

# Predator-free space, functional responses and biological invasions

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## Summary

1. Predator–prey interactions are mediated by the structural complexity of habitats, but disentangling the many facets of structure that contribute to this mediation remains elusive. In a world replete with altered landscapes and biological invasions, determining how structure mediates the interactions between predators and novel prey will contribute to our understanding of invasions and predator–prey dynamics in general.

2. Here, using simplified experimental arenas, we manipulate predator-free space, whilst holding surface area and volume constant, to quantify the effects on predator–prey interactions between two resident gammarid predators and an invasive prey, the Ponto-Caspian corophiid *Chelicorophium curvispinum*.

3. Systematically increasing predator-free space alters the functional responses (the relationship between prey density and consumption rate) of the amphipod predators by reducing attack rates and lengthening handling times. Crucially, functional response shape also changes subtly from destabilizing Type II towards stabilizing Type III, such that small increases in predator-free space to result in significant reductions in prey consumption at low prey densities.

4. Habitats with superficially similar structural complexity can have considerably divergent consequences for prey population stability in general and, particularly, for invasive prey establishing at low densities in novel habitats.

**Key-words:** *Chelicorophium curvispinum*, *Gammarus*, habitat complexity, nonlinear interactions, predator–prey dynamics, Type II, Type III

## Introduction

Predator–prey interactions can depend strongly on the spatial arrangement of surrounding objects that confer structural complexity to habitats (McCoy & Bell 1991). Structural complexity is frequently observed to increase prey survivorship by reducing direct predation, particularly at low prey densities (Humphries, La Peyre & Decossas 2011; Alexander *et al.* 2012; Toscano & Griffen 2013). Yet, structural complexity can also exert negative effects on prey by, for example interacting with predator risk to reduce fecundity (Orrock *et al.* 2013) and increasing direct predation (Marinelli & Coull 1987). Further, the mechanisms by which structural complexity mediates the establishment and persistence of invasive species are highly relevant to community ecology (e.g. Byers 2002), not least

because low population Allee effects can interact with biotic resistance offered by resident predators to determine invasion success (Taylor & Hastings 2005).

The apparent dichotomy of effects elicited by structural complexity on prey populations can stem from problems with defining and quantifying structural complexity itself (McCoy & Bell 1991; Beck 2000; Warfe, Barmuta & Wotherspoon 2008), but also to the numerous ways in which structural complexity can influence predator–prey interactions. These include, but are not limited to, the provision of camouflage (Farkas *et al.* 2013), the restriction of predator or prey movement (Manatunge, Asaeda & Priyadarshana 2000; Hauzy *et al.* 2010), and the availability of predator-free space *sensu* Humphries, La Peyre & Decossas (2011). Thus, structural complexity can simultaneously provide qualities that both facilitate and suppress the viability of predator and prey populations, the particulars of which are masked by the net effect. Further, many studies

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are experimentally confounded because they fail to separate distinct aspects of structural complexity: namely, that the quantity, or density, of certain structures within a habitat should not be conflated with their heterogeneity or diversity (McCoy & Bell 1991; Beck 2000; Warfe, Barmuta & Wotherspoon 2008). Careful manipulations can uncouple the separate effects of structural density and diversity (Beck 2000), but some aspects are indivisible: single structural units can alter multiple aspects of structural complexity. For example, a single macrophyte can simultaneously increase predator-free space, increase surface area (Warfe, Barmuta & Wotherspoon 2008) and reduce the effective volume for prey detection (Manatunge, Asaeda & Priyadarshana 2000).

Progress has been made in identifying useful metrics to measure complexity across a range of habitat types, which in turn have aided understanding of how structure alters ecological processes. In particular, the fractal dimension (D) of a surface quantifies its convolution. Large fractal dimensions indicate more convolution and have been shown to provide a reliable means to quantify complexity across a range of habitat types (Sugihara & May 1990; Warfe, Barmuta & Wotherspoon 2008). Because D depends on the scale at which habitats are viewed, explicit consideration of predator and prey size is required to understand how structure mediates predator–prey interactions. Further consideration of the scale-dependent nature of complexity has yielded methods that define the proportion of total space within a habitat that is unavailable to predators of a given size, but available to their prey (Bartholomew, Diaz & Cicchetti 2000; Warfe, Barmuta & Wotherspoon 2008). This predator-free space is spatially explicit, and thus distinct from the niche-based concept of enemy-free space, which incorporates morphological defences and temporal components (Jefferies & Lawton 1984).

