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LETTER

Colonisation rate and adaptive foraging control the emergence of trophic cascades

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Abstract

Ecological communities are assembled and sustained by colonisation. At the same time, predators make foraging decisions based on the local availabilities of potential resources, which reflects colonisation. We combined field and laboratory experiments with mathematical models to demonstrate that a feedback between these two processes determines emergent patterns in community structure. Namely, our results show that prey colonisation rate determines the strength of trophic cascades – a feature of virtually all ecosystems – by prompting behavioural shifts in adaptively foraging omnivorous fish predators. Communities experiencing higher colonisation rates were characterised by higher invertebrate prey and lower producer biomasses. Consequently, fish functioned as predators when colonisation rate was high, but as herbivores when colonisation rate was low. Human land use is changing habitat connectivity worldwide. A deeper quantitative understanding of how spatial processes modify individual behaviour, and how this scales to the community level, will be required to predict ecosystem responses to these changes.

Keywords

Adaptive foraging, colonisation, food webs, trophic cascades.

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INTRODUCTION

Anthropogenic habitat alteration is changing the spatial context in which species interactions occur. Human land use in particular is eroding historical patterns of habitat connectivity (Gibbs 2000; Foley *et al*. 2005), resulting in altered exogenous supplies of resources (e.g. prey resources for predators) to food webs (Hein & Gillooly 2011; Piovia-Scott *et al*. 2011; Fahimipour & Hein 2014; Stier *et al*. 2014). An important goal for efforts to predict and manage human effects on ecosystems is to understand how changes in spatial habitat features that govern resource supplies affect direct and indirect interactions in food webs, and how this in turn impacts emergent patterns of community structure (Holt 2010; Dreyer & Gratton 2013). Trophic cascades are the archetypical example of emergent outcomes of food web interactions, and occur when predators directly reduce prey populations, indirectly facilitating populations at lower trophic levels. But, despite the fact that cascades have been documented in virtually every type of ecosystem (Shurin *et al*. 2010), both conceptual and mathematical theories have been unable to fully explain widespread variation in observed cascade strength (Polis *et al*. 2000; Borer *et al*. 2005; Fox 2007; Holt *et al*. 2010; Shurin *et al*. 2010; Heath *et al*. 2013); predictions from mathematical models have received equivocal experimental support (Fox 2007; Shurin *et al*. 2010; Heath *et al*. 2013) and the mechanisms underlying spatial variation in cascade strength in nature remain largely unexplored (Holt *et al*. 2010).

Traditionally, cascade models that have provided predictions for experiments lump species into discrete trophic levels, and assume that species interactions are fixed and occur in closed systems (Oksanen *et al*. 1981; Nisbet *et al*. 1997; Terborgh *et al*. 2010; Heath *et al*. 2013). These assumptions are now being challenged (Shurin *et al*. 2010), however, by evidence that suggests many if not most predators feed across multiple trophic levels (i.e. omnivory) and forage adaptively or flexibly to some degree (Fryxell & Lundberg 1998; Kondoh 2003; Arim & Marquet 2004; Thompson *et al*. 2007; Abrams 2010). Moreover, ecological communities are open systems governed by exogenous spatial flows of colonists (MacArthur & Wilson 1967; Levin 1992; Hubbell 2001). In many communities, predator foraging behaviour and prey colonisation rates may be linked, because variation in the influx of different resources can influence predator foraging strategies, thereby altering direct and indirect food web interactions. It is therefore conceivable that these ubiquitous features of real food webs – omnivory, adaptive foraging and colonisation – influence one another through feedbacks that could help explain empirical deviations from cascade theory (Polis *et al*. 2000; Holt *et al*. 2010; Shurin *et al*. 2010). However, to our knowledge, no studies have investigated their joint effects on trophic cascades.

Here, we combine field and laboratory experiments with mathematical models to demonstrate that colonisation rate determines foraging strategies of top omnivorous predators and, therefore, how cascades manifest in food webs. Specifically, we manipulated colonisation rate in an array of experimental pond communities, and studied variation in the strength of cascades induced by an adaptively foraging omnivorous fish predator, *Gambusia affinis*, in these communities. We report that variation in colonisation rate among habitats strongly altered the strength and direction of cascades. We observed a traditional cascade, with fish strongly depressing prey (i.e. primary consumers) and facilitating producer biomass densities when colonisation rate was high. However, the facilitation effect was overridden by direct consumption of producers when colonisation rate was low. Mathematical models, gut content analyses and laboratory feeding experi-

ments reveal the underlying mechanism: experimentally reducing colonisation rate caused differences in the relative biomass of prey and producer resources at the community scale, which prompted an adaptive shift in the foraging effort of individual fish increasingly towards producers.

