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

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3   1   **How ecology shapes exploitation: a framework to predict the behavioural response of human**
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5   2   **and animal foragers along exploration-exploitation tradeoffs**
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7   3   Social dynamics of Natural resource consumers
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35 DIR & MB), MB & JRW developed the mathematical model, PR developed the lattice model,

36 CTM, JA & SN conducted the case study review, CTM & RA wrote the first draft and all authors

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48   **Abstract**

49   Understanding how humans and animals behave in response to changes in their environments

50   is vital for predicting population dynamics and the trajectory of coupled social-ecological

51   systems. Here, we present a novel framework for identifying emergent social behaviours in

52   foragers (including humans engaged in fishing or hunting) in predator-prey contexts based on

53   the exploration difficulty and exploitation potential of a renewable natural resource. A

54   qualitative framework is introduced that predicts when foragers should behave territorially,

55   search collectively, act independently, or switch among these states. To validate it, we derived

56   quantitative predictions from two models of different structure: a generic mathematical model,

57   and a lattice-based evolutionary model emphasizing exploitation and exclusion costs. These

58   models independently identified that the exploration difficulty and exploitation potential of the

59   natural resource controls the social behaviour of resource exploiters. Our theoretical

60   predictions were finally compared to a diverse set of empirical cases focusing on fisheries and

61   aquatic organisms across a range of taxa, substantiating the framework's predictions.

62   Understanding social behaviour for given social-ecological characteristics has important

63   implications, particularly for the design of governance structures and regulations to move

64   exploited systems, such as fisheries, towards sustainability. Our framework provides concrete

65   steps in this direction.

66 **Introduction**

67   The ecosystems in which animals, including humans, are embedded act as complex

68 adaptive systems, where outcomes at macro-scales, such as energy flow, population dynamics,

69 or sustainability emerge from micro-scale interactions among individual agents and ecosystem

70 components (Levin 1998; Holling 2001). Humans and ecosystems are further tightly linked

71 within coupled social-ecological systems (SESs) (Schlüter *et al.* 2012; Levin *et al.* 2013;

72 Arlinghaus *et al.* 2017). Key to addressing macro-scale ecological and socio-economic

73 challenges, such as fully understanding population dynamics of species, avoiding overharvest,

74 preventing biodiversity loss, optimizing species reintroductions, or mitigating the effects of

75 climate change, is improving knowledge about the dynamical feedbacks among agents and

76 between natural and human systems across scales (Levin 1998; Levin *et al.* 2013). Many key

77 interactions among individual animals or between animals and humans in SESs are initiated or

78 controlled by individual behavioural responses that affect collectives (Milner-Gulland 2011; Sih

79 *et al.* 2012; Ward *et al.* 2016). In this context, the emergence of particular resource use

80 patterns fundamentally affects animal population dynamics (Huey & Pianka 1981; Brown *et al.*

81 1999; Grant *et al.* 2017), the exploitation rates induced by fishers or hunters (Laundré *et al.*

82 2010; Januchowski-Hartley *et al.* 2011), and social conflicts in natural resource use contexts

83 (Gutiérrez *et al.* 2011). A better understanding of which human and animal behavioural

84 responses are expected for a given ecological state is an important step to move us forward

85 along a trajectory towards the ultimate normative goal of sustainability and resilience (Pine *et*

86 *al.* 2009; Berger-Tal *et al.* 2011; Mangel *et al.* 2015).

87   In many ecosystems, resource use patterns are dependent on foraging decisions made

88   by individuals or groups of individuals (Dill 1987; Lima & Dill 1990; Lima & Zollner 1996). Social

89   interactions form a major component of foraging decisions, which can encompass a range of

90   strategies, from territoriality, to collective search, to individualism (Grant 1993; Ranta *et al.*

91   1993; Giraldeau & Caraco 2000; Maher & Lott 2000). The dynamic and connected nature of

92   complex adaptive systems means social behaviours are constantly coevolving with the

93   environment, with individuals potentially switching among behavioural strategies as

94   environmental cues change (Elgar 1986; Higginson & Ruxton 2015; Tilman *et al.* 2016). An

95   improved understanding of the manifestation and switches among forms of social interaction in

96   both animal and human foragers has important consequences for wildlife management and

97   natural resource governance. For example, in coupled SESs a shift from communal information-