Predator–prey interactions are frequently density-dependent; the predator functional response describes the relationship between prey density and consumption rate (Solomon 1949). Functional responses are widely used by ecologists (e.g. Rall *et al.* 2012; Williams, Flaherty & Flaxman 2013) and, recently, have yielded insights into how invasive species affect recipient communities by, for example revealing how impacts on prey populations vary over space and time (Barrios-O'Neill *et al.* 2014c). Historically, ecologists have adopted a categorical approach to defining functional responses; Type I functional responses are linear; Type II functional responses are characterized by a decreasing proportion of prey consumed with increasing prey density; whilst Type III functional responses describe an initial increase of proportional prey consumption, followed by a decrease (Juliano 2001). Type II functional responses may destabilize predator–prey dynamics on account of high prey exploitation at low prey densities, whilst Type III functional responses may impart stability by providing prey refuge at low densities (Murdoch & Oaten 1975; Williams & Martinez 2004). Although empiri-

cally measured functional responses are frequently classified as Type II, the coexistence of commonly occurring predator–prey systems in nature suggests that Type III functional responses are more prevalent than previously anticipated (Sarnelle & Wilson 2008), often resulting from predator interference (Rall, Guill & Brose 2008), predator switching behaviour (Murdoch 1969), or the modification of interactions by habitat structure (Toscano & Griffen 2013). Predator–prey dynamical modelling has partially corroborated the notion that Type II functional responses drive destabilization, but also suggests that very small deviations from an absolute Type II shape are sufficient to impart stability (Williams & Martinez 2004). Similarly, analysis of functional response data using models that incorporate a scaling exponent ( $q$ : Real 1977; Vucic-Pestic *et al.* 2010) has demonstrated that functional responses can be quantified in a flexible, continuous manner (Vucic-Pestic *et al.* 2010; Kalinkat *et al.* 2013). Altogether, it is evident that empirically derived functional responses must be capable of resolving shape with considerable precision if the consequences for population stability are to be properly understood.

Exploration of the effects of structural complexity on functional response shape and magnitude remain comparatively rare (Lipcius & Hines 1986; Alexander *et al.* 2012; Toscano & Griffen 2013) and has often neglected quantification of the possible components of structure that may drive observed changes. Conversely, studies which focus primarily on structural complexity frequently fail to account for the density dependence of predator–prey interactions (Bartholomew, Diaz & Cicchetti 2000; Warfe & Barmuta 2004). A primary objective of the present study is to couple these two components to gain a more thorough understanding of how structural complexity alters functional response shape and magnitude. Because of the ubiquity of spatial refuge use by prey, and the myriad implications for resulting predator–prey dynamics (Orrock *et al.* 2013), we sought to manipulate predator-free space whilst holding D, surface area and volume constant. We use a freshwater amphipod study system consisting of two resident predators – the Irish native *Gammarus duebeni celticus* Stock and Pinkster, 1970, and the invasive *Gammarus pulex* (Linnaeus, 1758) – both preying on the invasive Ponto-Caspian corophiid, *Chelicorophium curvispinum* Sars, 1895. *C. curvispinum* is often a successful and numerically dominant invader that associates with structurally complex habitats (Van den Brink, Van der Velde & Bij de Vaate 1993; Noordhuis, Schie & Jaarsma 2009). Because other amphipods have been implicated as important predators of *C. curvispinum*, directly responsible for curtailing the growth of established populations (Bovy *et al.* 2014), a secondary objective of this study was to understand how predator-free space might mediate the successful establishment of this particular invader in novel habitats. We hypothesized that increasing predator-free space would (i) reduce the strength of predator–prey interactions, resulting in functional responses with lower magnitudes and (ii)

alter the character of predator–prey interactions, such that functional response shapes move from destabilizing Type II towards stabilizing Type III.