MATERIALS AND METHODS

Experimental design and sampling protocol of field experiment

On 12 June 2012, we deployed an array of 32 experimental pond mesocosms downwind from a permanent lake, which acted as a colonisation source, at the San Joaquin Marsh Reserve (SJMR) in Irvine, CA, USA. In this system, small natural ponds are seasonally filled with water and rapidly colonised by primary producers (e.g. wind-dispersed and hitch-hiking phytoplankton) and invertebrate prey (e.g. flying aquatic insects, oviposited insect larvae, wind-dispersed zooplankton; species list provided in Appendix S1) that immigrate from the nearby permanent lake. Increasing the *distance* between ponds and the nearest permanent lake reduces species' colonisation rates (Hein & Gillooly 2011; Fahimipour & Hein 2014). Thus, through a distance treatment, we created *high* and *low* colonisation rate communities by placing ponds either 30 or 300 m from the colonisation source respectively.

All mesocosms began the experiment at a state in which no species were present. We scrubbed with bleach, washed and placed 16 1-m diameter plastic wading pools at each of the two distances, filled them with a 25 mm layer of heat sterilised sand, 25 g of rabbit food (Small World, Manna Pro, St. Louis, MO, USA) to provide an initial source of nutrients and 70 L of filtered and treated tap drinking water. Tap water is the only available clean water source at the SJMR, and was treated for chloramines and chlorine; the absence of these and other contaminants was confirmed using water testing kits prior to the experiment.

We allowed communities to naturally assemble for 4 weeks, at which point we added two individual *G. affinis* mosquitofish *c.* 30 mm in length, collected from the permanent lake, to eight randomly selected mesocosms in each distance treatment (i.e. half of the ponds at each distance). *G. affinis* is a generalist adaptive omnivore that readily consumes resources in multiple trophic levels – both prey (e.g. zooplankton, aquatic macroinvertebrates) and producers (e.g. phytoplankton, diatoms). *Gambusia* have dorsally oriented mouths and dorsoventrally flattened heads, and are known to feed primarily on pelagic resources or near the surface, while largely avoiding the unpalatable $CaCO_3$-encrusting plankton that comprise benthic mats (Geddes & Trexler 2003; Pyke 2005). For these reasons, our sampling focused on the pelagic phytoplankton-zooplankton-insect community. Fish abundance and predation pressure were kept constant throughout the experiment by removing offspring in the event of a male-female pairing, and replacing dead individuals (< 18% of all individuals) or individuals who underwent significant growth with a new individual *c.* 30 mm in length, following surveys every 3–5 days. We also replaced evaporated water during surveys, to maintain pond volume at *c.* 70 L and control for variation in habitat size. Communities were sampled 2, 4, 6, 8, 10 and 12 weeks after the establishment of ponds; the average natural pond at the SJMR continuously contains water for 2–8 weeks (P.A. Bowler, *pers. comm.*). Thus, the length of our experiment is sufficient to capture relatively long-term changes in this system over 4–12 generations of an average member species, and 2–4 generations of the longest-lived taxa (Hein & Gillooly 2011).

During each sampling event, we counted all macroinvertebrates by sweeping a 1-mm mesh net through the water and benthos until no individuals were detected on three consecutive sweeps. We measured the body lengths of the first 20 individuals of each species with digital calipers before returning them to mesocosms. We then took four 250-mL zooplankton samples using an integrated depth sampler. Plankton samples were combined and filtered through 1-mm nitex mesh, anaesthetised with carbonated water, preserved with 10% acid Lugol's solution and enumerated and measured in the laboratory. All zooplankton and macroinvertebrates (i.e. prey) were identified to the highest possible taxonomic resolution (Appendix S1), and population biomass densities ($mg \times mL^{-1}$) were calculated as B_i/V, where $B_i = M_i \times N_i$; M_i and N_i are the average body mass (mg) and abundance of species i respectively and V is the measured habitat volume (mL). Body masses were estimated from measured lengths using a set of taxon-specific conversions for aquatic invertebrates compiled by Fahimipour & Hein (2014). Producer (e.g. phytoplankton, diatoms) biomass densities were estimated by measuring chlorophyll *a* fluorescence values from five vertical water samples collected with an integrated depth sampler, using a handheld AquaFluor fluorometer (Turner Designs, Sunnyvale, CA, USA).

