

Supporting Information for "How ecology shapes exploitation: a framework to predict the behavioural response of human and animal foragers along exploration-exploitation tradeoffs"

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Edge cases of the qualitative framework

Our qualitative framework (main text, Fig. 1) covers a wide range of behaviours, but it also suggests limits in which one can find yet other behaviours (which we refer to as edge cases). If exploration difficulty is small, all exploitation strategies tend toward equivalent benefits and it is possible to see more mixed strategies. If forager movement (which plays into exploration difficulty) is too limited compared to both exploitation potential and communication range, any shared information will be obsolete by the time other foragers arrive, and collective search can never emerge. In the extreme case where the resource moves or fluctuates faster than foragers can find it, searching provides no benefit over waiting for the resource to appear. However, scale must also be considered: on a regional level, the fast-moving resource may actually be concentrating in more permanent areas, and these regional patches might favor large-scale collective search or territoriality.

An additional edge case emerges when resource exploiters are satiated after a certain level of resource exploitation. When foragers can harvest resources freely and with ease, our model suggests patterns of social behaviour are unrelated to the absolute abundance of the resource. For instance, more efficient exploiters in a system with proportionally richer resource patches would encounter the same exploitation potential and exploration difficulty, and adopt the same behaviour. However, if resource users are satisficers – individuals whose goal is to attain a certain minimal amount of resource (Simon 1956), enough to satisfy a wage or a minimum energy density sufficient for reproduction for example – any gains beyond their threshold requirements are irrelevant, and they may see no benefit to optimizing their behavioural strategies as long as the resource is plentiful (Pazgal 1997).

General mathematical model: assumptions

The model makes the following assumptions, whose limitations are discussed below:

1. We have a population of N identical agents targeting a single resource type defined by its ecological traits (including spatial and temporal heterogeneity).

2. Agents are individually capable of search and exploitation, and identical in these capabilities: they cannot develop non-social strategies, such as adapting their level of effort (sit-and-wait strategies) or trading between traits such as resource extraction, detection and mobility.
3. Agents can develop two social strategies: information sharing, which allows other agents to skip search but splits the benefits of exploitation, and exclusion, which sacrifices part of the benefits of exploitation to prevent other agents from using the same resource.
4. All agents within the population express the same strategy, so we search for the strategy that maximizes total utility U for the group. Since all agents have the same level of effort and no extraneous costs, utility U is simply given by the average rate of resource extraction, or total value gained over a fixed time period.
5. The change in the resource's ecological traits (availability, heterogeneity, etc.) due to exploitation is a slow process compared to the choice of a strategy. Thus, we can first look at how the resource shapes the agents' behaviour, and only in a second time consider how the latter feeds back on the resource.
6. We ignore additional benefits or costs which might correlate with these strategies, such as grouping to reduce predation risks or facilitate exploitation or outgroup exclusion, travel costs to reach or return to known resource patches, and nonstationarity such as diminishing returns of exploitations.

The evolutionary model dispenses with assumptions 2 and 4, allowing agents to invest in non-social strategies (controlling their level of effort or resource extraction efficiency) and to exhibit different strategies within the same population adding an explicit spatial dimension which may favour this diversity of behaviours.

General mathematical model: behavioural states framework

Instead of explicitly modelling the agents' spatio-temporal behaviour, we divide it into discrete behavioural states of exploration and exploitation (see Fig. S1). By choosing a spatially implicit model, we ignore the effects of complex spatio-temporal couplings between agents and resources, such as pattern formation: however, we can capture the essential mechanisms that determine the rate of resource extraction.

Before adding in collective strategies, we can reframe classical ecological models of functional response (Holling 1959) in these terms, as shown in Fig S1 (left): a consumer spends a fraction s of its foraging time searching for a resource, and a fraction h exploiting it. Given the typical time T_s spent searching and T_h spent handling the resource, an agent should switch from search to exploitation with rate $1/T_s$ and back with rate $1/T_h$, so that at equilibrium:

$$\frac{s}{T_s} = \frac{h}{T_h}. \quad (1)$$

By considering only these average equilibrium values, we are ignoring complex spatiotemporal dynamics, instead constructing a simple Markov model of behavioural state switching.



Figure S1. Sketch of the behavioural states Markov model for the classic Holling functional response (left) and our functional response with consumer interference, temporal resource heterogeneity and information sharing (right). In Holling's (1959) reasoning, the rate of switching from searching to handling is proportional to some power R^q of resource density R .

An agent's average uptake efficiency or utility U is given by the fraction of time that is not spent searching

$$U \propto 1 - s = \frac{1}{\frac{T_s}{T_h} + 1}. \quad (2)$$

Finally, Holling (1959) assumes that search time simply decreases with some power of resource density: $T_s(R) = 1/R^q$ so that

$$U \propto \frac{R^q}{\frac{1}{T_h} + R^q}. \quad (3)$$

where $q = 1$ gives a Type II functional response, and $q > 1$ gives a Type III functional response. Drawing on more results on random search and foraging theory, we can much more precisely characterize T_s as a function of resource density and patchiness (Barbier & Watson 2016). For our purposes, it is sufficient to retain T_s as a parameter, since we assume that resource properties change slower than the social dynamics of users we wish to capture.

General mathematical model: exploitation potential and inference

The previous calculation assumes full exploitation potential, and no interaction between consumers. To connect to the qualitative framework, we must first add temporal heterogeneity of resource availability (e.g. mobility of prey species or ephemerality of resource influx), via the timescale T_r of resource persistence. Exploiters are thus sent back to the search state with rate $1/T_r$.

