

## IDEA AND PERSPECTIVE

# How ecology shapes exploitation: a framework to predict the behavioural response of human and animal foragers along exploration–exploitation trade-offs

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### Abstract

Understanding how humans and other animals behave in response to changes in their environments is vital for predicting population dynamics and the trajectory of coupled social-ecological systems. Here, we present a novel framework for identifying emergent social behaviours in foragers (including humans engaged in fishing or hunting) in predator–prey contexts based on the exploration difficulty and exploitation potential of a renewable natural resource. A qualitative framework is introduced that predicts when foragers should behave territorially, search collectively, act independently or switch among these states. To validate it, we derived quantitative predictions from two models of different structure: a generic mathematical model, and a lattice-based evolutionary model emphasising exploitation and exclusion costs. These models independently identified that the exploration difficulty and exploitation potential of the natural resource controls the social behaviour of resource exploiters. Our theoretical predictions were finally compared to a diverse set of empirical cases focusing on fisheries and aquatic organisms across a range of taxa, substantiating the framework's predictions. Understanding social behaviour for given social-ecological characteristics has important implications, particularly for the design of governance structures and regulations to move exploited systems, such as fisheries, towards sustainability. Our framework provides concrete steps in this direction.

### Keywords

Conflict, consumer-resource, cooperation, fish and fisheries, governance, human behaviour, predator–prey, social-ecological system, sustainability.

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## INTRODUCTION

The ecosystems in which animals, including humans, are embedded act as complex adaptive systems, where outcomes at macro-scales, such as energy flow, population dynamics or sustainability emerge from micro-scale interactions among individual agents and ecosystem components (Levin 1998; Holling 2001). Humans and ecosystems are further tightly linked within coupled social-ecological systems (SESs) (Schlüter *et al.* 2012; Levin *et al.* 2013; Arlinghaus *et al.* 2017). Key to addressing macro-scale ecological and socio-economic challenges, such as fully understanding population

dynamics of species, avoiding overharvest, preventing biodiversity loss, optimising species reintroductions or mitigating the effects of climate change, is improving knowledge about the dynamical feedbacks among agents and between natural and human systems across scales (Levin 1998; Levin *et al.* 2013). Many key interactions among individual animals or between animals and humans in SESs are initiated or controlled by individual behavioural responses that affect collectives (Milner-Gulland 2011; Sih *et al.* 2012; Ward *et al.* 2016). In this context, the emergence of particular resource use patterns fundamentally affects animal population dynamics (Huey & Pianka 1981; Brown *et al.* 1999; Grant *et al.* 2017),

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the exploitation rates induced by fishers or hunters (Laundré *et al.* 2010; Januchowski-Hartley *et al.* 2011), and social conflicts in natural resource use contexts (Gutiérrez *et al.* 2011). A better understanding of which human and animal behavioural responses are expected for a given ecological state is an important step to move us forward along a trajectory towards the ultimate normative goal of sustainability and resilience (Pine *et al.* 2009; Berger-Tal *et al.* 2011; Mangel *et al.* 2015).

In many ecosystems, resource use patterns are dependent on foraging decisions made by individuals or groups of individuals (Dill 1987; Lima & Dill 1990; Lima & Zollner 1996). Social interactions form a major component of foraging decisions, which can encompass a range of strategies, from territoriality, to collective search, to individualism (Grant 1993; Ranta *et al.* 1993; Giraldeau & Caraco 2000; Maher & Lott 2000). The dynamic and connected nature of complex adaptive systems means social behaviours are constantly coevolving with the environment, with individuals potentially switching among behavioural strategies as environmental cues change (Elgar 1986; Higginson & Ruxton 2015; Tilman *et al.* 2016). An improved understanding of the manifestation and switches among forms of social interaction in both animal and human foragers has important consequences for wildlife management and natural resource governance. For example, in coupled SESs a shift from communal information sharing to territorial behaviour, while under a common property regime, requires a new set of management rules to avoid subsequent overexploitation (Boserup 1965; Poteete & Ostrom 2004; Chabot-Hanowell & Smith 2012). As an example from animal populations, the facilitation of the invasion success of the Argentine ant (*Linepithema humile*) through the breakdown in territorial behaviour upon introduction to southern California, demonstrates how better predictions of changes in social behaviour could improve models of invasion risks (Holway *et al.* 1998; Holway & Suarez 1999). Importantly, shifts in the social behaviour of foragers can affect the harvested resource in ways that may in turn feed back to further influence the behaviour of the foragers (Wiens 1976; Schlüter *et al.* 2012; Stoop *et al.* 2012; Lade *et al.* 2015).

Our objective is to provide a novel theoretical framework for predicting both the level and form of social behaviour when foraging for renewable resources in both animals and humans. Our interdisciplinary work builds on literature from behavioural ecology (Brown 1968; Wiens 1976) and several anthropological works, which have proposed frameworks for understanding the emergence of territorial human behaviour in natural resource systems (Dyson-Hudson & Smith 1978; Acheson 2015). In particular, we were interested in predicting which social behaviour to expect in response to spatio-temporally varying ecological properties and whether such behavioural responses would be seen in both human and animal foragers. In this context, a classical anthropological framework based on the concept of 'economic defendability' proposed that property rights emerge from generic ecological properties (Dyson-Hudson & Smith 1978; Acheson 2015). We built our framework on this idea, but propose that the 'exploration difficulty' and 'exploitation potential' of a resource, and not economic defendability per se, are the two major determinants of the foragers' social behaviour and

that this applies generally across both animal and human foragers.

To develop our case, we first present a novel qualitative framework. We then use a general mathematical model and an agent-based evolutionary simulation model as a detailed validation of the expectations derived from the qualitative framework. Finally, we present results of a literature review of empirical case studies using fisheries as an example of SESs and studies on aquatic organisms to understand how well our models apply across a variety of empirical systems. We also discuss examples beyond fish and fisheries, but for space reasons do not present a comprehensive review of terrestrial literature. We conclude that our framework promises to generate robust predictions of the form of social behaviour shown by foraging animals, and in particular humans, in response to characteristic ecological or technological attributes of a given ecological system or SES. In particular, we propose that reflections along just two axes are sufficient to explain the emergence of a rich family of resource exploitation systems.

## A QUALITATIVE FRAMEWORK FOR UNDERSTANDING FORAGER BEHAVIOUR

Behavioural ecology has long inspired hypotheses about which forms of social foraging to expect under particular ecological contexts (Caraco & Giraldeau 1991; Grant 1993; Potts & Lewis 2014). In applications to animals, a classic framework by Wiens (1976) suggests that the social organisation should be a function of resource aggregation or unpredictability and the expense of resource defence. Herding and nomadism were predicted when defence costs were high and resources were unpredictable, territoriality was predicted when defence costs were low and resources were predictable, and coloniality or refuging were predicted at intermediate defence costs and resource predictability (Wiens 1976).