Following the field experiment's conclusion, we sacrificed fish in order to perform gut content analyses and determine whether fish diets depended on habitat colonisation rate. Gut contents were preserved in 70% ethanol and stained with 5% Lugol's solution before identifying and measuring food items using a stereomicroscope. The relative volumetric quantity of food in the gut was estimated by assuming the gut was cylindrical, measuring its dimensions, calculating total gut volume and then visually estimating the fraction of the gut occupied by food as a proxy for total food biomass. We then separated gut contents into two components, prey and producers, and estimated the fraction of prey in the gut by measuring body lengths and using taxon-specific length-volume conversions (McCauley 1984; see also references in Appendix S1 in Fahimipour & Hein 2014). The fraction of prey in fish diets sacrificed from mesocosms experiencing different colonisation rates were compared using ANOVA.

Laboratory feeding experiment

To characterise the foraging strategies of *G. affinis*, we performed laboratory feeding trials with individual mosquitofish in replicate 3.5 L aquaria. On 10 December 2013, we starved twelve fish for 5 h to establish a consistent intermediate hunger level (Pyke 2005), at which point we exposed them to *c.* 20 mg (dry biomass) of total food, varying only the ratio of producer (the algae, *Spirogyra spp.*; Carolina Biological Sup-

ply) to prey (mosquito larvae, *Culex quinquefasciatus* from laboratory stocks) biomass densities. We experimentally altered food availabilities to *c.* 1 : 3, 1 : 1 and 3 : 1 producer : prey biomass ratios. However, variation in the body masses of individual mosquito larvae caused slight variation about the precise ratios. Following a 24-h period, we measured the amount of prey and producer biomass consumed by each fish by calculating the difference between remaining (after 24 h) and initial prey and producer biomass densities. We used a second-order polynomial regression of the ratio of prey: producers eaten on the ratio available to determine whether fish foraged in a manner consistent with adaptive foraging models during laboratory feeding experiments, with a significant quadratic term being consistent with the hypothesis of adaptive foraging. Conversely, if *Gambusia* forages in a manner in which producers and prey comprise a fixed proportion of the total diet, then we would expect a linear relationship between the ratio eaten and the environmental ratio (q_R and q_N in eqn 1 are constants for fixed foragers, so the ratio of producers to prey consumed $\propto q_R/q_N \times R/N = wR/N$, where w is a constant).

Statistical analyses

To quantify trophic cascade strength, we calculated effect sizes according to convention (Shurin *et al*. 2002; Fox 2007) as $\log_e(X_{+P}/X_{-P})$, where X_{+P} and X_{-P} are the mean biomass densities, averaged over the final 6 weeks of the experiment, of resource X in the presence and absence of fish respectively. Habitat pairs (i.e. X_{+P} and X_{-P}) were assigned based on spatial proximity in the field, although randomly assigning habitat pairs did not affect the qualitative results presented below. We used ANOVA to determine whether producer and prey effect sizes were different in high- vs. low-colonisation rate ponds. Changing the number of post-fish addition sampling dates included in the cascade strength analyses did not change the qualitative results presented below (see Appendix S2 for cascade results when only week 12 is included).

To determine how biomass densities depended on time, fish presence and colonisation rate, we performed linear mixed effects (*LME*) model analyses on the producer and prey time series post-fish addition (Table 1). For each community property, Y (i.e. producer and prey biomass densities), we fit a model of the form $Y = B_1(time) + B_2(fish) + B_3(distance) + B_4(time \times fish) + B_5(time \times distance) + B_6(fish \times distance) + B_7(time \times fish \times distance) + G + E$, where B_1–B_7 are regression coefficients, G is a random effect of pond identity (to account for the fact that repeated measurements were made on each pond), and E is a vector of errors. To improve normality of residuals, producer biomass densities were fourth-root transformed and prey biomass densities were fifth-root transformed prior to analyses. We also examined whether local resource conditions at the time of fish additions were different in habitats experiencing different colonisation rates. To do this, we compared prey and producer biomass densities in low- and high-colonisation rate ponds immediately before fish additions (the week four censuses) using ANOVA. *LME* models were fitted using the *nlme* package in the statistical programming environment, R (R Core Team, 2014).

Table 1 Results from analysis of community properties

Property	Treatment	Sign	*F*(d.f.)	*P*-value
R	**Time**	+	19.14 (3,84)	< 0.001
	Distance	+	10.24 (1,28)	0.0034
	Fish	+	2.1 (1,28)	0.044
	Time × Distance	−	5.16 (1,92)	0.042
	Time × Fish	n.a.	1.48 (3,84)	0.23
	Distance × Fish	−	24.99 (1,28)	< 0.001
	Time × Distance × Fish	n.a.	0.344 (3,84)	0.793
N	**Time**	+	35.72 (3,84)	< 0.001
	Distance	−	31.12 (1,28)	< 0.001
	Fish	−	31.79 (1,28)	< 0.001
	Time × Distance	−	7.06 (3,84)	0.0003
	Time × Fish	−	2.92 (3,84)	0.039
	Distance × Fish	+	9.68 (1,28)	0.0043
	Time × Distance × Fish	n.a.	1.98 (3,84)	0.123

'Property' column indicates the community property to which statistics refer (either producer or prey biomass densities). 'Sign' column indicates whether the treatment variable resulted in an increase (+) or decrease (−) in the value of the community property. Significant effects ($P < 0.05$) are listed in bold.