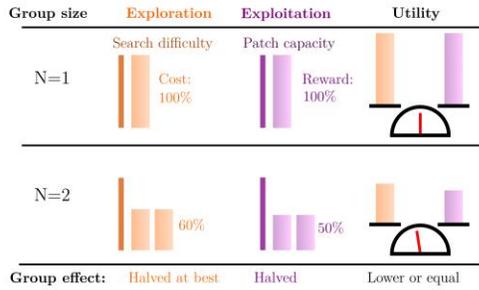
to model the benefits of exclusion and the costs of information sharing, we must also account for scramble interference between consumers: if n agents are exploiting the same resource patch, the rate at which this patch will be exhausted should not be $1/T_h$, but rather n/T_h (which can be generalized to n^v/T_h with $v > 1$ for active interference, and $v < 1$ for group facilitation). Combining these two factors, we obtain a total rate of return to the search state

$$\omega = \frac{1}{T_r} + \frac{n}{T_h}. \quad (4)$$

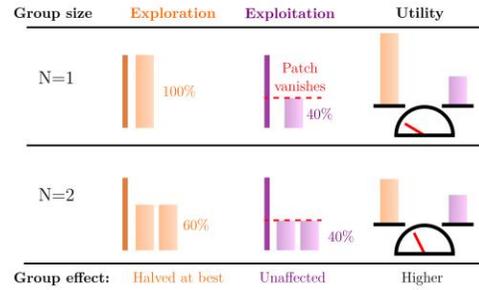
Where the rates can simply be added under the assumption that resource persistence and patch exhaustion both obey Poisson processes (Barbier & Watson 2016). This makes apparent the fact that exploitation potential T_h/T_r acts as threshold for the cost of scramble interference: if $n \ll T_h/T_r$, the interference term in ω can be neglected. This intuition is displayed in Fig S2 panel A.

A. Collective exploration and the role of temporal variability

1. High patch persistence:



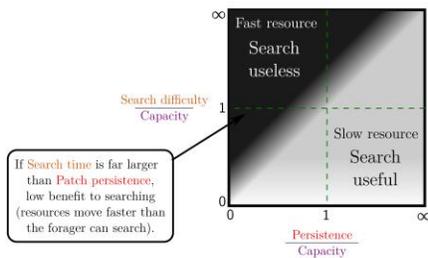
2. Low patch persistence:



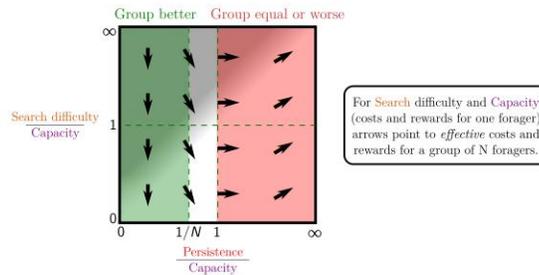
Three properties of environment and individuals control this tradeoff: **search difficulty** (maximum cost), **patch capacity** (maximum reward) and **patch persistence**. They can be made into ratios on the axes below by expressing them in the same units, e.g. time or effort. Social dynamics decide final **search cost** and **exploitation reward**.

B. Value of lone and collective search for one patch

1. Value of searching alone

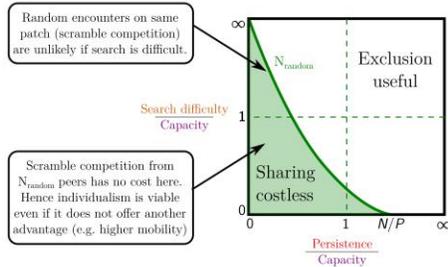


2. From lone forager (without competition) to collective search



C. When to search together and when to defend: strategies on P patches

1. Effect of scrambling competition



2. Optimal population-wide strategy

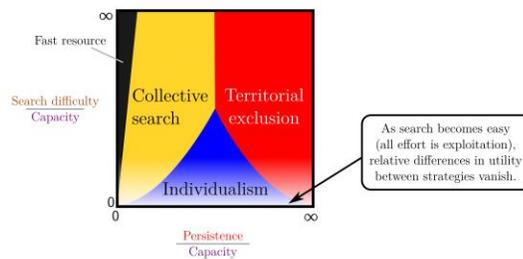


Figure S2. Summary of the various mechanisms in the model. A. Persistence of the resource controls the cost-benefit trade-off of information sharing: while the benefits remain the same, low persistence discounts the costs of sharing by limiting the potential of a single agent to exploit the resources. B. While exploitation potential controls the costs of sharing, its benefits depend on how worthwhile exploration is. The region of "fast resources" would be associated with sit-and-wait strategies if agents could control their level of effort. C. The value of exclusion depends on the likelihood of costly scramble interference. Combined with the previous panels, we finally obtain the overall map of expected strategies.

General mathematical model: social strategies

Finally, we must model the two social strategies. Let λ be the investment in collective search, and μ the investment in territorial exclusion.

To account for information sharing, we distinguish a new behavioural state, b , representing the fraction of time spent benefitting from resources that were found by another agent, see Fig S1 (right). As a searching agent finds resources with a rate $1/T_s$, it attracts (voluntarily via a call, or involuntarily via behavioural signals that cannot be concealed) a fraction λ of the other searching agents. Thus, the flux from s to b is given by $\lambda Ns/T_s$.