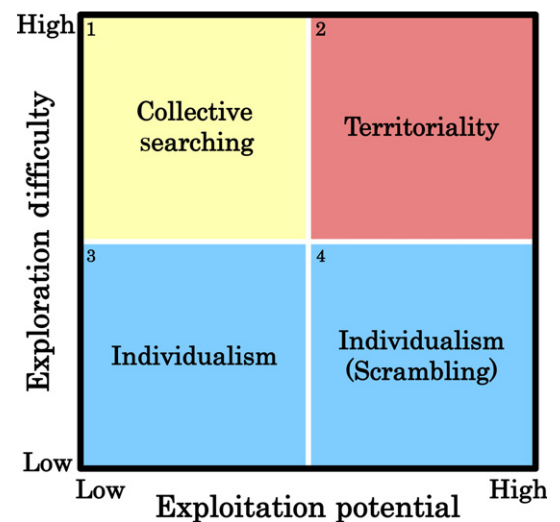
Anthropological models of human social behaviour have built on these ideas (Dyson-Hudson & Smith 1978), emphasising 'economic defendability' (Brown 1968) to determine the expected type of human territorial behaviour. It was suggested territoriality will form when the benefits from maintaining a territory are greater than the defence costs (Brown 1968). In contrast, when defence costs are greater, one should expect cooperative or individualistic behaviours over territorial resource use (Rubenstein 1981; Chabot-Hanowell & Smith 2012; Acheson 2015). Dyson-Hudson & Smith (1978) also proposed social behaviour responds to natural resources according to two factors (axes in a graph): resource density and the predictability of the resource (Brown 1968; Dyson-Hudson & Smith 1978). It was suggested that when both the resource density and predictability are low, foragers should be dispersed and mobile; when both the resource density and predictability are high, foragers should be territorial; when the resource density is low but the predictability is high, foragers should be in a non-territorial home-range system; last, when the resource density is high, but the predictability is low, foragers should be sharing information within spatio-temporally confined territories (Dyson-Hudson & Smith 1978). These ideas were consistent with the earlier models of animal social behaviour proposed by Wiens (1976).

There are several issues with applying the above-mentioned frameworks to forager behaviour as highlighted by several anomalous empirical case studies (summarised in Acheson 2015). The original axes – resource density and predictability – fall short of encompassing all relevant ecological and social factors affecting the pay-off of certain social behaviours. They do not allow robust metrics for comparing different empirical systems, where the dynamics of abundance or resource density may take on very different meanings. Resource density must be understood as the potential benefit gained from extracting the resource, accounting for factors such as resource value (in terms of either monetary value or energy for growth) as well as the ability to extract the resource (which relates to technology or competition with other foragers). The term ‘density’ will then be potentially misleading, as resources can be disproportionately valued because of their rarity within a given system: this is seen, for example, in recreational fisheries, where the presence of an individual trophy fish and not the density of fish per se can drive angler site choice behaviour (Arlinghaus *et al.* 2014). Abundance or density must thus be replaced by some relative measure of access to desired resources if a framework to predict social behaviour as a function of ecological factors is to be applied across different case systems.

Similar shortcomings can be expressed in relation to the axis ‘predictability’, which does not distinguish the various effects of predictability on foragers, in particular the ability to find the resource, and to exploit the resource once found. We consider the latter to be a more direct contributor to the emergence of social behaviours of resource exploiters than the predictability of a resource per se.

Developments in understanding when individuals are expected to behave territorially, or share information have diverged from one another (Ranta *et al.* 1993; Maher & Lott 2000; Danchin *et al.* 2004; Rendell *et al.* 2011; Potts & Lewis 2014; Higginson & Ruxton 2015; Smolla *et al.* 2015), and to our knowledge the shortcomings of the original frameworks (Wiens 1976; Dyson-Hudson & Smith 1978; Acheson 2015), have not yet been addressed. To advance the frameworks proposed by Wiens (1976) and Dyson-Hudson & Smith (1978), we redefined its axes into the more general ‘exploration difficulty’ and ‘exploitation potential’ (Fig. 1). This terminology follows the classic framing of forager behaviour as a trade-off between exploration and exploitation (Dugatkin & Wilson 1991; Enquist & Leimar 1993; Smaldino & Schank 2012; Hills *et al.* 2015; Barbier & Watson 2016). Exploration difficulty reflects the effort spent searching per unit of resource value found (independent of its abundance), while exploitation potential represents the fraction of the value that can be extracted by an individual once found. Each of these axes combine multiple properties of both environment and foragers (including gear and technology), so as to fully determine when it is more advantageous to be territorial, individualistic or search collectively.

We view foragers as searching the environment for and harvesting distinct patches of resources with varying degrees of mobility, temporal persistence and sparseness (Elton 1949; Kotliar & Wiens 1990; Barbier & Watson 2016). Accordingly, exploration difficulty (the y-axis in Fig. 1) is modified by both the distribution of the resource patches in the environment



**Figure 1** Conceptual model of how exploitation potential and exploration difficulty in natural resources should select for particular social behaviour by foragers.

and the ability of individual foragers to find new patches. It is, crucially, a *relative* metric: harder-to-find but richer patches may lead to the same search effort per unit value and therefore an equivalent ‘exploration difficulty’. While we generally think of patchiness as spatial, exploration may involve learning the resource’s temporal patterns, in which case temporal predictability is integrated into the exploration difficulty as well.

The second axis (the x-axis in Fig. 1) – exploitation potential – is the fraction of value that can be extracted by a lone forager from a resource patch after finding it, and also relates to a number of ecological and social factors, for example, how efficient the forager is at extracting the resource from a patch, and the temporal resource variability. Ephemeral resource patches (e.g. harvesting desert wildflowers) have low exploitation potential because, even when patches are discovered, the resource may disappear before it can be completely extracted. Patches may also disappear before complete extraction because other foragers are also harvesting the resource or because the resource patch may move (e.g. a fish school moving along a coastline). Conversely, a resource that can be continuously exploited at a given location has high exploitation potential. Again, the exploitation potential metric is relative as a resource patch that disappears more quickly, but can also be extracted more efficiently may result in an equivalent exploitation potential.

When resources have a high exploration difficulty and low exploitation potential (Fig. 1, Quadrant 1, ‘Collective Search’), it may be beneficial to share information as the resource is difficult to find and retain, and we expect to see collective searching behaviour in both animal and human foragers. If both exploration difficulty and exploitation potential are high (Fig. 1, Quadrant 2, ‘Territoriality’), for instance because of sparse but long-lasting resource patches, the value of defending the resource should be very high and the foragers should establish territories and exclude outsiders, either via formal or informal norms, or antisocially through

aggression. Where exploration difficulty is low, individuals can easily find more resources on their own, and the advantages of territorial exclusion or collective search vanish, leading to generally individualistic behaviour, more so if individualism comes with its own benefits (e.g. freedom of movement). Low exploration difficulty also means that more foragers are likely to find the same patch by chance over its lifespan. If exploitation potential is low (Fig. 1, Quadrant 3, 'Individualism'), the presence of other foragers on the same patch does not affect individual gains, and there is effectively no competition. If exploitation potential is high, however, (Fig. 1, Quadrant 4, 'Scrambling'), these foragers do interfere with each other and their utility is reduced by scramble competition, but the advantage that would be provided by territorial exclusion is still too weak to justify its costs (in terms of time, energy or risk). We propose any SES and any natural forager system, based on the exploitation of a natural resource can be located along the two axes of Fig. 1 (excluding several edge cases, see Supporting Information 1).