Mathematical model

Our model is a coarse-grained representation of our experimental study system and represents a straightforward alteration of traditional cascade models (Oksanen *et al*. 1981; Nisbet *et al*. 1997). A simple food chain model with the addition of colonisation and adaptive foraging strategies, in which the omnivore dynamically apportions foraging effort towards either producers or prey based on their availability and profitability, can be represented by

$$\begin{aligned} \frac{dR}{dt} &= I_R + rR\left(1 - \frac{R}{K}\right) - a_N RN - q_R a_P RP \\ \frac{dN}{dt} &= I_N + e_R a_N RN - q_N a_P NP - mN \\ \frac{dq_X}{dt} &= v q_X \left(\frac{\partial \beta}{\partial q_X} - \sum\nolimits_{k \in S} q_k \frac{\partial \beta}{\partial q_k}\right), \end{aligned} \quad (1)$$

where R is the producer biomass density, N is the prey biomass density and P is the omnivore biomass density, which we make constant to mirror experimental conditions, and q_R and q_N are the preferences of the omnivore for producers and prey respectively. The parameter v is a rate constant that sets the timescale upon which changes in foraging effort occur, β is the omnivore's per capita biomass production rate, $\beta = f_R q_R a_P R + f_N q_N a_P N$, and the sum is taken over all S species in the omnivore's diet. Producers and prey colonise the system at rates, I_R and I_N respectively. Other parameters are defined in Appendix S2, and correspond to a biomass interpretation of standard food chain models with Type I functional responses.

We incorporated adaptive foraging strategies using a pair of dynamical variables, denoted generally as q_X, which are based on replicator equations (e.g. Kondoh 2003) and represent the proportion of total foraging effort an omnivore will apportion towards one of its resource species, X (Kondoh 2003; Abrams & Fung 2010). In this context, the replicator equation implies a food choice rule that attempts to maximise biomass produc-

tion: the omnivore increases its foraging effort towards resource X (i.e. q_X) if a unit change in q_X causes the omnivore's biomass production to exceed that derived from current foraging effort. We revisit some of the assumptions behind the model, and present the results of simulations with Type II functional responses in Appendix S2.

To study the effects of colonisation rate on producer and prey effect sizes over a broad range of potential conditions, we simulated the model using 10^5 randomly generated parameter sets. We generated 100 values of colonisation rates, I_X, evenly spaced on the interval $1 \times 10^{-4} \leq I_X \leq 5 \times 10^{-1}$ and simulated the model 1000 times for each value of I_X, drawing all other parameter values (except P and a_P, which we make constant to mirror experimental conditions) independently from uniform distributions. To compare modelling results with our experimental results, equilibrium biomass' were summarised similarly to our data as log response ratios, where X_{+P} is the equilibrium biomass of resource X simulated with $P > 0$ and X_{-P} is the equilibrium biomass of X simulated with the same set of parameter values but with $P = 0$. Parameter distributions were based around values from the omnivory food chain model of McCann (2011) and ranges were chosen because they produced interior equilibria with positive values for R, N, q_N and q_R when matching parameter sets were used in models with omnivores ($P > 0$) and without omnivores ($P = 0$), and because they yielded realistic cascade strength values – for instance, effect sizes less than -3 or greater than 3 are rarely observed in nature (Shurin *et al.* 2002). This approach yields model results from thousands of unique 'communities', which allowed us to explore the generality of our findings without making specific assumptions about variation in community composition or particular species' characteristics in our mesocosm experiment. During each simulation, the model was run to equilibrium; simulations that did not generate fixed interior equilibria within 10^6 time steps were excluded from our analyses. To explore the importance of adaptive omnivory in generating empirically observed patterns, we also simulated fixed omnivory by performing the same procedure described above, except that we held q_R constant and $q_N = 1–q_R$. Numerical simulations were accomplished using the *deSolve* and *rootSolve* libraries in R (R Development Core Team 2014). For additional details on parameter ranges used and other modelling specifics, see Appendix S2.