Territorial exclusion is straightforwardly modeled as spending some of the time on a patch defending rather than exploiting it: to exclude a fraction μ of the n agents using the same resource patch, a fraction μc of an agent's exploitation time must be sacrificed, with c the cost of defence. since this cost typically depends more on characteristics of the users than characteristics of the resource, we do not attempt to model its origins explicitly here, and simply retain it as an auxiliary parameter which is shown below to change quantitative results, but not the qualitative picture painted by the model.

General mathematical model: equations

The utility of a resource user is proportional to the time spent exploiting the resource rather than searching or defending a patch:

$$U = (1 - s)(1 - \mu c). \quad (5)$$

To construct the maps of optimal social strategies in Figure S2 panel C and Figure S3, we must maximize U as a function of λ and μ at each point in the parameter space defined by exploration difficulty and exploitation potential.

Using the behavioural states and fluxes specified above, agents leave the searching state with a rate $1/T_s(1 + \lambda Ns)$ (including both finding resources and information sharing), and return to it with rate ω , hence the equilibrium condition becomes

$$\frac{1}{T_s}(N\lambda s^2 + s) = (1 - s)\omega. \quad (6)$$

where ω depends on s through n , and all other terms are constant parameters. Previous work (Barbier & Watson 2016) has shown that the main consequences of complex spatial dynamics are encapsulated in n , the expected number of users exploiting the same patch: it determines how fast a patch is harvested, but also how correlated the users are. High n means that they tend to move around as dense packs, and switch between behavioural states simultaneously,

while low n means that their exploitation patterns are not synchronized. While a complex analysis is required to model it precisely, its qualitative features are captured by the simple expression

$$n = (1 - \mu)(1 - \lambda)(1 - s) \frac{N}{P} + \lambda N. \quad (7)$$

where the two terms respectively define the benefit of exclusion μ and the cost of sharing λ .

The first term represents scramble competition between the $(1 - s)N$ agents extracting resources at any given time, if they have found the same resources by chance, which depends on the number P of resource patches, see Fig S2 panel B. This term decreases with investment μ in territorial exclusion. The second term represents the effect of collective search, causing agents to be present on the same resources. Note that if $\lambda = 1$, the agents are then fully correlated in space and time, and all N are present on the same patch rather than only the time-averaged number $(1 - s)N$ of agents extracting resources.

Equations 6 & 7 form a closed system with unknowns s and n .

$$\begin{aligned} \frac{1}{T_s}(N\lambda s^2 + s) &= (1 - s)\left(\frac{1}{T_r} + \frac{n}{T_h}\right) \\ n &= (1 - \mu)(1 - \lambda)d(1 - s)N + \lambda N. \end{aligned} \quad (8)$$

which can be solved exactly or numerically by root-finding. Then we compute U using (5), and we optimize it as a function of λ and μ , given the three timescales T_s , T_r , and T_h , and auxiliary parameters N and P (numbers or densities of agents and patches) and c (the cost of exclusion). We can consider various scenarios for c which move the boundaries of the various optimality regimes but do not change the qualitative picture (see Fig S3).

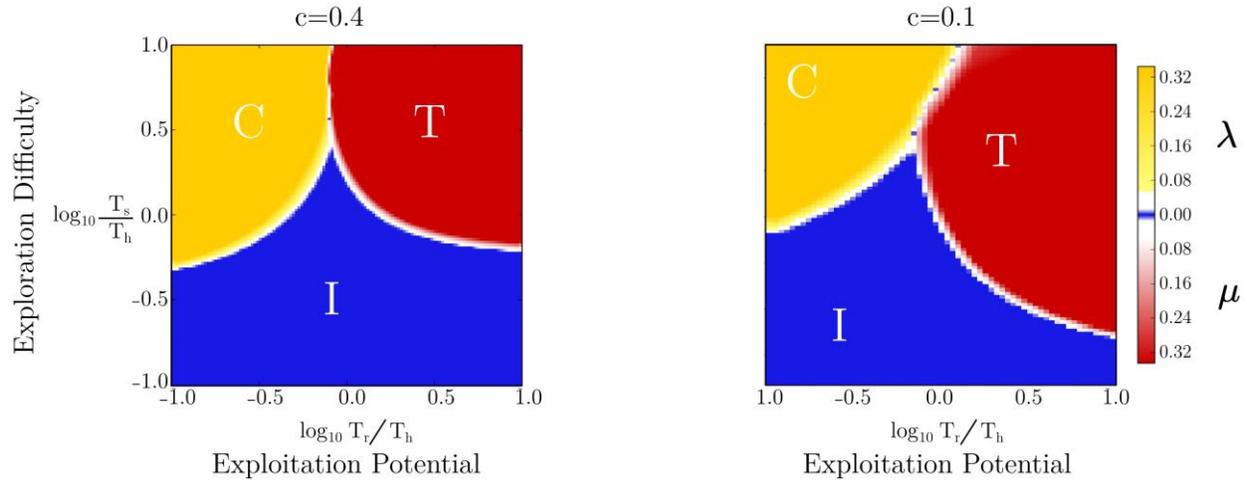


Figure S3. Optimal strategy given exploitation potential $\log_{10} T_r/T_h$ and exploration difficulty $\log_{10} T_s/T_h$ for $N = 30$ users. Three domains are made apparent: territorial (T), cooperative (C) and individualist (I) agents. For clarity, investment in territorial exclusion (red, μ) and communication (yellow, λ) are made mutually exclusive here. Left: the cost of exclusion is set to $c = 0.4$, meaning that agents must spend 30% of their time on a patch defending it to guarantee full exclusivity. Right: the cost of exclusion is set to $c = 0.1$, leading to a larger prevalence of territorial exclusion similar to the lattice model results.