## QUANTITATIVE MODELS FOR UNDERSTANDING FORAGER BEHAVIOUR

To better understand collective behaviour of foragers in the context of the novel framework we propose in Fig. 1, we performed a quantitative exploration of behavioural strategies across the full spectrum of exploration difficulty and exploitation potential. To do so, we developed two models. First, we propose a simple formalisation of the qualitative framework in Fig. 1, to understand its fundamental assumptions and test their consistency. Given a population of foragers in a fixed ecological setting, this mathematical model gives analytical predictions for collectively optimal strategies. However, it ignores the possibility of foragers exhibiting different individual behaviours, in particular via explicit spatial dynamics, which may allow the coexistence of diverse strategies. Therefore, we also implemented a lattice (grid-based) evolutionary simulation model to investigate the resulting spatial and temporal dynamics, abstracting out the search process and adopting discrete space and time for computational efficiency, so as to identify emergent strategies over many generations. While these two approaches differ significantly, we finally show that both models convey the same qualitative message in support of the predictions in Fig. 1. This provides evidence that the results we report are not model-dependent, but reflect generic social behaviour patterns in foragers within complex adaptive systems, as a function of exploration difficulty and exploitation potential.

### MODEL 1: GENERAL MATHEMATICAL MODEL

#### Description

Our mathematical model (see Supporting Information 1 for details and Table 1 for parameter definitions) closely follows the qualitative analysis above. To translate the framework's axes into definite quantities, they can be expressed in terms of timescales, taking a clue from ecological models of predation: the consumption efficiency of a predator can be expressed in terms of  $T_s$ , the time spent searching, and  $T_h$ , the time spent

**Table 1** Parameters and variables for the general mathematical model

| Parameters   | Symbol    |
|--|-----------|
| Number of users                                    | $N$       |
| Communication propensity                           | $\lambda$ |
| Exclusion propensity                               | $\mu$     |
| Cost of territorial exclusion                      | $c$       |
| Timescales   |           |
| Search time for a lone user                        | $T_s$     |
| Resource mobility time                             | $T_r$     |
| Harvest time for a lone user                       | $T_h$     |
| Variables  |           |
| Forager utility                                    | $U$       |
| Expected number of users exploiting the same patch | $n$       |

handling a prey (Holling 1959). The ratio of these timescales  $T_s/T_h$  corresponds to exploration difficulty, that is how much time it takes to find one unit of the resource, where units here are measured in terms of how long it takes to handle them. Adding  $T_r$ , the timescale of resource persistence, we can define exploitation potential as a second ratio,  $T_r/T_h$ , which is small for resource patches that are ephemeral compared to their richness.

All three time scales can be computed for various resource use settings, using specific models that integrate relevant environmental and socio-technological parameters, for example, for fisheries (Barbier & Watson 2016). They will be taken here as the external parameters that determine the social dynamics.

Given the three parameters and the number  $N$  of foragers, our goal is to compute the forager's utility  $U$ , specified as their average rate of resource extraction (or total value gained over a fixed time period), as a function of the adopted social strategy. An additional parameter must be provided:  $c$  the fraction of time spent defending a territory, if the territorial strategy is selected. Indeed, collective search naturally comes at the cost of sharing a patch, but territorial exclusion would always be preferable over individualism unless it is made costly, here in terms of lost exploitation time. It is then possible to abstract all spatial dynamics by simply considering the 'behavioural states' of the foragers, and their transition rates (see Supporting Information 1 for details of the model). The state-based description can easily be extended to account for other processes of interest. Spatial patterns are sufficiently captured by  $n$ , the expected number of foragers exploiting the same patch, either due to voluntary sharing or scrambling, which can be computed as a function of the three timescales and the social strategy. Despite this simplicity, the mathematical model, previously implemented without consideration of territoriality, has been shown to agree qualitatively and quantitatively with spatially explicit agent-based simulations (Barbier & Watson 2016). We thus present only the mathematical model outcomes here.

#### Results

Figure 2 validates the outcomes of the qualitative analysis by demonstrating that domains with distinct strategies corresponding to the quadrants of the qualitative Fig. 1 emerge



## Box 1 Evolutionary lattice-based model

### EVOLUTIONARY SIMULATIONS

We consider the evolution of behavioural strategies in populations of agents which compete with each other for the resource assuming a finite lifetime of the resource landscape  $T_r$ . At each generation, we perform  $N_{rounds}$  of independent “competition” bouts, each with a random resource landscape. Each bout consists of the following sequence: (1) generation of a random resource distribution, (2) random agent placement on the lattice, (3) signalling and corresponding movement, (4) exclusion and corresponding movement and (5) exploitation over the lifetime of the resource.

The pay-offs of an individual per generation are determined by its average benefits, given by the average amount of resource gathered  $\langle g_i \rangle$  multiplied by the resource ‘value’  $v$  and reduced by the costs of the strategy  $P_i = v \langle g_i \rangle - C$ . Based on the pay-offs of the population, we calculate the relative fitness  $f_i = 2(P_i - P_{min}) / \Delta P - 1$  ( $f_i \in [-1, 1]$ ) with  $P_{min}$  being the minimal pay-off in the population and  $\Delta P = P_{max} - P_{min}$  being the range of individual pay-offs. The fitness determining the reproductive success is calculated according to  $F_i = 1 + \omega f_i$  with  $\omega \in [0, 1]$  setting the strength of selection. After each generation, the strategies are updated according to a roulette-wheel algorithm (Guttal *et al.*, 2012). The initial behavioural trait vectors are randomly picked assuming a uniform distribution on the simplex defined by  $c_{upt} + c_{rep} + c_{sig} = C$ , with  $c_x$  corresponding to the investment into different traits (fitness costs). Following a selection each ‘trait’ undergoes random mutation:  $c_x \rightarrow c_x + \mu x$ , with  $\mu x$  being independent random increments drawn from a normal distribution with zero mean and standard deviation  $\sigma_{mut}$ . The mutated costs are rescaled again to fall on the simplex.

### BEHAVIOURAL PHENOTYPES

Each agent can invest into three different behaviours: signalling, excluding others or harvesting. The behavioural phenotype of an agent is characterised by the vector  $\{\alpha_i, \beta_i, \gamma_i\}$ . The increase in any of those above a base-level vector  $\{\alpha_0, 0, 0\}$  is associated with costs  $c_{upt,i}$ ,  $c_{rep,i}$  and  $c_{sig,i}$  according to a simple linear relationship:

$$\alpha_i = \alpha_0 + a_{upt} c_{upt,i}, \quad \beta_i = a_{rep} c_{rep,i}, \quad \gamma_i = a_{sig} c_{sig,i} \quad (1)$$

where  $\alpha_0$  is the base uptake rate and  $a_x$  are constants defining the increment in traits per capita. The investment into the three behaviours are constrained by:  $c_{upt,i} + c_{rep,i} + c_{sig,i} = C$ . Here, we use  $a_{upt} = a_{rep} = a_{sig} = 1$  and  $C = 1$ . The behavioural phenotype is uniquely defined by any two values of the costs. In general, we can define three general behavioural strategies: (1) ‘Individualist’ (I): primary investment into uptake  $c_{upt,i} > c_{rep,i}, c_{sig,i}$  (2) ‘Territorial’ (T): main investment into repulsion  $c_{rep,i} > c_{upt,i}, c_{sig,i}$  and (3) ‘Communicator’ (C): primary investment into signalling  $c_{sig,i} > c_{upt,i}, c_{rep,i}$ .

### RESOURCE DISTRIBUTION

The resource is randomly distributed on a two-dimensional lattice of size  $L \times L$ , so that we have either lattice sites with a fixed resource amount  $r$  (resource patches) or empty sites. The number of non-empty lattice sites is  $A_c$ , and the area fraction covered is  $f_c = A_c / L^2$ . Without loss of generality, the average resource density is set to 1. Thus, the amount of a resource per patch depends on the area fraction covered,  $r = 1/f_c$ . Large  $f_c$  ( $\lesssim 1$ ) corresponds to an almost homogeneous landscape, whereas for a small area covered ( $f_c \ll 1$ ) we have few high-resource patches.