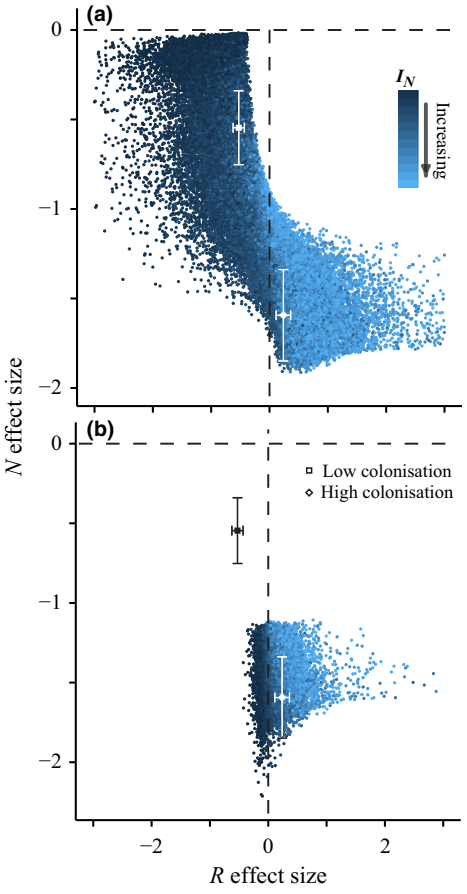

Figure 1 Effects of colonisation rate on cascade strength (± SEM) from experimental ponds (squares = low colonisation rate ponds; diamonds = high colonisation rate ponds) superimposed over results of mathematical models (coloured points). Producer and prey effect sizes are on the x- and y-axes, respectively. (a) Results from 10^5 simulations of the adaptive foraging model. (b) Results of 10^5 simulations of the fixed foraging model with $q_R = 0.2$. Points represent stable internal equilibria resulting from individual simulations and are shaded according to the associated value of I_N, with lighter colours corresponding to higher colonisation rates. Experimental points and error bars are shaded only for contrast against the background.

RESULTS

Effects of colonisation rate on trophic cascades in mesocosms

Cascade strengths in field mesocosms depended on colonisation rate (Fig. 1a). Fish facilitated producer biomass densities, inducing a classic cascade, in communities experiencing high colonisation rates (Fig. 1a; ANOVA; $F_{1,14} = 23.51$, $P = 0.0003$). When colonisation rate was low however, fish depressed producer biomass densities. Likewise, fish effects on prey depended on colonisation rate (Fig. 1a; ANOVA; $F_{1,14} = 10.18$, $P = 0.007$): higher colonisation rates led to an increasingly strong depression of prey biomass by omnivores. In short, differences in colonisation rates in our study system generated consistent spatial variation in fish effects on both producers and prey; as colonisation rate increased, fish effects shifted from a relatively weak depression of prey and depression of producers, to a relatively strong depression of prey and facilitation of producers.

Analyses of biomass dynamics confirmed that fish had qualitatively different effects on producers in high- (positive effect of fish, Table 1) compared to low- (negative fish × distance interaction, Table 1) colonisation rate ponds (compare Figs. 2a and 2b). We did not detect an interaction between time and fish presence for producers in ponds experiencing either colonisation rate. Fish had a negative effect on prey in both high- and low-colonisation rate ponds (compare Figs. 2c and 2d; negative effect of fish, Table 1). The effect of fish on prey biomass densities was weaker in low colonisation rate ponds however (positive distance × fish interaction, Table 1), consistent with the results of the cascade analysis. Producer and prey biomass densities increased through time in all meso-

cosms (Table 1). We also detected a negative interaction between time and fish presence for prey, indicating that prey biomass increased more slowly in the presence of fish in these mesocosms (Table 1).

We compared prey and producer biomass densities from the week four census (immediately preceding fish additions) in all ponds to show that local resource conditions at the time of fish arrivals depended on colonisation rate. At this time (Fig. 2, vertical dashed lines), our colonisation rate treatment had generated differences in producer and prey biomass densities, indicating that fish experienced different resource conditions upon entering their respective webs, and that this depended on colonisation rate. Specifically, fish added to high colonisation rate communities entered webs with higher prey (Fig. 2c and d, vertical dashed lines; ANOVA; $F_{1,30} = 51.56$, $P < 0.001$) and lower producer (Fig. 2a and b, vertical dashed lines; ANOVA; $F_{1,30} = 31.91$, $P < 0.001$) availabilities, whereas fish added to low colonisation rate communities experienced lower prey and higher producer availabilities. These differences were present not only at the time of fish additions, but could be detected throughout the experiment by analysing the dynamics of fishless ponds. Reducing colonisation rate (i.e. increasing distance from the source lake) had a positive effect on producers and a negative effect on prey (Fig. 2; Table 1) in these ponds, again indicating that resource conditions shifted from relatively low producer and relatively high prey, to high producer and low prey biomass densities as colonisation rate decreased.