General mathematical model: depletion and multitrophic dynamics

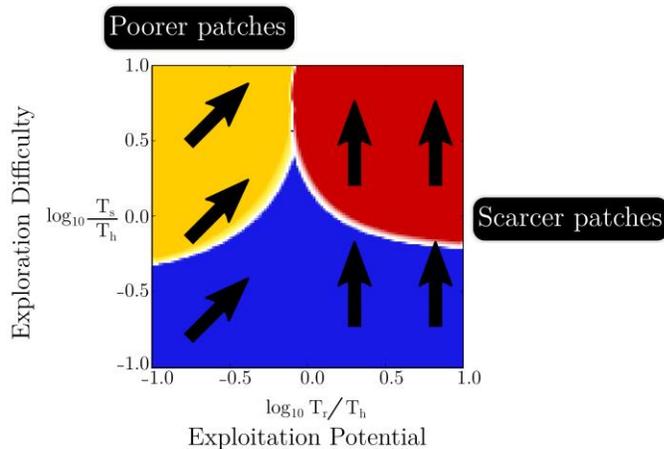
All previous results were obtained under the assumption that, while local resource patches could be exploited and exhausted, the overall resource distribution was not significantly affected, so that search would not become more difficult or less rewarding over time. However, they can be directly extended to coupled user-resource dynamics, as long as the choice of collective strategy happens on a shorter time scale than their feedback on the resource's ecological attributes. This feedback translates to a slow change in the parameters of the model, so that a population represented by one point in the parameter space in Fig S3 may change slowly, as shown in Fig S4.

There are two main ways in which depletion can change resource traits: either it makes resources more patchy (or these patches scarcer), thus increasing exploration difficulty, or it makes each patch less valuable, thus reducing their total value and increasing a single user's exploitation potential. These correspond to the two types of arrows in Fig S4. We can generally expect the first to occur in the right half of the map, and the second in the left half: if $T_r > T_h$, a local patch can be permanently exhausted, and it is likely that global depletion will make patches scarcer and harder to find, leading to higher T_s . If $T_r < T_h$, then a resource patch (e.g. a fish school) tends to move away or fluctuate before it is locally depleted, and therefore global depletion will take the form of all patches growing poorer, leading to constant T_s but lower T_h .

These two effects lead to a trend toward territoriality with overall depletion, although there may first be transition from individualism to collective search.

The same reasoning can also be applied in a multitrophic setting: depletion of a population in which itself consumes other resource means that, from its perspective resource user number N decreases. This in turn causes both the value of exclusion and the cost of sharing to decrease (see Fig S4 right). Thus, in general we may expect top predators to exhibit more territoriality, and to induce more group searching in their prey, even without accounting for additional benefits such as protection for the latter.

Resource depletion



Consumer rarefaction

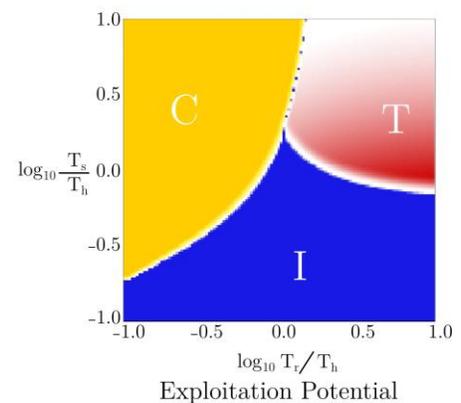


Figure S4. Long-term effects of global resource depletion (left) and consumer rarefaction (right). Left: If patches are not persistent compared to extraction (low T_r/T_h), it is more likely that the resource will be uniformly depleted, leading to poorer patches (lower T_h). If patches are persistent compared to extraction, it is more likely that the resource pattern will be permanently depleted in a given location, leading to fewer and fewer patches and harder search (higher T_s). Right: In the case of multitrophic dynamics, consumers can themselves be depleted, leading to a decrease in the prevalence of territoriality and an increase in information sharing, as seen here in the case $N = 5$.

Lattice-based evolutionary model: basic model structure

We consider a population of N agents competing for a finite resource heterogeneously distributed on a $L \times L$ square lattice under temporal constraints. Each agent follows an individual strategy regarding social interactions and resource exploitation characterized by its behavioural phenotype. This behavioural phenotype evolves according to the relative fitness of individuals after M competition bouts. As described in the main text, each competition bout consists of the following sequence:

1. Random placement: each individual is randomly placed on the lattice and has the probability f_c to land on a lattice site containing resources (see below).
2. Communication phase: each individual may signal the presence of resources at its location to other agents in close vicinity ($l_{sig} = 8$) to attract them.
3. Competition phase: If more than one agent is on a resource site, they have a finite probability to "fight", the losing agent has to move to a neighbouring lattice site.
4. Exploitation phase: all agents on a resource patch harvest the resource in parallel for a finite time, given by the resource lifetime T_r .

The first two phases can be viewed together as a search phase, subdivided into the individual search (random placement and collective search (signalling)). The above sequential structure of a competition bout allows for a very efficient numerical implementation. In particular, instead of explicitly simulating the harvesting process, it allows a calculation of the harvesting payoff during the exploitation phase analytically, assuming a fixed exploitation time (resource lifetime T_r) and a given number of agents on a resource patch, each with individual uptake rates.