## Materials and methods

### ANIMAL COLLECTION AND MAINTENANCE

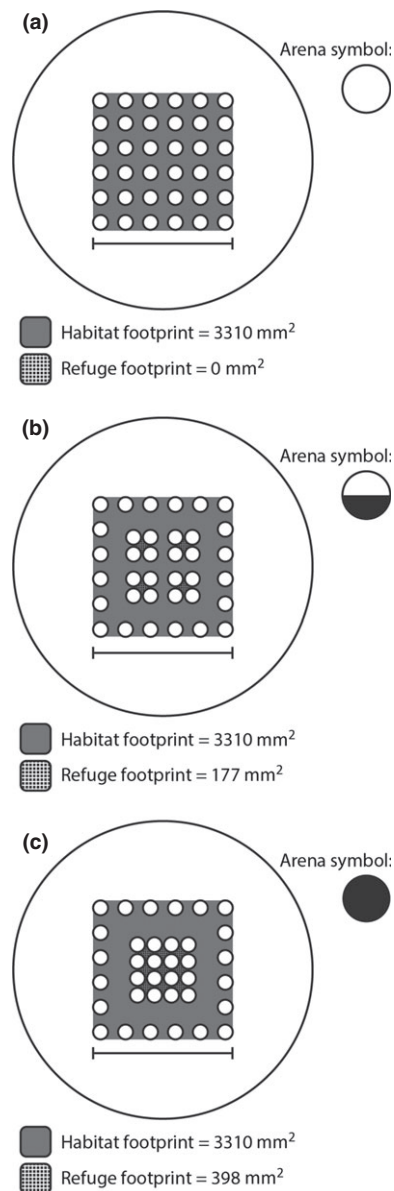
During February 2013, *G. pulex* and *G. d. celticus* were collected from a tributary of the River Lagan, Co. Antrim (54.50914° N, 5.97018° W) and the Gransha River, Co. Down (54.5484° N 5.81950° W), respectively. Large individuals of both species were isolated for subsequent experimental trials, and closely matched for size (mean body mass ± SE: *G. pulex* = 96.9 mg ± 2.5, and *G. d. celticus* = 94.2 mg ± 4.0,  $t_{50} = 0.57$ , NS). Prey *C. curvispinum* (5.4 mg ± 0.3) were collected from Lough Derg, Co. Tipperary (52.92583° N, 8.27913° W). Each species was maintained separately in aerated source water (Lagan, Gransha or Derg as appropriate), with leaf litter and associated substrate, at 12 °C and on a 12 L: 12 D photoperiod. Predators were starved in isolation for 24 h prior to experimental trials.

### DESIGN OF EXPERIMENTAL ARENAS

Artificial habitats were constructed from vertically oriented plastic tubes (7.5 mm Ø); these are often used as habitat analogues of reedy margins (e.g. Mattila 1992). Predator-free space was manipulated by altering the interstitial distance between vertically oriented tubes. Tubes were arranged in grids with varying internode distances, thus allowing changes to be quantified in two dimensions rather than three. Each habitat was constructed from 36 tubes arranged in six-by-six grids such that the total footprint of each habitat was 70 mm × 70 mm, with surface area and volume held constant among manipulations. For habitats lacking any predator-free space (Fig. 1a) grids were uniform, yielding gaps of 5 mm throughout. Pilot trials indicated that predators and prey moved freely between gaps of this size and that a gap size which consistently prevented predators from moving between areas was ~ ≤1 mm. Consequently, predator-free space was increased by altering the positions of the inner four-by-four tubes within each habitat grid; first by creating four small refugia of two-by-two tubes each, where gap size was 1 mm (Fig. 1b) and, to increase predator-free space further, by creating one large refuge of four-by-four tubes where gap size was 1 mm (Fig. 1c). For simplicity, the three habitat types are qualitatively referred to as low, medium and high refuge treatments. Each habitat was supported by a plywood template above water level, and set into a 3-mm bed of nontoxic mounting putty in the centre of glass arenas (150 mm Ø).

### QUANTIFYING STRUCTURAL COMPLEXITY

Because habitats were horizontally uniform, structural complexity [i.e. predator-free space and the fractal dimension (D)] was calculated from two dimensional schematics (Fig. 1). Predator-free space was expressed as a ratio, calculated as the total available refuge area (Fig. 1b,c, black tiles) divided by the total available area (Fig. 1b,c, grey areas), with the low refuge habitat (Fig. 1a) having a ratio of 0. The fractal dimension, D, is a noninteger value between 1 and 2 that expresses the degree of convolution within a structure; higher values indicate increased complexity. Here, we use the general grid method (Sugihara & May 1990) to determine D by overlaying grids of 16<sup>2</sup>, 32<sup>2</sup>, 64<sup>2</sup> and 128<sup>2</sup> squares (yielding characteristic scales, δ, between 0.55 and 4.38 mm) on the schematics and counting the squares in which sections of structure



**Fig. 1.** Schematics of experimental arenas (outer circles) containing habitats (inner grids). Open circles within habitat footprints (grey areas) represent vertically orientated tubes. Black tiled areas within habitat footprints represent refuge areas of predator-free space. Scale bars are 70 mm. Symbols for each habitat type are used in Figs 2 and 3: open circles (a) denote the low refuge treatment, half-filled circles (b) denote the medium refuge treatment, and filled circles (c) denote the high refuge treatment.