98   sharing to territorial behaviour, while under a common property regime, requires a new set of

99   management rules to avoid subsequent overexploitation (Boserup 1965; Poteete & Ostrom

100   2004; Chabot-Hanowell & Smith 2012). As an example from animal populations, the facilitation

101   of the invasion success of the Argentine ant (*Linepithema humile*) through the breakdown in

102   territorial behaviour upon introduction to southern California, demonstrates how better

103   predictions of changes in social behaviour could improve models of invasion risks (Holway *et al.*

104   1998; Holway & Suarez 1999). Importantly, shifts in the social behaviour of foragers can affect

105   the harvested resource in ways that may in turn feed back to further influence the behaviour of

106   the foragers (Wiens 1976; Schlüter *et al.* 2012; Stoop *et al.* 2012; Lade *et al.* 2015).

107   Our objective is to provide a novel theoretical framework for predicting both the level

108   and form of social behaviour when foraging for renewable resources in both animals and

109 humans. Our interdisciplinary work builds on literature from behavioural ecology (Brown 1968;

110 Wiens 1976) and several anthropological works, which have proposed frameworks for

111 understanding the emergence of territorial human behaviour in natural resource systems

112 (Dyson-Hudson & Smith 1978; Acheson 2015). In particular, we were interested in predicting

113 which social behaviour to expect in response to spatio-temporally varying ecological properties

114 and whether such behavioural responses would be seen in both human and animal foragers. In

115 this context, a classical anthropological framework based on the concept of "economic

116 defendability" proposed that property rights emerge from generic ecological properties (Dyson-

117 Hudson & Smith 1978; Acheson 2015). We built our framework on this idea, but propose that

118 the "exploration difficulty" and "exploitation potential" of a resource, and not economic

119 defendability *per se*, are the two major determinants of the foragers' social behaviour and that

120 this applies generally across both animal and human foragers.

121 To develop our case, we first present a novel qualitative framework. We then use a

122 general mathematical model and an agent-based evolutionary simulation model as a detailed

123 validation of the expectations derived from the qualitative framework. Finally, we present

124 results of a literature review of empirical case studies using fisheries as an example of SESs and

125 studies on aquatic organisms to understand how well our models apply across a variety of

126 empirical systems. We also discuss examples beyond fish and fisheries, but for space reasons do

127 not present a comprehensive review of terrestrial literature. We conclude that our framework

128 promises to generate robust predictions of the form of social behaviour shown by foraging

129 animals, and in particular humans, in response to characteristic ecological or technological

130 attributes of a given ecological or socio-ecological system. In particular, we propose that

131   reflections along just two axes are sufficient to explain the emergence of a rich family of

132   resource exploitation systems.

133   A Qualitative Framework for Understanding Forager Behaviour

134   Behavioural ecology has long inspired hypotheses about which forms of social foraging

135   to expect under particular ecological contexts (Caraco & Giraldeau 1991; Grant 1993; Potts &

136   Lewis 2014). In applications to animals, a classic framework by Wiens (1976) suggests that the

137   social organization should be a function of resource aggregation or unpredictability and the

138   expense of resource defence. Herding and nomadism were predicted when defence costs were

139   high and resources were unpredictable, territoriality was predicted when defence costs were

140   low and resources were predictable, and coloniality or refuging were predicted at intermediate

141   defense costs and resource predictability (Wiens 1976).

142   Anthropological models of human social behaviour have built on these ideas (Dyson-

143   Hudson & Smith 1978), emphasizing "economic defendability" (Brown 1968) to determine the

144   expected type of human territorial behaviour. It was suggested territoriality will form when the

145   benefits from maintaining a territory are greater than the defense costs (Brown 1968). By

146   contrast, when defense costs are greater, one should expect cooperative or individualistic

147   behaviours over territorial resource use (Rubenstein 1981; Chabot-Hanowell & Smith 2012;

148   Acheson 2015). Dyson-Hudson & Smith (1978) also proposed social behaviour responds to

149   natural resources according to two factors (axes in a graph): resource density and the

150   predictability of the resource (Brown 1968; Dyson-Hudson & Smith 1978). It was suggested that

151   when both the resource density and predictability are low, foragers should be dispersed and

152   mobile; when both the resource density and predictability are high, foragers should be

153   territorial; when the resource density is low but the predictability is high, foragers should be in

154   a non-territorial home-range system; last, when the resource density is high, but the

155   predictability is low, foragers should be sharing information within spatio-temporally confined

156   territories (Dyson-Hudson & Smith 1978). These ideas were consistent with the earlier models

157   of animal social behaviour proposed by Wiens (1976).