Stationary phenotype distributions and parameter dependence

Typically the phenotype distributions converge within a few hundred generations to a stationary distribution (see Fig. S2). We note that in particular for intermediate exploration difficulties and exploitation rates, we rarely observe "pure" strategies (Fig. S6), where agents only invest into one behaviour. For example in Fig. S2a, although most investment goes into signalling, we see also a significant average investment into repulsion. In the vicinity of the boundary between C and T, we may also observe bistable phenotype distributions and coexistence of communicators and territorial agents (Fig. S3 & S5).

Whereas the general structure of the strategy phase space, with the three different regimes as proposed by our qualitative framework holds across wide parameter ranges, the exact boundaries between the different regimes will depend on the various parameters in our model (see Table 2 main text). For example, if we reduce the size of the system, while maintaining the number of agents constant, we will increase the expected number of agents that land on the same resource patch, thus investing into exclusion becomes more beneficial for a larger range of exploitation potentials and exploration difficulties. On the other hand, increasing the system size for a constant number of agents decreases the probability of several agents landing by chance on the same resource patch. Thus investing into repulsion becomes unnecessary even for high exploitation potentials, instead individuals should preferably invest into harvesting or communication based on the exploration difficulty.

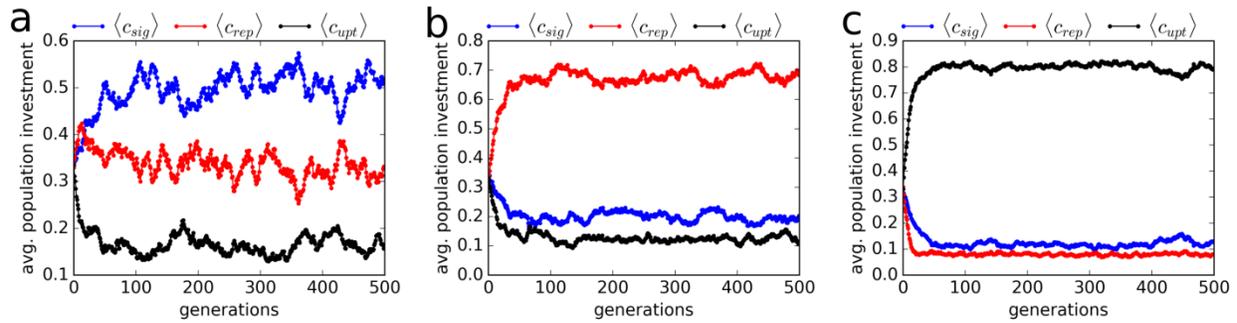


Figure S5. Evolution of average population investments into the three behavioural traits or the first 500 generations. The three panels correspond to the three example distributions shown in the main text exemplifying the different regimes: (a) communication (C), (b) territorialism (T) and (c) individualism (I). The corresponding values for exploration difficulty and exploitation potential are indicated as dots in the main text Fig. 3 (panel a), Fig. S6 and Fig. S7.

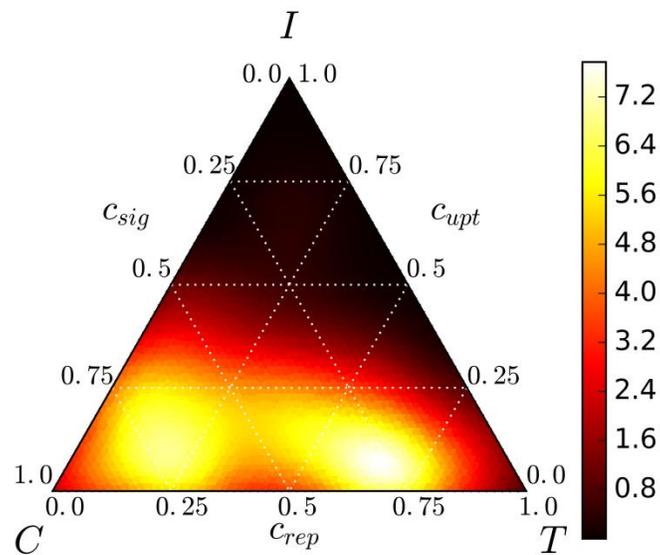


Figure S6. Example of an evolved bistable distribution showing a coexistence of two distinct behavioural strategy, information sharing (C) and territoriality (T). For the corresponding parameters $f_c = 0.03$ ($T_a \approx 32$) and $T_r = 0.01$, the evolutionary stable state yields most individuals belonging to the communicator phenotype ($c_{sig} > c_{rep}, c_{upt}$), yet a significant portion of the evolved population belongs to the territorial phenotype ()