### INTERACTION STRATEGIES

#### Information sharing (Cooperation)

First, after random placement on the resource landscape, agents are able to cooperate with others in their local neighbourhood (within range  $l_{sig}$ ), by signalling the presence of resources at their position and attracting others. The probability of sending as well as understanding a signal is set by the communication capability  $\gamma_i$ . The communication ability of agent  $i$  is a monotonously increasing function of its investment into signalling  $\gamma_i = \gamma_i(c_{sig,i})$ . The total probability of successful communication, with agent  $i$  sending, and agent  $j$  understanding a signal is  $p_{sig} = \gamma_i \gamma_j$ . Thus, both agents need to invest into signalling in order to ensure successful communication. An agent, which received and understood a signal, moves only to the signaller if there are no resources in its current position.

#### Repulsion (Territoriality)

Second, all agents at the same lattice site compete directly with each other by ‘fighting’ (exclusion process). The probability of fighting is reduced by the communication ability according to:  $p_{fight} = 1 - (\gamma_i + \gamma_j)/2$ . Thus, two fully information-sharing agents  $\gamma_i = \gamma_j = 1$  never fight. The losing agent has to move to random neighbouring lattice. All competitions are binary with the probability of agent  $i$  winning against agent  $j$  given by:

$$p_{win,i} = \frac{1}{1 + \exp(b(\beta_j - \beta_i))} \quad (2)$$

with  $\beta_i$ ,  $\beta_j$  being the repulsion strengths of the focal individual and its neighbour respectively. The parameter  $b$  sets the sensitivity with respect to the repulsion strength difference  $\beta_j - \beta_i$ .

### Resource exploitation

Finally, all agents remaining on a resource patch harvest it in parallel. Here, different harvesting rates lead to indirect competition. For  $n$  agents present at a patch  $k$ , each with an individual harvesting rate  $\alpha_i$  the resource  $r_k$  is assumed to follow a simple (linear) depletion dynamics:

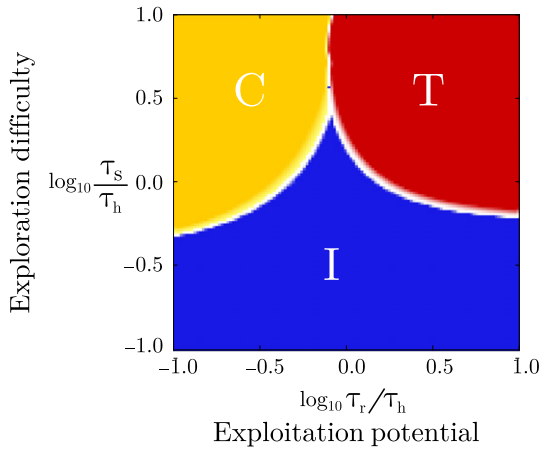
$$\frac{dr_k}{dt} = - \left( \sum_n \alpha_i \right) r_{kj}.$$

The resources gathered by an individual during a finite time interval  $\Delta t$  are thus

$$g_i(\Delta t) = r_k^{(0)} \frac{\alpha_i}{\sum_n \alpha_j} \left( 1 - e^{-(\sum_n \alpha_j) \Delta t} \right)$$

with  $r_k^{(0)} = r$  being the initial amount of resource at site  $k$ . Thus, it will gather the ratio  $\alpha_i / \sum_n \alpha_j$  of the total exploited resource.

Due to the finite lifetime of the resource, we set  $\Delta t = T_r$ . The absolute amount of resource harvested depends exponentially on the resource lifetime  $T_r$ .



**Figure 2** Results of the general mathematical model for  $N = 30$  users. Optimal behaviour versus exploitation potential  $\log_{10} T_r/T_h$  and exploration difficulty  $\log_{10} T_s/T_h$ . For clarity, investment into territorial exclusion (red,  $\mu$ ) and communication (yellow,  $\lambda$ ) are made mutually exclusive here. The cost of exclusion is set to  $c = 0.3$ , meaning that agents must spend 30% of their time on a patch defending it to guarantee full exclusivity. Three domains are made apparent: territorial ( $T$ ), collective searching ( $C$ ) and individualistic ( $I$ ) agents.

straightforwardly from the mathematical model. In the left panel of Fig. 2, the  $y$ -axis is exploration difficulty and the  $x$ -axis exploitation potential, as defined from the key timescales in the previous section. We focus here on collective optima: all foragers can either communicate to a degree  $\lambda \in [0, 1]$  (yellow), or put an effort  $\mu \in [0, 1]$  (red) into excluding others from their territory. The colour pictured represents the one that maximises the average intake of any individual forager in the group, and therefore the best strategy for the population as a whole.

## MODEL 2: EVOLUTIONARY LATTICE MODEL

### Description

We complement our mathematical modelling approach by introducing a simple, yet generic, evolutionary simulation model of interacting agents, which compete for a temporally variable finite resource that is spatially distributed on a lattice (see Box 1 for implementation details and Table 2 for parameters). The model is computationally inexpensive and enables simulations of large (evolving) agent populations. It focuses on competition among exploiters in terms of resource access and exploitation, as well as on collective searching via information sharing. The evolutionary lattice-based model does not explicitly model individual search strategy, but studies the selection operating on behavioural strategies. The evolutionary aspect of this model accounts for the opportunity for learning, to transmit foraging strategies culturally, or to transfer resources through inheritance. It thus applies to both animal and human foragers.

We consider the exploitation of a resource, randomly distributed on a two-dimensional discrete lattice, by a population of  $N$  agents. Each lattice site either contains a constant amount of the resource or is empty. The spatial distribution of the resource is characterised by the area fraction covered  $f_c$ . The average density of the resource in the environment is fixed, thus depending on the area covered there exists either few high-yield sites given a low  $f_c$  or many low-yield sites given a large  $f_c$ . In the simplest case considered here, there is no spatial correlation in the resource distribution (see Supporting Information 1 for more details).

The distribution of the resource is assumed to have a finite lifetime,  $T_r$ , setting a characteristic timescale, during which the agents may harvest the resources. Once the lifetime of the resource distribution is reached it is replaced by a new

**Table 2** Parameters and variables for the lattice model with the specific definitions as well as values used to obtain the presented results

| Parameters   | Symbol/definition | Values   |
|--|-------------------|----------|
| <b>General parameters</b>  |                   |          |
| System size (linear dimension)                                   | $L$               | 80       |
| Total resource present   | $R$               | $L^2$    |
| Area fraction covered  | $f_c$             | 1–1.0    |
| Exploration difficulty   | $T_0 = 1/f_c - 1$ | 0–100    |
| Lifetime of resource landscape                                   | $T_r$             | 0.01–100 |
| Number of agents   | $N$               | 1024     |
| Base uptake rate   | $\alpha$          | 1        |
| <b>Evolutionary and interaction parameters</b>                   |                   |          |
| Number of generations  | $N_{gen}$         | 1000     |
| Number of independent bouts per generation                       | $N_{rounds}$      | 40       |
| Value of resource  | $v$               | 20       |
| Cost factor for increasing uptake                                | $a_{upt}$         | 1        |
| Cost factor for increasing repulsion                             | $a_{rep}$         | 1        |
| Cost factor for increasing communication                         | $a_{sig}$         | 1        |
| Strength of selection  | $\omega$          | 0.8      |
| Mutation noise for investment $x$                                | $\sigma_x$        | 0.05     |
| Steepness of sigmoidal competition function                      | $b$               | 10       |
| Signalling range   | $l_{sig}$         | 8        |
| <b>Evolvable traits and corresponding behavioural parameters</b> |                   |          |
| Investment into uptake   | $c_{upt}$         |          |
| Investment into repulsion  | $c_{rep}$         |          |
| Investment into signalling                                       | $c_{sig}$         |          |
| Individual uptake rate   | $\alpha$          |          |
| Individual repulsion strength                                    | $\beta$           |          |
| Individual communication capability                              | $\gamma$          |          |

random distribution with the same area covered. Thus, the resources can represent ephemeral stationary natural resources or mobile ones.