(i.e. tubes) intersect (giving a value of C at each δ). The log of C plotted against the log of δ yields a linear relationship where the slope is 1/D. The predator-free space ratio and D are given for each habitat in Table 1.

### EXPERIMENTAL TRIALS

Trials were conducted in continuously aerated experimental arenas filled with 500 mL of dechlorinated tap water. Prey were introduced into experimental arenas at seven densities (2, 4, 6, 8, 15, 25 and 40; n = 4 each) 2 h before the introduction of single starved predators. Controls were predator-free arenas at all prey densities

**Table 1.** Structural complexity metrics of each habitat: total refuge areas, predator-free space ratios and the fractal dimension (D)

Refuge treatment	Total habitat footprint (mm <sup>2</sup> )	Total refuge footprint (mm <sup>2</sup> )	Predator-free space ratio	Fractal dimension (D)
Low	3309.6	0	0	1.84
Medium	3309.6	112.3	0.034	1.91
High	3309.6	252.6	0.076	1.90

and across all habitat complexities,  $n = 4$  each. Trials ran for 24 h, after which predators were removed and surviving prey counted.

#### STATISTICAL ANALYSES

All statistical analyses were undertaken in R (R Development Core Team 2013). Functional response types can be defined categorically by using logistic regression to determine the shape of the relationship between proportional consumption and prey density. Decreasing proportional consumption with increasing prey density is indicated by a negative first-order term, where the functional response can be classified as Type II. Increasing then decreasing proportional consumption corresponds to positive first and negative second-order terms, and indicates a Type III response (Juliano 2001).

Alternatively, flexible functional response models that incorporate a scaling exponent ( $q$ ) can be fitted, allowing a continuum of shapes between categorical Types I, II and III to be defined (Real 1977). Here, we adopt both categorical and flexible approaches to compare their suitability using Akaike's Information Criterion ( $\Delta$ AIC). Functional responses were subsequently fitted using maximum likelihood estimation (MLE; Bolker 2010):

Categorical Type II functional responses were modelled for nonreplacement of prey (Rogers 1972):

$$N_e = N_0(1 - \exp(a(N_e h - T))) \quad \text{eqn 1}$$

where  $N_e$  is the number of prey eaten,  $N_0$  is the initial density of prey,  $a$  is the attack rate,  $h$  is the handling time and  $T$  is the total time available.

The flexible model accounting for nonreplacement of prey amounts to a modification of eqn 1 with the scaling exponent,  $q$  (Real 1977; Vucic-Pestic *et al.* 2010):

$$N_e = N_0(1 - \exp(bN_0^q(hN_e - T))) \quad \text{eqn 2}$$

where  $N_e$  is the number of prey eaten,  $N_0$  is the initial prey density,  $b$  is the search coefficient,  $h$  is the handling time,  $q$  is the scaling exponent and  $T$  is the total time available.

Categorically, Type II functional responses are  $q = 0$ , and where  $q > 0$  functional responses become increasingly sigmoidal, or Type III. Note that the attack rate,  $a$ , in eqn 1 is fixed regardless of initial prey density,  $N_0$ , but that in eqn 2 the search coefficient,  $b$ , combines with  $N_0$  and  $q$  to yield attack rates that vary with prey density ( $a = bN_0^q$ ). Although theoretical ecologists favour flexible models such as eqn 2, empirical data which are strongly Type I ( $h = 0$ ) or Type II ( $q = 0$ ) may yield a poorer fit with a flexible model than with a categorical equivalent.

Raw data were nonparametrically bootstrapped ( $n = 2000$ ), and eqn 1 or 2 was applied to each new data set to construct 95% confidence intervals around functional response curves (Pritchard 2013). Finally, bootstrapped estimates of model parameters [(1):  $a$ ,  $h$  (2):  $b$ ,  $q$ ,  $h$ ] and associated 95% confidence intervals were plotted against predator-free space ratios (Table 1) to quantify systematic changes in functional response parameters with predator-free space.

## Results

Survival of *C. curvispinum* in controls was 100%, thus we attribute experimental mortality to predation by *G. pulex* or *G. d. celticus*. In addition, predators were directly observed preying upon *C. curvispinum*. Prey were distributed throughout habitats, regardless of available predator-free space.