158   There are several issues with applying the above-mentioned frameworks to forager

159   behaviour as highlighted by several anomalous empirical case-studies (summarized in Acheson

160   2015). The original axes – resource density and predictability — fall short of encompassing all

161   relevant ecological and social factors, affecting the pay-off of certain social behaviours. They do

162   not allow robust metrics for comparing different empirical systems, where the dynamics of

163   abundance or resource density may take on very different meanings. Resource density must be

164   understood as the potential benefit gained from extracting the resource, accounting for factors

165   such as resource value (in terms of either monetary value or energy for growth) as well as the

166   ability to extract the resource (which relates to technology or competition with other foragers).

167   The term "density" will then be potentially misleading, as resources can be disproportionally

168   valued because of their rarity within a given system: this is seen for example in recreational

169   fisheries, where the presence of an individual trophy fish and not the density of fish per se can

170   drive angler site choice behaviour (Arlinghaus *et al.* 2014). Abundance or density must thus be

171   replaced by some relative measure of access to desired resources if a framework to predict

172   social behaviour as a function of ecological factors is to be applied across different case

173   systems.

174   Similar shortcomings can be expressed in relation to the axis "predictability", which

175   does not distinguish the various effects of predictability on foragers, in particular the ability to

176   find the resource, and to exploit the resource once found. We consider the latter to be a more

177   direct contributor to the emergence of social behaviours of resource exploiters than the

178   predictability of a resource *per se*.

179   Developments in understanding when individuals are expected to behave territorially,

180   or share information have diverged from one another (Ranta *et al.* 1993; Maher & Lott 2000;

181   Danchin *et al.* 2004; Rendell *et al.* 2011; Potts & Lewis 2014; Higginson & Ruxton 2015; Smolla

182   *et al.* 2015), and to our knowledge the shortcomings of the original frameworks (Wiens 1976;

183   Dyson-Hudson & Smith 1978; Acheson 2015), have not yet been addressed. To advance the

184   frameworks proposed by Wiens (1976) and Dyson-Hudson & Smith (1978), we redefined its

185   axes into the more general "exploration difficulty" and "exploitation potential" (Fig. 1). This

186   terminology follows the classic framing of forager behaviour as a trade-off between exploration

187   and exploitation (Dugatkin & Wilson 1991; Enquist & Leimar 1993; Smaldino & Schank 2012;

188   Hills *et al.* 2015; Barbier & Watson 2016). Exploration difficulty reflects the effort spent

189   searching per unit of resource value found (independent of its abundance), while exploitation

190   potential represents the fraction of the value that can be extracted by an individual once found.

191   Each of these axes combine multiple properties of both environment and foragers (including

192   gear and technology), so as to fully determine when it is more advantageous to be territorial,

193   individualistic, or search collectively.

194   We view foragers as searching the environment for and harvesting distinct patches of

195   resources with varying degrees of mobility, temporal persistence and sparseness (Elton 1949;

196   Kotliar & Wiens 1990; Barbier & Watson 2016). Accordingly, exploration difficulty (the y axis in

197   Fig. 1) is modified by both the distribution of the resource patches in the environment and the

198   ability of individual foragers to find new patches. It is, crucially, a *relative* metric: harder-to-find

199   but richer patches may lead to the same search effort per unit value and therefore an

200   equivalent "exploration difficulty". While we generally think of patchiness as spatial,

201   exploration may involve learning the resource's temporal patterns, in which case temporal

202   predictability is integrated into the exploration difficulty as well.

203   The second axis (the x axis in Fig. 1) – exploitation potential – is the fraction of value

204   that can be extracted by a lone forager from a resource patch after finding it, and also relates to

205   a number of ecological and social factors, for example, how efficient the forager is at extracting

206   the resource from a patch, and the temporal resource variability. Ephemeral resource patches

207   (e.g., harvesting desert wildflowers) have low exploitation potential because, even when

208   patches are discovered, the resource may disappear before it can be completely extracted.