All agents (i.e. foragers) may invest in three different strategies to try to maximise their harvesting pay-off: (1) faster *exploitation* of the resources by increasing their harvest rate ( $c_{upt}$ ), (2) *information sharing* via investing into their communication ( $c_{sig}$ ) and (3) effective *exclusion* of competitors from resources by investing in their ‘repulsion’ strength ( $c_{rep}$ ). We distinguish three main strategies based on the primary investment of the respective agents: ‘Individualists’ with the main

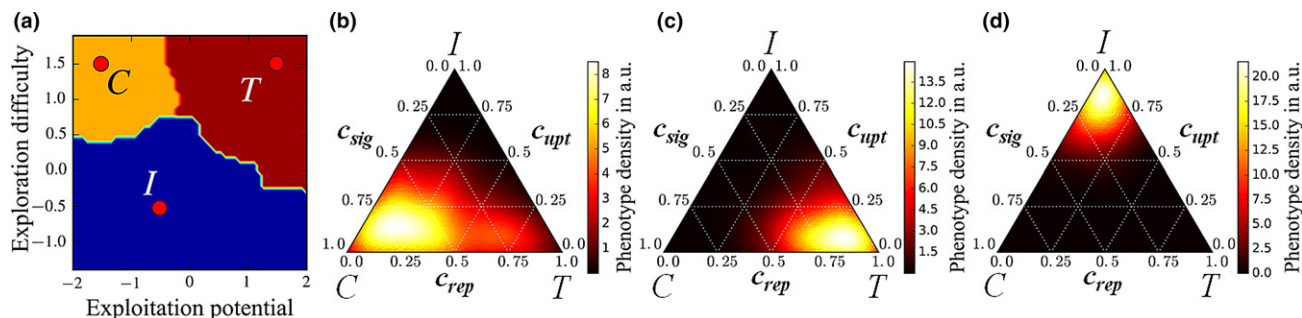
investment into increasing their harvesting rate, ‘Communicators’ (or ‘Information Sharers’) who invest primarily in their communication ability, and ‘Territorial’ agents who invest most into excluding others from resource patches.

For computational simplicity we assume a sequential structure of a single competition bout, consisting of the following steps: (1) random placement on a randomly generated resource landscape (abstract search process), (2) signalling phase (communication) where agents on resource patches may attract others based on their communication phenotype, (3) competition phase with all agents at the same location performing pair-wise fights, where the losing agent is displaced from the location to a neighbouring lattice site and finally (4) the exploitation phase, where all agents remaining on the same resource patch harvest it in parallel constrained by the finite lifetime of the resource.

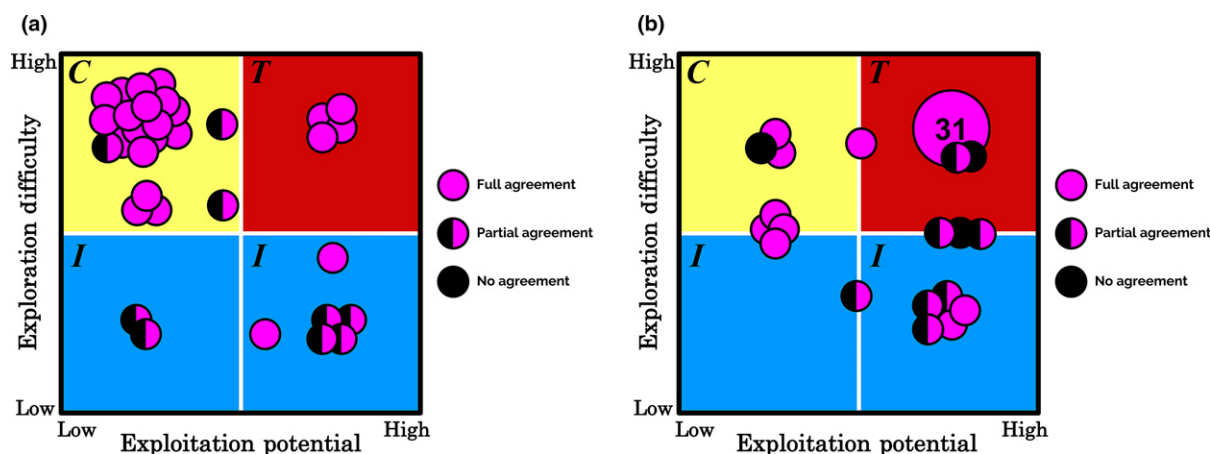
In the evolutionary lattice model we employ a minimal search process: a random placement of agents on the resource landscape. Here a key parameter is the probability that an individual finds a resource patch, which equals the area fraction covered  $f_c$ . Reinterpreting this probability as a rate of ‘landing’ on a resource patch allows us to define a characteristic ‘search time’ in dimensionless units as the inverse probability,  $T_s = 1/f_c$ , which we then can use to quantify the exploration difficulty (Fig. 3). The exploitation potential of the resource landscape is quantified simply by the lifetime of the resource  $T_r$  (Fig. 3). Note that in the lattice model there is no fixed timescale associated with the resource exploitation, as the uptake rate is an evolvable parameter. However, we can consider a corresponding handling timescale set by the base uptake rate  $T_0 = 1/\alpha_0 = 1$ .

## Results

In Fig. 3 we summarise exemplary results for the evolved stationary strategies as a function of the exploitation potential (resource lifetime  $T_r$ ) and exploration difficulty (dimensionless search time). For long-lived and sparse resources  $T_r \gg 1$ ,  $T_r \gg 1$ , the predominant evolved strategy corresponds to ‘Territoriality’ with high investments in repulsion  $c_{rep} > c_{upt}$ ,  $c_{sig}$ , whereby the largest evolved  $c_{rep}$  corresponds to highest resource sparseness. For short-lived resources ( $T_r \ll 1$ ), and high exploration difficulty, the most frequent behavioural



**Figure 3** Evolutionary lattice model: (a) Behavioural map obtained from the evolutionary simulations distinguishing three regimes based on most frequent strategy in the population: Communication (C) with  $c_{sig} > c_{rep}, c_{upt}$ , Territoriality (T) with  $c_{rep} > c_{sig}, c_{upt}$  and Individualism (I) with  $c_{upt} > c_{sig}, c_{rep}$ . The red dots show parameter values corresponding to the ternary plots (b, c and d) of the evolved phenotype distribution for different regimes: (b) Communication, (c) Territorial, (d) Individualistic.