#### MODEL SELECTION AND FITTING

Logistic regressions indicated that the functional responses of *G. pulex* and *G. d. celticus* across all refuge treatments could be appropriately described by Type II models, since the first-order terms were all negative and significant (all:  $P < 0.05$ , Table 2). Two-term logistic regressions lacked any significant positive first-order terms (Table 2), indicating that categorical Type III functional response models were inappropriate. Both categorical Type II and flexible functional response models could be applied to each predator treatment combination, yielding estimates for all parameters (Fig. 2). The flexible model had comparable  $\Delta$ AIC values to the categorical Type II model despite containing an extra parameter and was more appropriate for describing the functional responses of *G. pulex* in the high refuge treatment and *G. d. celticus* in the low and high refuge treatments (Table 2).

#### FUNCTIONAL RESPONSE COMPARISONS

Generally, *G. pulex* and *G. d. celticus* had similar functional responses towards *C. curvispinum* at each refuge level, because 95% CIs of bootstrapped parameter estimates overlapped at high, medium and low refuge treatments for categorical Type II models (Fig. 2a,b), and for flexible models (Fig. 2c–e).

The systematic effects of increasing predator-free space on functional response parameters were evident for both predators. For categorical functional responses, attack rates generally declined; for both *G. pulex* and *G. d. celticus*, attack rates were significantly lower in the medium and high as compared to the low refuge treatments (Fig. 2a). Handling times remained comparable among treatments for both predators because 95% CIs overlapped throughout (Fig. 2b). Systematic reductions in attack rates for categorical Type II models translated to systematic reductions in the overall functional responses of both predators with increasing predator-free space (*G. pulex*; Fig.

**Table 2.** Results of logistic regressions for selecting categorical Type II or III functional response models; Akaike Information Criterion ( $\Delta$ AIC) for fitted categorical Type II (eqn 1) and flexible (eqn 2) functional response models

Refuge treatment	Predator	Logistic regression Type II		Logistic regression Type III				$\Delta$ AIC: categorical Type II model	$\Delta$ AIC: flexible model
		1st term	P	1st term	P	2nd term	P		
Low	<i>G. pulex</i>	-0.040	<0.001	-0.057	0.156	<0.001	0.664	113.757	113.817
Medium	<i>G. pulex</i>	-0.031	<0.001	-0.059	0.135	0.001	0.478	134.585	134.351
High	<i>G. pulex</i>	-0.054	<0.001	-0.138	0.001	0.002	0.040	112.275	113.565
Low	<i>G. d. celticus</i>	-0.034	<0.001	-0.042	0.315	<0.001	0.854	123.131	121.232
Medium	<i>G. d. celticus</i>	-0.038	<0.001	-0.053	0.168	<0.001	0.686	121.448	123.377
High	<i>G. d. celticus</i>	-0.045	<0.001	-0.192	<0.001	0.003	<0.001	111.860	110.363

3a–c, *G. d. celticus*; Fig. 3d–f). The functional response of *G. pulex* in the medium refuge treatment was lower than in the low refuge treatment, up to prey densities of 20 (Fig. 3b). Comparison of high and low refuge treatments demonstrated that the functional response in the high refuge treatment was lower across prey densities up to 30 (Fig. 3c). For *G. d. Celticus*, there were similar reductions in the functional response between medium and low refuge treatments (Fig. 3e) and between high and low refuge treatments (Fig. 3f).

Flexible functional response model parameters also highlighted systematic effects of predator-free space. The search coefficients of both predators generally decreased with increasing predator-free space with significant reductions in the medium and high as compared to the low refuge treatments (Fig. 2c). The handling times of both predators increased with predator-free space (Fig. 2d), and for *G. d. Celticus*, handling times were significantly longer in the high as compared to the medium and low refuge treatments (Fig. 2d; open squares). For both predators, there was a trend towards higher scaling exponent values and thus increasingly stabilizing (i.e. Type III) functional response shape with predator-free space (Fig. 2e). The resulting functional response shapes systematically changed from Type II (*G. pulex*; Fig. 3 h & i, dotted curves; *G. d. celticus*, Fig. 3k & l, dotted curves) towards Type III (*G. pulex*; Fig. 3 g & i, solid curves; *G. d. celticus*, Fig. 3j & l, solid curves) with increasing predator-free space. Thus, reductions in functional responses at low prey densities emerged at high and medium refuge treatments; the sigmoidal shapes of high and medium refuge flexible functional responses resulted in lower predicted prey consumption at the lowest prey densities than categorical equivalents for both predators (Fig. 3; solid and dashed curves throughout).