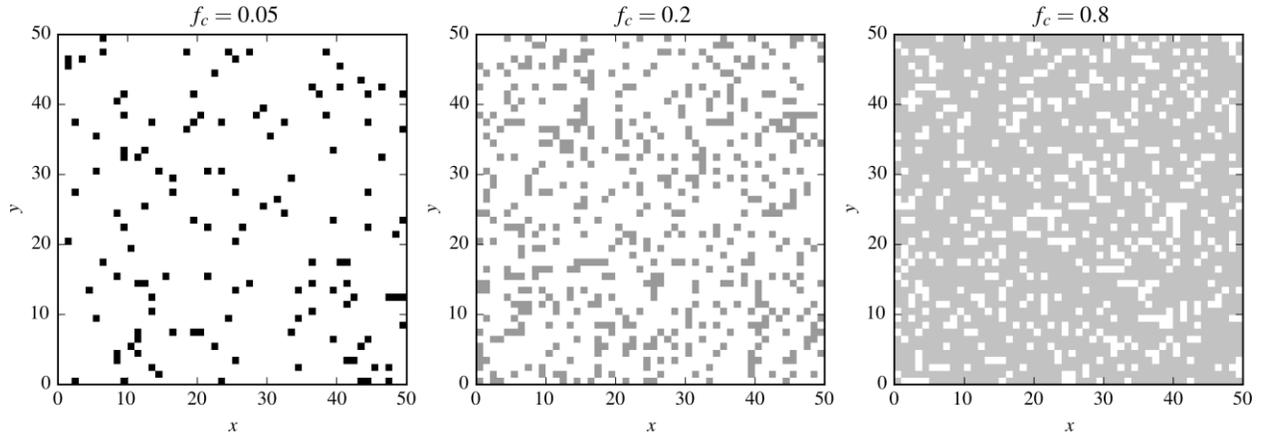


Figure S7. Examples of resource landscapes for three different values of $f_c = 0.05, 0.2$ and 0.8 . Lattice size is 50×50 .

Random resource landscape

We assume here a simple scenario of the resource being randomly distributed on a two-dimensional discrete lattice with linear dimension $L \in \mathbb{N}$. Each lattice-site k contains either a fixed amount $r_k > 0$ of the resource (\rightarrow resource patch), or is empty. The total resource present is $R = \sum_k r_k$, and the area fraction of the lattice covered is $f_c = A_c/L^2$ with $A_c = \sum_k \delta(r_k > 0)$ being simply the number of resource patches (non-empty lattice sites). The average density of the resource in the environment is fixed to one, which is equivalent to fixing the total amount of resource to $R = L^2$ for a lattice of size L^2 . Thus the amount of resource at a patch depends on the fraction of the area covered $r_k = 1/f_c$. So large areas covered $f_c \lesssim 1$ corresponds to almost homogenous landscape with low density of resources, whereas small area covered $f_c \ll 1$ corresponds to few patches with a large amount of resource in each.

A landscape has a finite lifetime T_r , during this time resource patches remain stationary and may be only depleted through harvesting (exploitation, see Fig. S10). After T_r , all non harvested resources vanish and a completely new random landscape is generated. This can be interpreted as a complete renewal of the resource after each bout, which does not consider any correlations between resource landscapes in different bouts. In particular, we do not consider here any explicit regrowth of the resources between different bouts. This allows parallel simulation off all bouts for each generation, which leads to a massive speed up of the evolutionary simulations.

For simplicity, we assume a completely random distribution of resource patches on the lattice, thus the patch positions are completely uncorrelated in space. Here, we note that for large f_c , resource patches will always border other resource patches (see Fig. S4).

We have also tested the role of spatial correlations of the resource patches on our final result, by enforcing a specific correlation length on the landscape. However, spatial correlations

played only a minor role in comparison to the area fraction covered f_c . Specifically, introducing spatial correlations (increasing correlation length) leads only to small shifts in the boundaries between the different regimes. The small impact of spatial correlation of the resource landscape can be understood through the initial random placement of the agents on the lattice, instead of an actual search process by random walk on a lattice. For a random placement, the resulting exploration difficulty does not depend on the correlation length, but only on area covered f_c . Thus, the correlation length affects only the relative payoffs of the strategies. A larger correlation length implies on average larger connected regions covered by the resource. As a consequence for large correlation lengths, we obtain a higher probability of an agent losing a fight and moving to a neighbouring lattice site also containing resources. On the other hand, local neighbours of an agent in the middle of an extended resource region are very likely to be on lattice sites containing resources as well. Thus on average fewer agents are attracted through signalling.

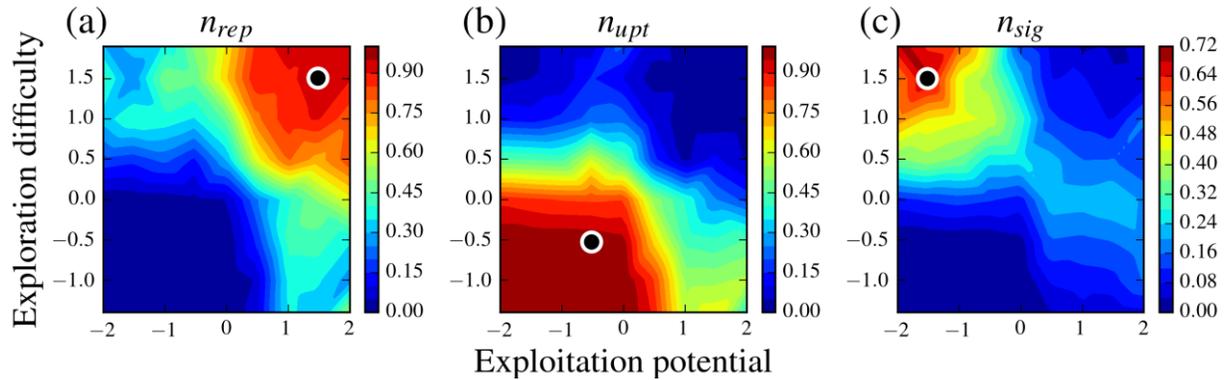


Figure S8. Evolved relative frequencies of the three different behavioural phenotypes defined via primary investments: (a) Territorialism), (b) Individualism and (c) Communication. The black dots correspond to the three example cases shown in the main text Fig. 3 (panels b-d) and Fig. S3 (a-c).