**Figure 4** Placement of empirical case studies within the qualitative framework (see Fig. 1), based on agreement with predictions. Panel (a) shows placement for fisheries case studies, and panel (b) shows placement for aquatic organism cases. In both panels, the yellow quadrant corresponds to collective searching, the red quadrant corresponds to territoriality and the blue quadrants correspond to individualism. Each small circle represents one empirical cases, while the large circle in panel (b) represents 31 cases. In both panels, the yellow quadrant corresponds to collective searching (C), the red quadrant corresponds to territoriality (T) and the blue quadrants correspond to individualism (I).

phenotype is ‘Communicator’, with the highest investments into signalling. Finally, for low exploration difficulty the dominant strategy is ‘Individualism’, with the highest investments in increasing harvest rate for short resource lifetimes. The resulting strategy space closely resembles the predictions of our qualitative framework and the general mathematical model. Although this general structure is conserved for a wide range of model parameters (see Table 2), the detailed shape and extension of the different regions will depend on specific parameter choice (see Supporting Information 1 for details).

## EMPIRICAL EVIDENCE IN FISHERIES AND AQUATIC ORGANISMS AS CASE STUDIES

We searched the literature (see Supporting Information 1 for methods) for empirical cases in aquatic systems that describe the social behaviour of foragers (‘harvesters’ in the case of fisheries) in response to the ecology of food patches or fish stocks and, in human cases, technology. We focused on capture fisheries and aquatic systems as empirical cases because of the relatively high uncertainty in outcomes and patterns of property rights formation in capture fisheries systems (Acheson 2015) and the complementary wide behavioural diversity within aquatic animal systems, particularly fish (Keenleyside 1979). We briefly touch on terrestrial cases in the Discussion because we think the framework (Fig. 1) should apply generally. Our aim was to gather examples across diverse systems to evaluate empirical support for our framework and not to collect all known cases.

## Results

We retained 84 empirical cases (33 from capture fisheries and 51 from aquatic organisms; see Supporting Information 2). These cases covered a diversity of systems, from small-scale multi-species fisheries, to large-scale commercial fishing fleets, targeting species across trophic levels from urchins (*Strongylocentrotus* spp.) to lobsters (*Homarus americanus*), to tuna (*Thunnus* spp.). Furthermore, the cases examined animal

populations in a range of ecological conditions, including deep-sea abyssal plains, caves, lakes, reefs, rivers and the marine pelagic. We thus feel confident that our cases are sufficient to examine our framework’s support.

The majority of evaluated fisheries systems corresponded primarily to collective searching ( $n = 21$  out of 33). Published cases with primarily territorial or individualistic behaviour were less common in fisheries systems, with only five and seven cases respectively. In contrast, cases specific to aquatic organisms corresponded primarily to territoriality ( $n = 35$  out of 51), while nine cases and seven cases corresponded to collective searching and individualism respectively.

When judging the social outcomes in each of the examined 84 cases against our predictions, we found strong support that the forager’s key social strategies – collective searching, territoriality and individualism – followed our model predictions as a function of exploitation potential and exploration difficulty (see Supporting Information 2). In fact, our predictions were supported in 66 of 84 cases, partially supported in 15 cases and completely unsupported in only three fish cases (Fig. 4). To our surprise, there were very few cases of complete disagreement. A partially supported case included a mixture of the predicted and unpredicted social behaviours existing within the same system, such as the glass shrimp, *Pasiphaea japonica*, fishery in Toyama Bay, Japan where individualistic fishers fish on opposite days to a group of cooperative, catch sharing fishers, despite targeting the exact same resource with comparable fishing gear (Carpenter & Seki 2011). Ayu, *Plecoglossus altivelis*, are an additional example from aquatic organism cases, where 30–50% of individuals defend rich algal patches as predicted, while the remaining individuals of the population shoal and intrude the defended patches (Kawanabe 1969).

Collectively, our case studies indicate – in agreement with our qualitative framework and two quantitative models – that key ecological and social properties subsumed in the exploration–exploitation trade-off lead to the emergence of characteristic behavioural strategies of the average forager. For example, in fisheries systems, pot and trap fisheries, targeting



lobsters and crayfish tended to show territoriality, and were characterised by medium to high exploration difficulty and high exploitation potential (Acheson 1975; Levine 1984; Wagner & Davis 2004; Acheson & Gardner 2005; Turner *et al.* 2013, 2014). In contrast, shellfish fisheries which target molluscs such as cockles and scallops and also sea urchins, were characterised by low to high exploitation potential and low exploration difficulty and thus tended to show individualism (Murray *et al.* 2011; Johnson *et al.* 2012; Beitel 2014, 2015; Lynham 2017). Moreover, large-scale commercial pelagic fishing fleets, targeting mobile and sparse (high exploration difficulty and low exploitation potential) pelagic species such as tuna and billfish with trawls or long-lines, showed high degrees of collective searching (Mangel & Clark 1983; Dreyfus-Leon & Kleiber 2001; Curtis & McConnell 2004; Gaertner & Dreyfus-Leon 2004; Dreyfus-Leon & Gaertner 2006; Girardin *et al.* 2016).

Cases of aquatic organisms also mostly showed characteristic social behaviours according to our framework. We found territoriality in river- and stream-dwelling fish feeding on drifting invertebrates (e.g. Slaney & Northcote 1974; Grant & Noakes 1987; Blanchet *et al.* 2006; Steingrímsson & Grant 2008) and in reef fish-exploiting algal patches or corals (e.g. Brawley & Adey 1977; Roberts & Ormond 1992; Letourneur 2000; Hamilton & Dill 2003) as both environments are characterised by sparse, yet rich patches of small prey, which relates to a high exploration difficulty and exploitation potential. Collective searching tended to occur in organisms hunting mobile shoaling pelagic prey as predicted by our framework (e.g. Schmitt & Strand 1982; Parrish 1993), but in contrast to the fisheries cases, collective search was commonly paired with other social strategies, such as collective hunting and anti-predator behaviour, suggesting differences between animal and human foragers. Finally, individualism was recorded in deep-sea scavengers (Priede *et al.* 1990a) and pelagic filter feeders (Sims & Quayle 1998; Sims 2008), which is understandable because deep-sea food falls are scarcely, but randomly distributed and consumed quickly (i.e. scramble competition), and pelagic plankton blooms are relatively easily found (low exploration potential) and have high exploitation potential. The resemblance of various case studies from similar, but geographically separate aquatic systems and fisheries overall supported our proposition that the properties of finding and harvesting a given resource systematically relate to the emergence of specific social behavioural patterns of the foragers.

Importantly, we found three cases, all examples of foraging fish, in complete disagreement with our qualitative framework. First, in experiments within drainable ponds, group-foraging adult Eurasian perch, *Perca fluviatilis*, captured more prey and grew faster compared to solitary perch (Eklöv 1992). Perch are known to be social foragers and group naturally in the wild even when prey fish are abundant and widely distributed (Nakayama *et al.* 2018), which we predict fosters individualism bordering territoriality depending on spatial patchiness. Adult northern pike, *Esox lucius*, in contrast, forage on the same prey species in the same habitats as perch, but showed agonistic reactions and avoidance behaviour and were most successful when foraging alone (Eklöv 1992), as predicted by our framework. Telemetry studies show pike are

usually solitary, forming home ranges, and do not like to feed in the presence of conspecifics (Nilsson *et al.* 2006; Kobler *et al.* 2009; Rosten *et al.* 2016). Second, several surgeonfish species (*Acanthurus* spp.), feeding on algal patches and expected to behave territorially, were unable to dominate individual damselfish (*Stegastes* spp.) defending algal patches in reef systems and therefore, counter to predictions, surgeonfish either formed groups to overwhelm the damselfish and access preferred patches, or foraged individually and suffered from increased damselfish attacks (Foster 1985; Reinthal & Lewis 1986). Lastly, Parrish (1993) found green jacks, *Caranx cabal-lus*, and black skipjacks, *Euthynnus lineatus*, foraged for herring alone; however, in agreement with our framework, the most efficient foraging strategy was found to be collective searching. The low number of cases in complete disagreement indicates exceptions to our framework may be rare, but the causes of such exceptions appear to be variable and often involve a survival risk from predation or threatening inter-specific interactions.