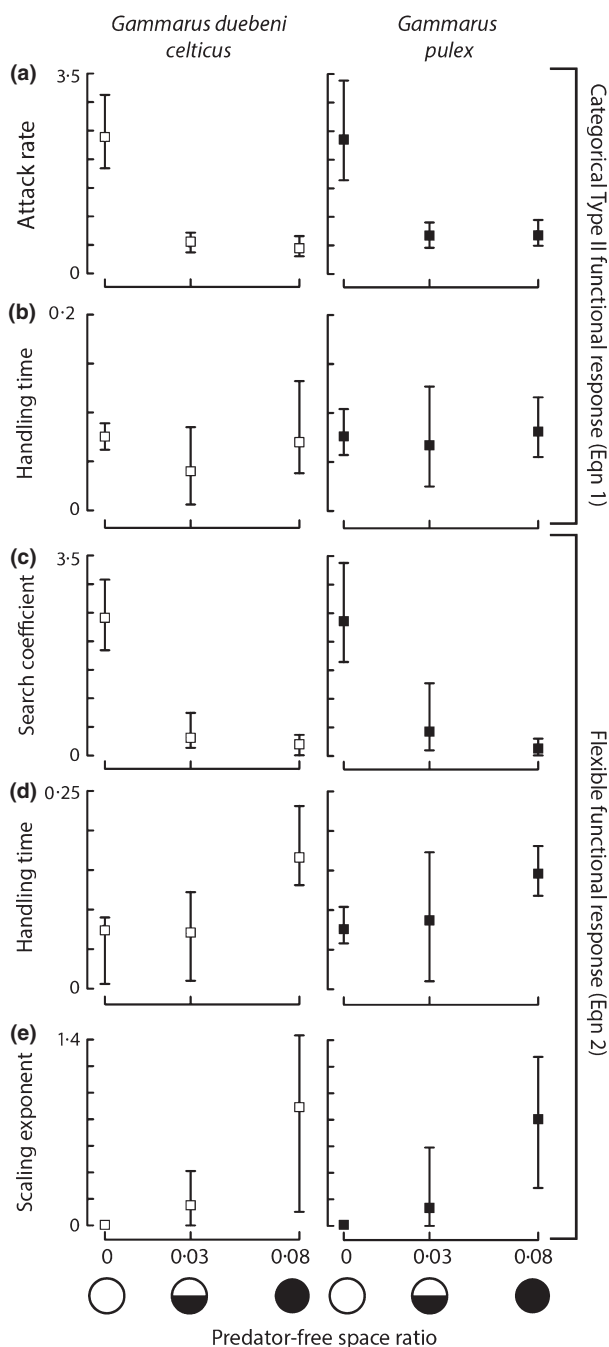
### Discussion

In this study, we provide the first evidence linking systematic increases in predator-free space to reductions in functional response magnitude, and also to subtle changes in functional response shape. In doing so, we demonstrate how predator-free space – as a discrete component of habi-

tat structure – can impart stabilizing effects on predator–prey dynamics. These findings suggest that habitats with superficially similar structural complexity can harbour subtle differences in predator-free space that considerably alter the outcomes of interspecific interactions.

Differences such as these are likely to be of particular importance to prey attempting to establish and persist in novel habitats (e.g. Byers 2002), because even invasions founded by a large influx of propagules may only provision a recipient habitat with low densities of invaders. At such densities, the distinction between the Type II and Type III functional response is an acutely important determinant of extinction (Sinclair *et al.* 1998), more so than the absolute magnitude of the interaction. Further, although the interaction between habitat structure and biological invasions is increasingly regarded as a fundamental component of understanding the effects of invasive species (Petren & Case 1998; Didham *et al.* 2007), expectations regarding the capacity of *C. curvispinum* to persist in novel habitats may be confounded without detailed consideration of the variable capacity of resident predators to attenuate its establishment (Bovy *et al.* 2014), and of the micro-scale variability in available predator-free space. Undoubtedly, these factors, and myriad others, contribute to the prevailing perception that invader impacts are idiosyncratic (Ricciardi *et al.* 2013).