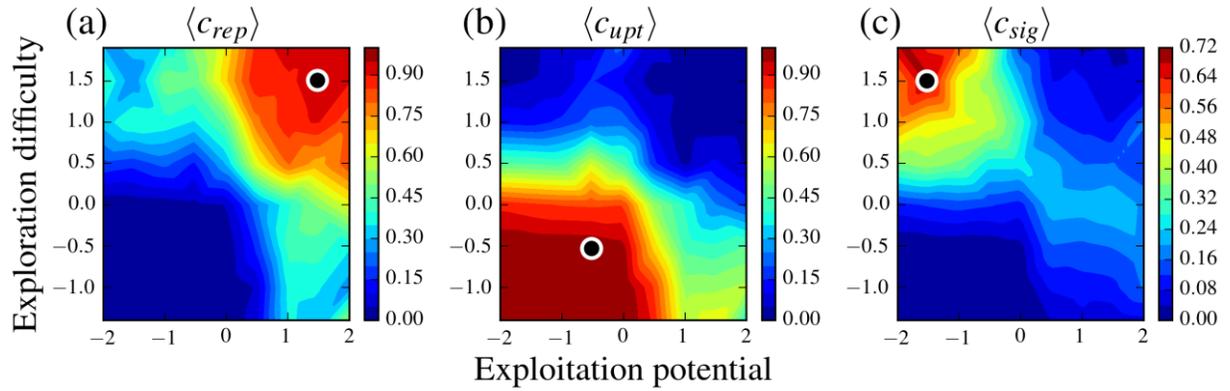


Figure S9. Evolved average population investments into the three different behavioural strategies: (a) Territorialism), (b) Individualism and (c) Communication. The black dots correspond to the three example cases shown in the main text Fig. 3 (panels b-d) and Fig. S3 (a-c).

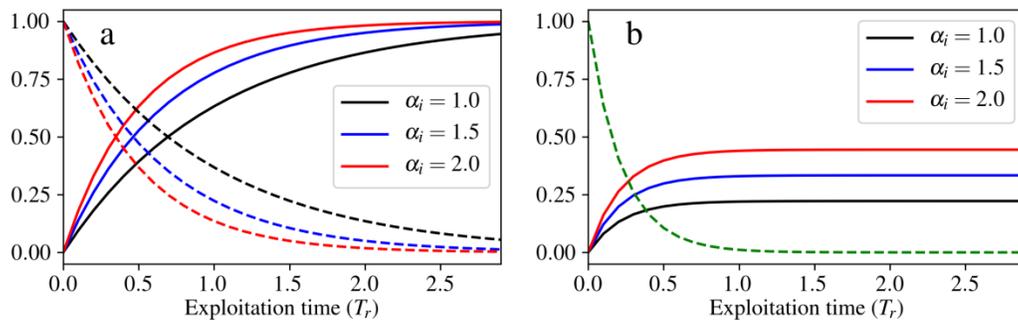


Figure S10. Role of harvesting rate: (a) Resource gathered by single agents on a resource path, with solid lines showing the resource gathered versus exploitation time for the different harvesting rates ($\alpha_i = 1.0, 1.5, 2.0$), and the dashed lines showing the remaining resources for the different α_i . (b) Resources gathered for three individuals with different harvesting rates ($\alpha_i = 1.0, 1.5, 2.0$) exploiting a resource patch in parallel. The different solid lines show the resource gathered by each of the three individuals versus exploitation time. The single dashed line show the amount of resource at the corresponding lattice site over time. (Initial resource amount in both panels $r = 1$).

Communication - Reciprocity and Cooperation

An assumption of the evolutionary lattice model is the symmetry of the communication trait, where investing into signaling increases both: the probability of receiving and sending information. Such communication "reciprocity" does not allow for explicit free-riding regarding information sharing, where an agent invests into "understanding" the signals from others, but does not share information if it lands on a resource patch. This assumption of "direct reciprocity" regarding communication was motivated mainly by our focus on socio-ecological systems. We emphasize however that this constrain of the strategy space is a significant simplification. The general question of evolution of cooperation is a fundamental problem that has received a lot of attention (see Nowak 2006, and references therein) and is clearly beyond the scope of our work. Many processes have been identified which favor evolution of cooperation and reciprocity, e.g. repeated interactions (Axelrod & Hamilton 1981), indirect reciprocity (Nowak 2006), kin selection (Hamilton 1964; Alexander 1974), spatially local interactions or network reciprocity (Nowak 2006; Nadell *et al.* 2008), punishment and social norms (Trivers 1971; Riolo *et al.* 2001; Ehrlich & Levin 2005). All these different mechanisms can lead to evolution of reciprocity regarding information sharing as assumed here, however these processes are not accounted for in our minimal lattice model.

Empirical case study search methods

Our literature search to locate empirical fisheries papers proceeded in three steps. First, we examined all fisheries cases in the recent literature reviews by Acheson (2015) and Girardin *et al.* (2016) and aquatic organism cases in (Grant 1993), (Maher & Lott 2000), and (Hart 1997). Acheson (2015) focused either on reviewing the emergence of property right systems in response to ecological characteristics and Girardin *et al.* (2016) or reported meta-analyses of determinants of site choice behaviour by commercial fisheries. Secondly, we used a standardized search in Google Scholar using the following search terms: "fleet + dynamics + collective + behaviour + fisher", "fleet + dynamics + fisheries", "cooperation + fisheries + fleet", "fishing + effort + collective + behaviour", "optimal + search + pattern + fisheries", "fleet + dynamics + social + information + fisheries", "recreational angler + information sharing", "recreational angler + territoriality + territory + territorial", "angler + site + choice", "angler + search + behaviour", "fishers + fishery + behaviour + space + time", "Fish OR aquatic organism and Individualism or nomadism", "solitary fish", "fish solitary foraging", "asocial fish foraging", "(solitary or asocial or non-social) pelagic fish", "private information foraging fish", "behaviour + space + time + territoriality + aquatic", "foraging + food + territory + marine + lake + river", "territorialism + fish + crabs + crustacea + aquatic", "territoriality + behaviour + foraging + marine", "territoriality + behaviour + foraging + freshwater", "territoriality + behaviour +

