the space in which consumers and resources move; (2) ***Confounded experimental designs.*** Experiments that quantify the effects of habitat structure often inadvertently manipulate multiple facets of structure simultaneously (e.g. simultaneously changing surface area and volume; Fig 1)[11]; (3) ***The Appeal to Nature.*** Natural structures are often preferentially employed in experiments. Although valid for applied reasons, natural structures are not superior where the goal is to quantify the effects of structure *per se*, because it is impossible to precisely manipulate or scale their facets; (4) ***Limited data on well-characterised interactions***. At minimum, well-characterised interactions should estimate consumer capture rates and handling times. Across the ecological literature, such data are in the order of 100s[12,13] of consumer-resource pairs: fewer data points than there are links in typical food webs. This fellowship will avoid methodological pitfalls (1-3) by focusing on designed, 3D printed structures that can be scaled and manipulated in precise ways (Fig 2a). The fellowship will increase the globally available data on interactions (4), providing a means to address a **CENTRAL AIM**:

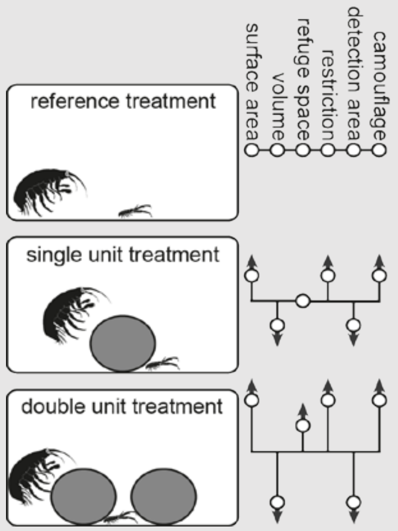

Fig 1 Experimental designs commonly manipulate multiple facets of habitat structure simultaneously, obscuring causality.

To develop a theoretical basis for understanding the effects of habitat structure on trophic interactions, and to understand if these effects of scale to population stability and coexistence.

Three objectives result from the overarching aim of the fellowship, each of which will underpin a discrete work package. **OBJECTIVE 1** Generate predictions of how the following quantities modify the underlying size-scaling of interaction strengths: (i) interference between consumers; (ii) interaction space dimensionality, and; (iii) interaction space complexity (specifically, obstacle density and predator-free space: Fig 2a). By combining established expectations from metabolic theory[14], and predator interference[15] with structural complexity[8], objective 1 seeks to develop a new standard model for interactions by treating consumers and resources as particles with generalisable behaviours.

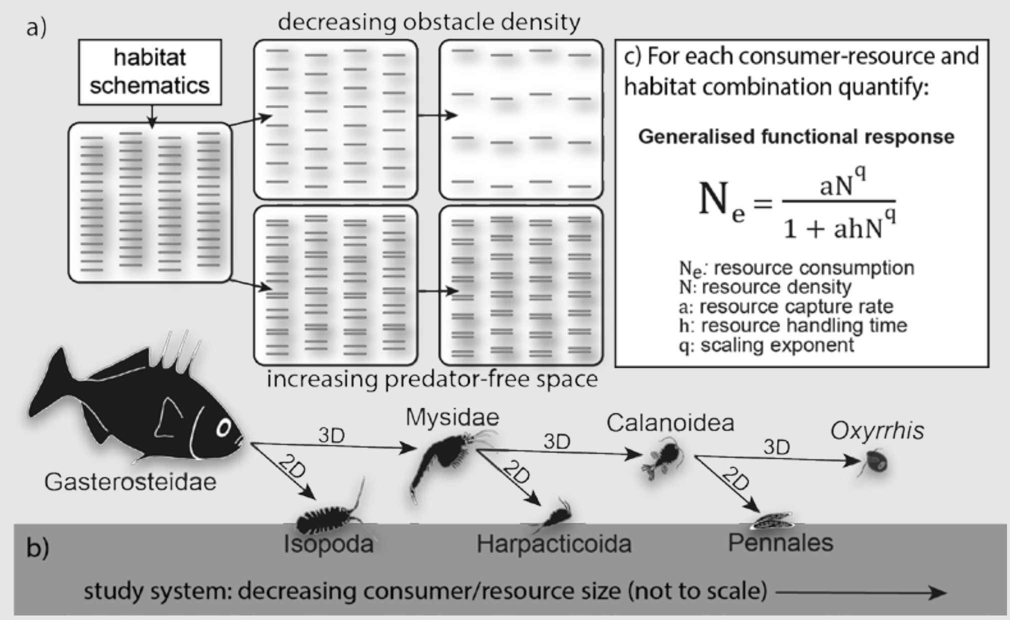

Fig 2 Systematic habitat structure manipulations (a) and consumer-resource pairs (b) designed to test the effect of search dimensionality, obstacle density, predator-free space and body size on generalised interactions (c).

OBJECTIVE 2 Generate an unparalleled open access dataset of empirically-measured interaction strengths. By systematising the collection of data from short-term feeding trials between a range of consumer types (i.e. active capture, sit and wait, grazing) across orders of magnitude in body size (10^{-7}-10^{-1}g: from protists to small teleosts), and using precise manipulations of continuously variable facets of habitat structure, this fellowship seeks to provide the data necessary to parse new patterns of resource consumption, and use these to validate and refine predictions generated by objective 1.

OBJECTIVE 3 Determine whether the signal of systematic changes to habitat structure—and concomitant changes in interaction strengths—can be detected in the stability of populations and community structure through time. This objective seeks to understand whether the alterations to habitat structure that typify the Anthropocene have consequences that are predictable from first-principles. Thus, the long-term vision is to provide knowledge that can be leveraged to mitigate against undesirable changes to ecosystems.