Whilst categorical approaches to defining functional responses can capture the broad effects of structural complexity – in terms of changes in magnitude and shape (Alexander *et al.* 2012) – our findings imply that such approaches can miss subtle but important changes, particularly at low prey densities. Indeed, analysis of large functional response data sets with flexible models has revealed that shape scales predictably with predator–prey body mass ratios (Vucic-Pestic *et al.* 2010; Kalinkat *et al.* 2013). This indirectly implies that many functional responses previously classified as Type II have some degree of low-density inflection characteristic of Type III. Although extensive empirical studies have the power to resolve patterns from noise, modelling has cast doubt on whether targeted empirical data are capable of resolving differences in shape to an adequate level on a case-by-case basis



**Fig. 2.** Parameter estimates from categorical Type II (a and b) and flexible (c–e) functional responses. Points are original MLE values and error bars are bootstrapped 95% CIs. Refer to Fig. 1 for symbol key.

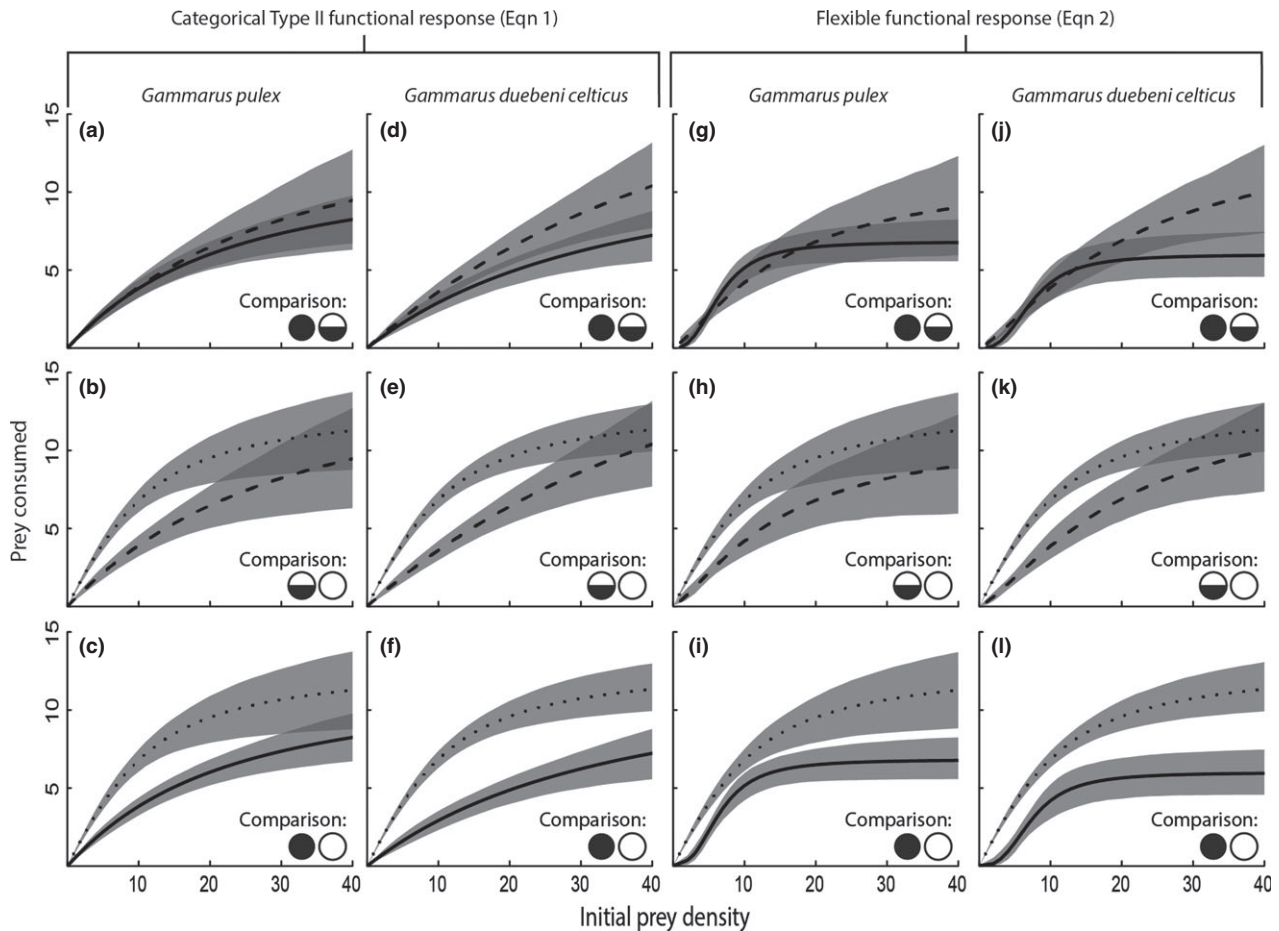
(Williams & Martinez 2004). Simply, the degree of inflection required to impart stability may be small (moving the scaling exponent from 0 to 0.2 is sufficient), and empirical functional response data are noisy. Nevertheless, case-specific empirical data can track systematic changes in shape (Toscano & Griffen 2013), and here we show that small increases in scaling exponent values, which may not be statistically distinguishable from one another, can yield functional responses with significant differences in prey consumption at low prey densities. Empirical functional