## DISCUSSION

### General assessment

Our framework integrates ideas from behavioural ecology, evolutionary biology, anthropology and complex adaptive systems theory. It offers a qualitative baseline for an improved understanding of the expected feedbacks between social behaviour and the ecology of renewable resources within animal populations and coupled SESs. The framework accounts for technological factors affecting consumption efficiency and resource discovery. The framework we derived qualitatively was supported by two distinct models, and also draws empirical support from a diversity of reviewed empirical cases in fisheries and aquatic animals. We thus contend our framework provides an important conceptual advance towards understanding how social-ecological feedbacks operate at the individual level, ultimately giving rise to macro-level outcomes relevant for management, conservation and understanding animal behaviour.

Although we restricted our empirical evaluation to aquatic and marine systems, our framework should also apply to terrestrial systems. To provide some examples, with respect to humans, food sharing is commonly observed in hunter-gatherer societies (Gurven 2005; Gurven & Jaeggi 2015), where the exploration difficulty is high – 4% of hunting trips are successful for the Hadza (Gurven & Jaeggi 2015) – and the exploitation potential is low – meat left in the open draws attention and is eaten quickly (Hawkes *et al.* 2001). As hunter-gather societies have transitioned to agricultural practices, where the exploitation potential and exploration difficulty are high, because farming requires high inputs of time and energy and offers high yields, private property systems were quickly implemented (Kaplan & Gurven 2005). Indeed, agriculture appears to consistently tend towards private property systems (i.e. territorial behaviour) (Acheson 2015).

There is also much support for our predictions in terrestrial animals. Increased clumping, or increased predictability of food patches tends to result in territoriality across a variety of

taxa as expected (see Maher & Lott 2000 for a comprehensive review of vertebrate territoriality). Information sharing has been observed in patchy resource environments, where food cannot be consumed completely alone (Stevens & Gilby 2004) (i.e. high exploration difficulty and low exploitation potential). For example, Elgar (1986) showed that when presented food was divisible, house sparrows, *Passer domesticus*, were more likely to recruit conspecifics to the food source. Furthermore, in mesic habitats with abundant, evenly distributed, long-lasting, quickly regenerated food sources (low exploration difficulty, high exploitation potential), family groups of Plains zebras, *Equus burchelli*, show overlapping home ranges and no territoriality, as predicted (Rubenstein 2010). By comparison, in nearby xeric habitats, where food is patchy and long-lasting (high exploration difficulty and exploitation potential), Grevy's zebras, *Equus grevyi*, show characteristic territorial behaviour (Rubenstein 2010).

Our combined results of conceptual theorising, quantitative modelling and empirical cases suggest it may indeed be possible to identify characteristic social behaviours within specific SES types or animal populations on average across empirical systems. Hence, it may be possible to make generalisations about broad groups of SESs regarding how they exploit natural resources of given ecological properties (see types of fisheries placed on Fig. S12). We suggest the consistent highly communicative behaviour of pelagic fishing fleets, territoriality of trap fishers, stream-dwelling juvenile salmonids or herbivorous reef fish, and the independence of shellfish divers and trawlers and of many recreational fisheries found in our case studies can largely be caused by the ecological properties of the targeted natural resources, specifically in terms of exploration difficulty and exploitation potential, in light of biological or technological foraging constraints.

Although our qualitative framework predicts one dominant social strategy, a number of empirical cases showed multiple behavioural strategies coexisting within the same system. A stable coexistence of multiple social strategies is a possible outcome according to the lattice model (see Supporting Information 1, Fig. S4) and is commonly reported in natural populations in terms of animal personalities (Kobler *et al.* 2009; Spiegel *et al.* 2017). Hence, mixed strategies may naturally emerge. For example, in two SESs dominated by individualism (diving for urchins and bottom trawling for hoki, *Macruronus novaezelandiae*) tracking the movement of other boats without explicit communication was common (Vignaux 1996; Lynham 2017). Similarly, abyssal grenadiers, *Coryphaenoides* spp., foraging on deep-sea food falls not only behave individualistically but may also minimise turbulence while swimming to avoid the risk of alerting other individuals to potential food sources (Priede *et al.* 1990b, 1991). These cases with multiple coexisting strategies are likely positioned closer to boundaries between the qualitative framework's quadrants (Fig. 1).

Other mixed strategy cases can be better explained through mechanisms unaccounted for in our framework. In some SES cases the ability to defend a territory or search collectively related to membership in an exclusive group requiring strong social ties (Gatewood 1984; Carpenter & Seki 2011; Beil 2014, 2015) or to a historical separation of communities (Krause & Ramos 2015), stressing the relevance of social

norms, social and personal capital, social identity, the need for repeated interactions and path dependencies of property rights. Additionally, mixed strategies may be the result of different top-down governmental controls emerging from development of a fishery under different political systems (e.g. socialist to democratic political systems, Daedlow *et al.* 2011), or biological constraints such as the threat of predation pressure (James 1987; Hoare *et al.* 2004). These processes, in addition to the three empirical cases in complete disagreement with our predictions, emphasise limitations to our qualitative framework and quantitative modelling.

### Framework and model limitations

Our model is based on a number of assumptions, notably that foragers maximise their fitness through resource exploitation and natural selection or cultural evolution has guided foragers towards optimal behaviour (Pyke 1984). In reality, behaviour, even of commercial fishers, is guided by multiple factors, some of which are unrelated to the expected utility derived from resource intake (Dall *et al.* 2005; Arlinghaus 2006; Girardin *et al.* 2016). For example, recreational anglers frequently cite non-catch-related benefits, such as experiencing nature or social experiences, as more important than catch related ones for determining whether, when and where to fish (Fedler & Ditton 1994; Beardmore *et al.* 2011; Hunt *et al.* 2011). If the currency on which foraging decisions are based is misidentified, then predictions from our framework will collapse. Accordingly, we expect our models will be most appropriate in contexts where behaviour is mainly harvest-oriented, such as in top predators, or commercial fisheries where mortality risk is relatively low.

Furthermore, we expect our framework will be more accurate when applied to SESs than to animal populations. Studies of optimal foraging in animal populations frequently observe deviations from predictions because behaviours are constrained by unaccounted factors, such as predation risk, sensory or memory limitations or incomplete information (Perry & Pianka 1997; Matsumura *et al.* 2010). An enduring mortality threat is a critical factor in an animal's behavioural decisions (Werner *et al.* 1983; Boutin 1990; Laundré *et al.* 2010), which does not exist to the same extent in human foragers. Accordingly, because shoaling has multiple advantages for fish against predation risks (Pitcher & Parrish 1993), foraging in groups to combat predation threats regardless of resource distribution or exploitability may be more common in fish populations (e.g. James 1987; Hoare *et al.* 2004). However, human foragers will also experience constraints on social behaviour such as harvest regulations or other institutions (e.g. Acheson & Gardner 2005). Our framework cannot represent such transitory institutional influences on social behaviour.