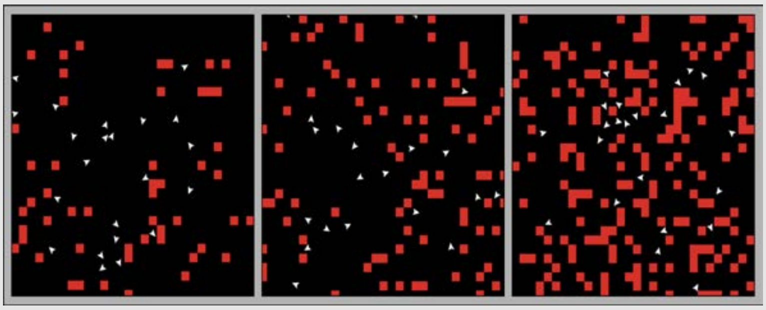

Fig 3 Consumers moving *in silico* through randomly generated habitat structures (Barrios-O'Neill, unpublished NetLogo model).

Methodology: A central novelty of this fellowship will be the use of an unparalleled size range of aquatic consumers, between 10^{-7}-10^{-1}g in size (Fig 2b). To ensure high turnover, species used will necessarily be logistically easy to maintain in culture or field-source in quantity (see[7]). The novelty of this fellowship's approach to manipulating habitat structure is threefold: (i) scalability of the designs allows for direct comparisons of the effects of habitat structure *per se* across orders of magnitude in body size; (ii) use of 3D objects that are manipulated on a two-dimensional plane (Fig 2a) to allow direct comparisons between consumers that have 3D and 2D search spaces (Fig 2b); (iii) precise changes in continuous, quantifiable facets of habitat structure will allow for specific hypothesis testing with respect to the basic components of predation (Fig 2c). **Work Package 1 (WP1):** Agent-Based Modelling (ABM: NetLogo 6.0.1, Fig 3) will be employed to rapidly test the effects of: consumer search space (2D or 3D); errant and sessile consumer-resource combinations; consumer-resource size, and size ratios; interference, and; facets of habitat structure (Fig 2a). ABM will facilitate hypothesis testing as to the mechanisms (Fig 2c) that drive any differences in interaction strengths. For example, increasing obstacle density can be hypothesised to reduce capture rates (*a*: Fig 2c) by reducing velocity and subsequent encounter rates and/or reducing detection regions. **Work Package 2 (WP2):** Hypothesis testing in WP1 informs WP2 by providing initial expectations for consumer behaviour in experimental trials. Fish and larger invertebrates will be field-sourced using kick nets and traps, and maintained in CT aquaria (Penryn). Cultures of smaller consumers will be purchased and maintained in the Yvon-Durocher lab. 3D printed habitats will be produced for 0.5 L (Myside) and 2 L (Gasterosteidae) aquaria (habitats: 10 levels of obstacle density and 10 of predator-free space—subset shown in Fig 2a). 3-6 h trials will run at a range of prey densities (>20 data points) over which consumption will be recorded to generate functional responses (Fig 2c) and the following behaviours will be recorded in a random subset of trials: (i) space use; (ii) movement; (iii) encounters and captures; (iv) handling times. Habitats will be downscaled using Nanoscribe 3D printing and the experiment will be downscaled (aquaria <0.1 L) and replicated for smaller consumers. WP1 & 2 will run in parallel for 2 years. **Work Package 3 (WP3):** Data from WP2 will identify combinations of structure that dampen or enhance short-term interactions between specific consumer-resource pairs. A controlled microcosm experiment (Fig 3: 10 L aquaria) will inoculate two replicated experimental treatments (Fig 3: enhancing vs dampening) with identical starting communities consisting of copepods protists and autotrophs that form part of the WP2 study-system. This experiment will run for 6 months+ in light and temperature-controlled conditions. The following will be quantified at weekly-to-monthly intervals: (i) abundance and individual size distribution by flow cytometry (BD Accuri C6 flow cytometer) and inverted light microscopy; (ii) respiration and primary production using light-dark incubations.

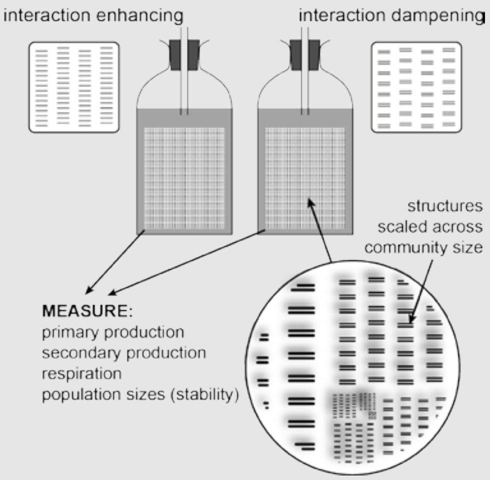

Fig 3 Microcosms with habitat structures designed to dampen or enhance short term interactions.

Outcomes: This fellowship will provide novel insight into the systematic effects and ecological consequences of habitat structure via the following outputs: **(i)** an open access, standardised dataset of functional responses; **(ii)** two hypothesis-led papers on obstacle density, predator-free space and scaling of interactions; **(iii)** one theoretical paper on developing functional response models to incorporate habitat structure, resulting from a specialist workshop on the subject; **(iv)** one empirical paper on long term population stability and habitat structure; **(v)** two international conferences (ESA & BES).

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