response comparisons must therefore consider both the individual component model parameters and functional response curves in their entirety to draw any meaningful conclusions about differences. Given that the stability of predator–prey dynamics can hinge on very small differences in functional response shape, however, a lack of statistical significance should not necessarily be conflated with a lack of ecological significance.

Case-specific comparisons of the functional responses of invasive and native species offer a pragmatic means to assess the impacts of invasive species, whether considering impacts on native prey, biotic resistance by resident predators (MacNeil *et al.* 2013) or both (Barrios-O'Neill *et al.* 2014b). Such comparisons are reductive in the sense that they do not consider community-level impacts, but their immediate use as impact assessment tools (Dick *et al.* 2014) belies their general value: functional responses are a fundamental component of ecological networks (Jeschke, Kopp & Tollrian 2002; Kalinkat *et al.* 2013). Although it would be impractical to resolve every possible pairwise interaction within ecological networks, and size-based models can provide useful generalizations in this respect (Kalinkat *et al.* 2013), the importance of species-specific effects should not be underestimated (Rall *et al.* 2011). Therefore, a continuing and major goal of empiricists should be to generate high-quality functional response data, both to answer case-specific questions and to elucidate more general patterns (e.g. Pawar, Dell & Savage 2012). As a result, we can hope to improve understanding of how invasive species elicit impacts, and how factors such as structural complexity mediate these impacts.

Isolating distinct components of habitat structure to quantify effects on predator–prey interactions remains difficult. In the present study, manipulating predator-free space in reedy-margin analogues still resulted in some variation in fractal geometry, and in certain other measurable aspects of complexity, such as number of refugia. That said, data presented here and in other studies allude to the importance of predator-free space in mediating predator–prey interactions (Bartholomew, Diaz & Cicchetti 2000; Humphries, La Peyre & Decossas 2011; Toscano & Griffen 2013). In contrast, although fractals have many applications in ecology (Sugihara & May 1990) they are often inappropriately applied (Halley *et al.* 2004) and offer no mechanistic insight into why interactions are mediated by structural complexity. Therefore, efforts to understand the effects of structural complexity should focus on metrics, which offer some degree of explanatory power.

Manipulations of these metrics may necessitate a move away from the use of analogues of natural structures, such as macrophytes (Warfe & Barmuta 2004), towards artificial structures, which provide means to continuously vary specific facets of complexity. Although some have adopted such an approach (Huffaker 1958; Bartholomew, Diaz & Cicchetti 2000; Hauzy *et al.* 2010), it has also attracted criticism (Beck 2000). In practice, however, these approaches are complementary, with highly abstracted



**Fig. 3.** Functional responses of gammarid predators towards *C. curvispinum*: (a–f) are categorical Type II models and (g–l) are flexible models. Solid curves are high refuge treatments, dashed curves are medium refuge treatments and dotted curve are low refuge treatments. Shaded areas are 95% bootstrapped CIs.

manipulations providing a means to identify fundamental relationships between discrete components of structure and interactions, and increasingly realistic manipulations facilitating a more complete understanding of how such components combine to shape interactions in the real world. Here, we provide further evidence for the value of an abstracted approach. Beyond the vertical orientation of the habitat structures, we deliberately made no attempt to further mimic a reedy-margin habitat to effectively manipulate predator-free space. Clearly, analogous natural structures contain myriad areas of predator-free space, each specific to certain predator–prey size combinations.

In conclusion, we reiterate that subtle changes in structural complexity can have important effects on the functional responses of predators. A thorough understanding of these effects will in turn improve our understanding of predator–prey dynamics, and of the success of invasive species. We encourage empirical ecologists to think creatively about how to address questions pertaining to structural complexity and, particularly, to consider separating the component parts of complexity systematically without necessarily resorting to mimicry of natural structures. By quantifying the important effects of individual compo-

nents, we can make progress towards a more complete understanding of an intrinsically and metaphorically complex challenge in ecology.

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### Data accessibility

Underlying functional response data are available on the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.v56t9> (Barrios-O’Neill *et al.* 2014a).

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