foraging + crustacea", "territory + optimal + foraging + aquatic", "fish + social information + foraging + (prey distribution OR resource distribution OR prey availability OR resource availability)", "fish + foraging + (prey distribution OR resource distribution OR prey availability OR resource availability) + group", "fish + foraging + (prey distribution OR resource distribution OR prey availability OR resource availability) + predictability + social", "fish + foraging +(prey distribution OR resource distribution OR prey availability OR resource availability) + predictability + social", fish + foraging + (prey distribution OR resource distribution OR prey availability OR resource availability) + value + (shoal or school)", "fish + foraging + (cooperative OR cooperation OR collective) + (unpredictable OR predictable OR unpredictability OR predictability)", "fish + public information + (unpredictable OR predictable OR unpredictability OR predictability)", "fish + (predictable OR unpredictable OR predictability + forage + social", "fish + collective search + (unpredictable OR predictable OR unpredictability OR predictability)", "fish + (cooperat* OR collaborat*) search + (resource OR prey)", "fish predator foraging schooling prey", "information fish predator foraging cooperative", prey profitability collective fish foraging social", "fish collective forag*" and "fish predator foraging schooling prey". From each query, we investigated the first 100 results.

Our search was not designed to provide an exhaustive list of primary publications and instead was meant to cover a sufficient diversity of cases to examine the qualitative and quantitative predictions of our framework. Finally, the authors searched their own databases and networks for studies devoted to social dynamics of the fishing fleets or recreational anglers. After filtering through the search results via an initial assessment of the paper's title and abstract, all potentially relevant publications were examined in detail and if needed supporting papers dealing with the same fishery were identified and screened.

From our search, we retained only cases from which we could derive at least qualitative information on the exploration difficulty and exploitation potential of the resource. To that end, we assessed various indicators related to the spatio-temporal dynamics of the targeted resource in light of the organism's ecology or the common technology and catchability in the fishery. The social behaviour of the foragers (or lack thereof) was required to be stated clearly in terms of collective searching, individualism or territoriality for a study to be considered in our review. The exact mechanism or extent of territory defense or collective searching is not represented in our quantitative models and therefore we included all cases regardless of the mechanism noted in the primary publications. However, we noted the details of the social behaviour, in terms of whether territoriality was competitive, with active defense or agreed avoidance, whether territories were shared or held individually and whether collective searching was active or passive (e.g. using public information, or monitoring others). We preferred empirical studies, but retained theoretical investigations if the model predictions were calibrated against empirical information in the original source or associated references.

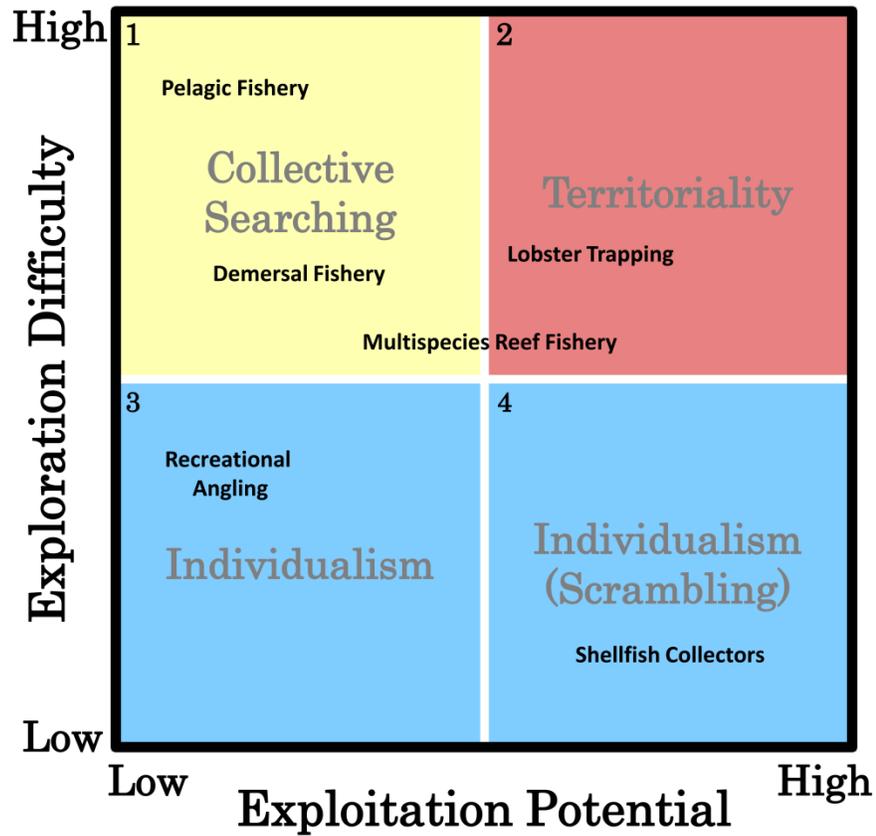


Figure S12 Conceptual model of how exploration difficulty and exploitation potential in natural resources with should select for particular social behaviour by human natural resource users, with hypothesized positions of characteristic fisheries based on findings from empirical case studies.

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