Our case studies highlight additional important differences between fish and fisher behaviour, further challenging whether our framework can be similarly applied to animal populations and SESs. Animals often lack the sophisticated communication technology of modern humans, which allows instant and complex information sharing across long distances. However, differences in communication range and ability between human and animal foragers may be rectified by adjusting the

scale of patch and patch lifetime definitions, which are context dependent (Wu & Loucks 1995; Marceau 1999). Human foragers are additionally affected by strong social norms (Tavoni *et al.* 2012; Kinzig *et al.* 2013; Tilman *et al.* 2016), cultural values (Manfredo *et al.* 2017), governance systems and associated institutions (Branch *et al.* 2006; Ostrom 2007; Lubchenco *et al.* 2016), market mechanisms and associated prosociality (Basurto *et al.* 2016) and historical path dependencies (Levin *et al.* 2013); phenomena which may not translate directly into animal populations. Although some of these factors are conceptually integrated in the two axes of our framework, others are not, specifically the overwhelming importance of social norms and culture. Experimental and empirical studies are needed to analyse how well our framework approaches behavioural reality in a range of contextual conditions.

### Empirical measurement

A critical step forward is to translate exploration difficulty and exploitation potential into empirical measurements in real systems. Specifically, three factors must be measured to test our framework: the relative exploration difficulty of a resource, the relative exploitation potential of a resource and the social behaviour of the foragers. The three factors must be measured according to the correct currency (e.g. net energy gain, or monetary gain) of patch value and defence costs (Higginson & Ruxton 2015). To measure exploration difficulty, one may measure the time (or cost) of the average search investment (e.g. during a fishing trip or foraging bout) or the investment into attractants, such as fish-chum, to discover the targeted resource. To measure exploitation potential, one must be able to measure the proportion of a patch/resource unit harvested before it is lost. In animal populations the individual consumption rate relates to the functional response (Holling 1959). In fisheries the harvest rate relates to the catchability coefficient  $q$ , the fraction of the resource unit harvested per unit effort (Arreguín-Sánchez 1996). If the typical resource patch lifespan is known (e.g. how fast a fish school leaves an area), and the individual-specific (or gear-specific) functional response or  $q$ , is also known, then an individual's effort to exploit a full patch can be calculated. The effort exerted before the patch disappears can then be divided by the effort to exploit a full patch as an indication of the exploitation potential. If the definition of a patch is unclear, or the ability to measure the full amount of a resource within a patch is impossible before resource exploitation can begin, then the functional response, or  $q$  alone, can provide a reasonable relative approximation when comparing foragers exploiting environments with identical resource properties. To estimate the foragers' social behaviour one can use bio-logging techniques when possible (Krause *et al.* 2013; Lennox *et al.* 2017) or more standard methods such as surveys, participant observation and semi-structured interviews (Acheson 1975; Neis *et al.* 1999; Acheson & Gardner 2005; Mueller *et al.* 2008). We suggest experimental and observational tracking studies where both foragers and resources are followed in real-time (Hussey *et al.* 2015; Monk & Arlinghaus 2018; Stowers *et al.* 2017) as direct measurements of forager–resource interactions, uptake rate and other parameters key to empirical tests of our framework.

### Implications for policy and management

Our framework offers some implications for governance and management systems as they may emerge from the behavioural patterns shown by humans in response to spatio-temporal natural resource variability or technological change (Wilson *et al.* 2013). Depending on whether local and regional outcomes are judged as desirable or not, institutions could be tuned to incentivise certain social behavioural strategies for improved biological and socio-economic outcomes (Lubchenco *et al.* 2016). These policy options will strongly differ depending on whether exploiters' behaviour is individualistic, collective searching or territorial. Individualistic behaviours tend to be associated with the race-for-fish, with overexploitation in open access systems being a likely outcome (Hardin 1968). In particular, individualistic behaviour may be associated with scrambling behaviour to collect resources before others, which creates excess and wasteful investment into new technologies required to keep up with competitors (Homans & Wilen 1997). Such situations are particularly hard to manage, and building proper incentives usually means forceful implementation of harvest regulations (e.g. effort controls, licensing, individual quotas in fisheries). Under these situations, incentivising proper behaviour could be improved by implementation of some form of access or harvest rights, for example, individual transferable quotas (Copes 1986; Costello *et al.* 2008), which often promotes efficiency and long-term planning. With respect to territoriality, the primary management issues may be antisocial behaviours related to territory defence and possibly equity. Explicitly acknowledging and legally enforcing the emerging territories through traditional user rights to fishing (TURFs) could reduce conflicts (Acheson & Gardner 2005) and split the costs of territory enforcement evenly among all foragers. Shared costs may not only increase the economic rent from the resource (Humphries *et al.* 2012) but also introduce the substantial equity-based issue of defining who is entitled to become a territory member. There are few panaceas: depending on the context, even community-based management may lead to resource overuse, for instance when there are abundant actors, few alternatives to fishing and good access to markets (Cinner *et al.* 2012). Finally, systems where collective searching behaviour is prominent fall somewhere in-between individualistic and territorial systems in terms of biological and socio-economic sustainability. Collective search not only improves a management body's monitoring capabilities and the ability to feed information into the fleet or community but may also contribute to inequalities in success among foragers under certain conditions (Klein *et al.* 2017). In this context, it would be important to detect leaders in the social network and to work proactively with these individuals (Gutiérrez *et al.* 2011; Barnes *et al.* 2016). Lastly, collective information sharing increases the likelihood informal institutions, such as agreed-upon rules of proper behaviour through self-enforcement, will develop (Ostrom 2007).

The ability to identify characteristic social behaviours within animal populations can also inform management decisions. For example, territorial defence of high-quality patches could lead to range contraction as territorial individuals are



harvested and replaced, which can facilitate overharvesting (Post *et al.* 2002; Burgess *et al.* 2017). When range contractions cannot be directly observed, the foraging ecology of a target species could provide early indications of potential overharvesting. Changes in social behaviour may also alter the exposure of individuals to predation risk and increase the natural mortality rate (Huey & Pianka 1981; Werner *et al.* 1983; Brown *et al.* 1999). Anticipating changes in natural mortality rates would help fine tune population assessments, and adjust conservation measures, or harvest rates accordingly (Clark 1999; Laundré *et al.* 2010). Importantly, our framework highlights that social behaviour is dynamic and changes in the social behaviour of the predators and prey feedback to one another through changes in space use, resource depletion or consumer rarefaction (See Fig S4). Therefore, if these dynamics do not stabilise, policy implementations may require temporal updates or re-evaluations.

## CONCLUSIONS

We have developed a novel framework for predicting social forager behaviour, demonstrating that the exploration difficulty and exploitation potential of a given SES gives rise to three social strategies – territoriality, collective search and individualism. Our framework received substantial empirical support when judged against a set of cases from fisheries and aquatic organisms. Going forward, it is important that the framework be tested with a range of new empirical and experimental studies, to systematically understand whether the predictions we offer are accurate. To that end, we proposed measures that could be used to quantify the exploration difficulty and exploitation potential. In the case of fisheries, novel Global Positioning System and biotelemetry technology can be used to study the spatial behaviour of fish and fishers in almost real-time, which is particularly useful to advance the empirical understanding of how the ecology of renewable natural resources interfaces with human factors to determine outcomes of harvesting patterns. If the amount of empirical support for our framework continues to grow, it may advance context-specific governance and management solutions and help support sustainable fisheries and other natural resource systems.

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## AUTHOR CONTRIBUTIONS

All authors developed the framework (substantial contributions from DIR and MB), MB and JRW developed the mathematical model, PR developed the lattice model, CTM, JA and SN conducted the case study review, CTM and RA wrote the first draft and all authors provided subsequent revisions and feedback.

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## SUPPORTING INFORMATION

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