Mathematical models and diet information reveal underlying mechanism

Our modelling analyses suggest that when omnivores forage adaptively, variation in prey colonisation rate, I_N, generates a dramatic spatial gradient of omnivore effects on both producers and prey highly consistent with results of the mesocosm experiment (Fig. 1a). This, however, does not occur when foraging preferences q_R and q_N are fixed (Fig. 1b), suggesting that a switch in preference towards producers in low colonisation ponds is required for the spatial patterns we observed. Observed changes occurred through the strong influence of prey colonisation rate, I_N, on omnivore foraging strategies (i.e. q_X; eqn 1). As I_N increases, prey become increasingly biomassive and the omnivore shifts its foraging effort increasingly away from the nutritionally inferior producers (Fryxell & Lundberg 1998). The topology of the system becomes more like a linear food chain, with increasingly strong omnivore–prey interactions and increasingly weak omnivore–producer interactions, as prey colonisation rate increases.

In contrast, producer colonisation rate, I_R, has little impact on either producer or prey effect sizes (Fig. S2.1, Appendix S2). This is due to the high sensitivity of q_N and q_R to the influx of the more profitable resource, which we assume are the prey. Thus, although our experiment's distance treatment potentially altered both prey and producer colonisation rates, our model analyses suggest that changes in prey colonisation rate, I_N, generated the observed shift in cascade strength, and

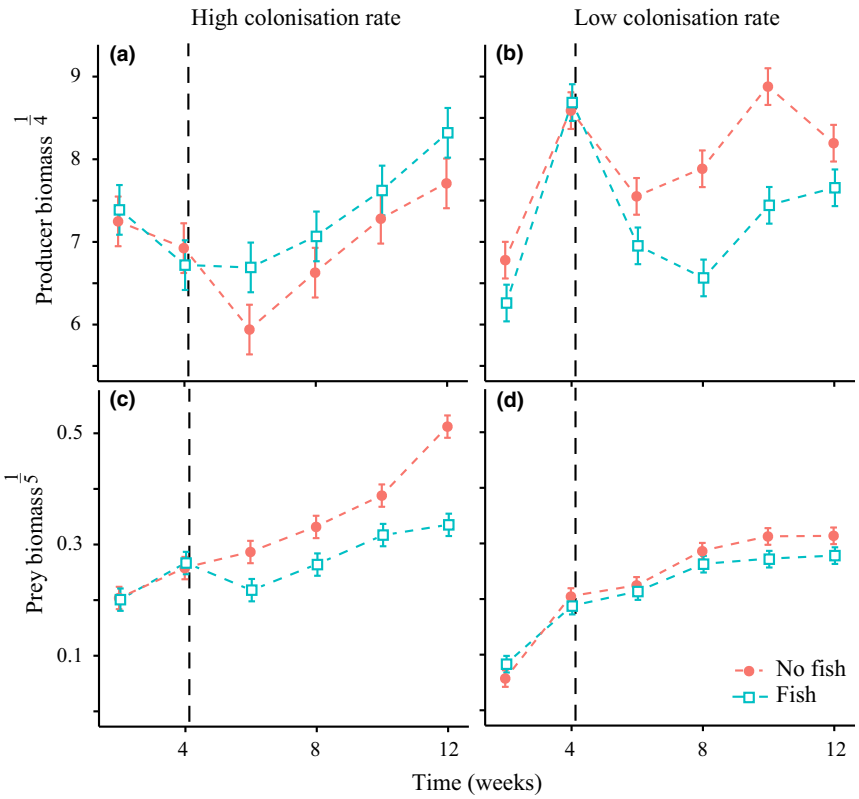

Figure 2 Effects of fish and colonisation rate on producer and prey biomass dynamics. Fish- and fishless ponds are indicated by blue squares and red circles, respectively. Dynamics of mean producer fluorescence (as a proxy for biomass) are shown for (a) high- and (b) low-colonisation rate ponds (± SEM). Dynamics of mean prey biomass densities (mg mL^{-1} ± SEM) are shown for (c) high- and (d) low-colonisation rate ponds.

that this holds across a range of assumed relationships between distance from the source pool, I_N and I_R. The relative effects of I_N and I_R also hold across a range of values in the other parameters; the average impact of each model parameter on cascade strength is discussed in Appendix S2 and shown in Fig. S2.1.

Differences in the gut contents of fish from ponds at different distances supported the hypothesis that spatially mediated shifts in fish foraging strategies altered the effects of fish on lower trophic levels in our study system. The guts of fish taken from high colonisation rate ponds contained a significantly higher fraction of prey than those taken from low colonisation rate ponds (Fig. 3a; ANOVA; $F_{1,7} = 17.53$, $P = 0.0041$), suggesting that fish foraging strategies depended on the habitat colonisation rate.

Data from laboratory feeding trials confirmed that *G. affinis* is an adaptive forager. If fish foraged in a manner consistent with a fixed omnivory model, then we would have expected the ratio of prey to producer biomass consumed by individual fish to increase linearly as a function of the prey to producer biomass ratio in the environment. But, this was not the case. Instead, this relationship displayed nonlinearities (Fig. 3b; significant quadratic term; $P < 0.001$), again suggesting that producers and prey do not comprise a fixed proportion of the total diet and that the fish forage adaptively depending on producer and prey availabilities in the environment.

DISCUSSION

Trophic cascades may be influenced by many factors that have so far received little empirical attention (Holt *et al.* 2010). Here, we demonstrate that cascade strength is strongly influenced by a feedback between organismal movement at the landscape scale, resource conditions at the community scale and foraging behaviour at the scale of the individual predator. Moreover, our study provides new empirical evidence that spatial variation in the strength of omnivory that likely exists within many landscapes (Kratina *et al.* 2012; Fig. 3) has important consequences for emergent patterns in community structure and system dynamics.

Although we use experimental pond mesocosms to demonstrate the effects of colonisation-foraging feedbacks on the emergence of cascades, we expect many of the qualitative features observed in this study to apply to other ecological systems. One requisite feature for this feedback to emerge is an omnivorous top predator that is capable of exhibiting rapid behavioural responses to changes in resource conditions. Food web data show that omnivory is pervasive, with most predators feeding from more than one trophic level to some degree (Arim & Marquet 2004; Thompson *et al.* 2007). One caveat is that, although omnivory is ubiquitous in food webs, this does not necessarily imply that omnivores consume both animal prey and primary producers (e.g. intraguild predators and hyperparasitoids are omnivores that do not necessarily consume producers), as in our system. However, the general result – that variation in the exogenous supplies of resources in a consumer's diet can influence its foraging strategies and, therefore, how top-down control manifests in food webs – is one that likely extends to many organisms facing diet choices regardless of resource types they exploit (Kondoh 2003; Beckerman *et al.* 2010). For instance, adaptive carnivores can prompt changes in the composition of lower trophic levels, with implications for key system properties like nutrient flux rates (Schmitz 2006) and food web persistence (Kondoh 2003).

Behavioural changes in individuals' foraging strategies have now been observed in taxa as diverse as rodents (Fryxell & Lundberg 1998), birds (Krebs *et al.* 1977), large mammals (Raynor *et al.* in press), arthropods (Egas *et al.* 2003) and fish (Dill 1983), many of which are high level consumers in their respective webs. The empirical patterns we observed emerge in models over a wide parameter range when we included adaptive behaviour (Fig. 1a), but did not emerge when trophic preferences were fixed (Fig. 1b). This result highlights the importance of how diet choice is represented in theoretical studies; for instance, adaptive vs. fixed models of omnivory (McCann & Hastings 1997; Abrams & Fung 2010). That adaptive and fixed diet choice models yield qualitatively different dynamics is well known for communities of several interacting species in closed systems (Abrams 2010). These disparate outcomes may be especially important for the study of spatially assembled habitats where resource dynamics can be strongly influenced by habitat connectivity and exogenous processes.

The behavioural mechanism we have identified altered community structures in response to spatial heterogeneity in coloni-

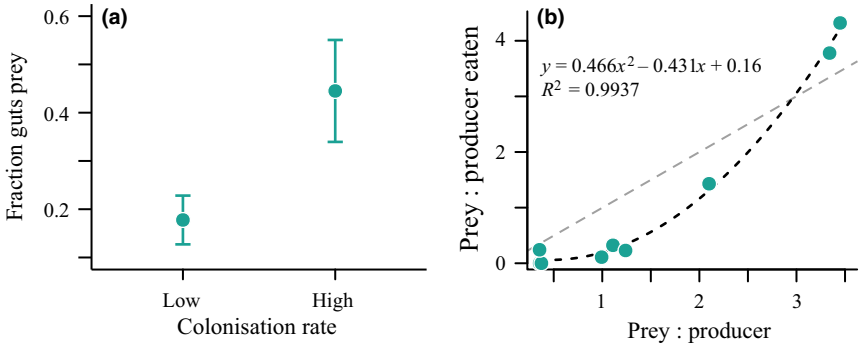

Figure 3 Adaptivity in fish foraging in response to local resource conditions. (a) The fraction of fish guts occupied by prey (± 2 SEM) was higher in fish sacrificed from high colonisation rate ponds. (b) Results of laboratory feeding trials show *G. affinis* exhibits a non-linear relationship between the ratio of prey:producers in the diet and the prey:producer biomass ratio in the environment. This non-linearity is consistent with predictions from adaptive foraging models.

sation rates. Yet, it is possible that spatial variation in other factors could influence the outcomes we observed. Mesocosms in our study were placed in an open field with very little variation in other factors that could have influenced community structure, such as shading and allochthonous nutrient inputs. Additionally, our mesocosms were the same size and experienced identical initial conditions. However, variation in habitat size and initial conditions do influence natural systems; pond size in particular varies naturally across the SJMR landscape. At least one experiment has demonstrated that predators have stronger effects on prey in small habitats compared to large ones (Schoener & Spiller 1999), although the opposite can be true depending on the particular relationships between habitat size and colonisation rate for species in a given food web (Holt 2010). Predicting the effects of habitat size on cascade strengths in our system would require a detailed understanding of the effects of pond diameter and depth on colonisation success and biomass distributions for species in basal, mid and top trophic levels. Uncovering the interactions between habitat distance, size and the adaptive foraging strategies of consumers therein is an important enterprise for future research.

Some species in our system (e.g. plankton) are capable of forming egg banks in dry sediment that individuals emerge from when ponds are inundated. This generates a lagged impulse of individuals following rewetting, separate from colonisation processes, at both producer and prey trophic levels. Some zooplankton eggs for instance can remain diapaused for decades, and emergence rates display complex relationships with numerous abiotic factors like dissolved oxygen, pH and the recurrence interval of flooding events (Hairston 1996). Because our observed outcomes are driven in large part by the presence of spatial variation in local resource conditions, the potential for egg banks to mask the patterns we observed would be limited to scenarios in which emergence forces homogenous resource conditions across a landscape. Insofar as egg banks do not erase spatial variation in local resource conditions, we expect that the behavioural mechanism we have identified would still influence cascades.

An alternative potential explanation for the observed spatial variation in cascade strength is that it was driven by isolation's effect on species richness rather than biomass densities among trophic levels. In our field experiment, we observed that ponds experiencing low colonisation rates had nearly half the number of prey species that ponds experiencing high colonisation rates contained, on average (Appendix S2). However, current cascade theory would predict cascades to be stronger (i.e. larger in magnitude) in low colonisation rate ponds, all else constant, because of this reduced prey species richness (Borer *et al*. 2005; Fox 2007; Shurin *et al*. 2010). Instead, we saw the strongest cascades in nearby, high richness ponds and trophic depression of producers by fish in isolated, low richness ponds. Changes in species composition could have also caused the observed spatial variation in cascade strength. It is possible that certain prey species in this system are less edible to *Gambusia*, and that these species preferentially colonised isolated ponds, which prompted the observed behavioural shift. However, *G. affinis* is a well-documented generalist (Pyke 2005); we detected confamilials of most encountered prey taxa in the guts of sacrificed fish, suggesting a low sensitivity to taxonomic composition (Appendix S1). Included in the gut contents were other predator species (e.g. *Libellulid* dragonflies), which tended to be rare and are generalist carnivores (Voshell 2002), making them unlikely candidates for depressing prey and producer biomasses in low colonisation rate ponds.

Finally, our modelling analysis suggests that the patterns we observed hold despite a wide range of "community compositions", which is reflected in the broad range of parameter space over which the empirical patterns are maintained in the model. Thus, it is unlikely that these patterns were driven by differences in prey community composition *per se*. Moreover, we did not detect an effect of habitat colonisation rate on the probability that a fish had to be replaced due to mortality or somatic growth (Appendix S2); we did not find evidence that changes in aspects of omnivores other than foraging strategies occurred in response to manipulating colonisation rates. Instead, our modelling, laboratory, and field results point to the strength of cascades being controlled by prey colonisation rate, local producer and prey dynamics and omnivore foraging strategies.

Prior work has demonstrated that spatial isolation can modify cascades through effects on the composition and body masses of the predator guild (Chase *et al*. 2010) and predator extinction frequencies (Crooks & Sanjayan 2006). Our results suggest that even when predator populations remain intact or vary on much slower timescales, changes in local foraging behaviour driven by exogenous resource supplies can have equally dramatic effects. A deeper quantitative understanding of how food web interaction strengths are influenced by features of the spatial environment will be required to predict ecosystem responses to changing environmental conditions.

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AUTHORSHIP

AKF and KEA designed the experiments, AKF performed experiments and collected data, AKF and KEA performed analyses and AKF and KEA wrote the manuscript.

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