209   Patches may also disappear before complete extraction because other foragers are also

210   harvesting the resource or because the resource patch may move (e.g., a fish school moving

211   along a coastline). Conversely, a resource that can be continuously exploited at a given location

212   has high exploitation potential. Again, the exploitation potential metric is relative as a resource

213   patch that disappears more quickly, but can also be extracted more efficiently may result in an

214   equivalent exploitation potential.

215   When resources have a high exploration difficulty and low exploitation potential (Fig. 1,

216   Quadrant 1, "Collective Search"), it may be beneficial to share information as the resource is

217   difficult to find and retain, and we expect to see collective searching behaviour in both animal

218   and human foragers. If both exploration difficulty and exploitation potential are high (Fig. 1,

219   Quadrant 2, "Territoriality"), for instance because of sparse but long-lasting resource patches,

220   the value of defending the resource should be very high and the foragers should establish

221   territories and exclude outsiders, either via formal or informal norms, or antisocially through

222   aggression. Where exploration difficulty is low, individuals can easily find more resources on

223   their own, and the advantages of territorial exclusion or collective search vanish, leading to

224   generally individualistic behaviour, more so if individualism comes with its own benefits (e.g.

225   freedom of movement). Low exploration difficulty also means that more foragers are likely to

226   find the same patch by chance over its lifespan. If exploitation potential is low (Fig. 1, Quadrant

227   3, "Individualism"), the presence of other foragers on the same patch does not affect individual

228   gains, and there is effectively no competition. If exploitation potential is high, however, (Fig. 1,

229   Quadrant 4, "Scrambling"), these foragers do interfere with each other and their utility is

230   reduced by scramble competition, but the advantage that would be provided by territorial

231   exclusion is still too weak to justify its costs (in terms of time, energy or risk). We propose any

232   social-ecological system and any natural forager system, based on the exploitation of a natural

233   resource can be located along the two axes of Fig. 1 (excluding several edge cases, see

234   Supporting Information 1).

235   **Quantitative Models for Understanding Forager Behaviour**

236   To better understand collective behaviour of foragers in the context of the novel

237   framework we propose in Fig. 1, we performed a quantitative exploration of behavioural

238   strategies across the full spectrum of exploration difficulty and exploitation potential. To do so,

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239   we developed two models. First, we propose a simple formalization of the qualitative

240   framework in Fig. 1, to understand its fundamental assumptions and test their consistency.

241   Given a population of foragers in a fixed ecological setting, this mathematical model gives

242   analytical predictions for collectively optimal strategies. However, it ignores the possibility of

243   foragers exhibiting different individual behaviours, in particular via explicit spatial dynamics

244   which may allow the coexistence of diverse strategies. Therefore, we also implemented a lattice

245   (grid-based) evolutionary simulation model to investigate the resulting spatial and temporal

246   dynamics, abstracting out the search process and adopting discrete space and time for

247   computational efficiency, so as to identify emergent strategies over many generations. While

248   these two approaches differ significantly, we finally show that both models convey the same

249   qualitative message in support of the predictions in Fig. 1. This provides evidence that the

250   results we report are not model-dependent, but reflect generic social-behaviour patterns in

251   foragers within complex adaptive systems, as a function of exploration difficulty and

252   exploitation potential.

253   **Model 1: General Mathematical Model**

254   **Description**

255   Our mathematical model (see Supporting Information 1 for details and Table 1 for

256   parameter definitions) closely follows the qualitative analysis above. To translate the

257   framework's axes into definite quantities, they can be expressed in terms of timescales, taking a

258   clue from ecological models of predation: the consumption efficiency of a predator can be

259   expressed in terms of T_s, the time spent searching, and T_h, the time spent handling a prey

260   (Holling 1959). The ratio of these timescales T_s/T_h corresponds to exploration difficulty, that is

261   how much time it takes to find one unit of the resource, where units here are measured in

262   terms of how long it takes to handle them. Adding T_r, the timescale of resource persistence, we

263   can define exploitation potential as a second ratio, T_r/T_h, which is small for resource patches

264   that are ephemeral compared to their richness.

265   All three time scales can be computed for various resource-use settings, using specific

266   models that integrate relevant environmental and socio-technological parameters, e.g. for

267   fisheries (Barbier & Watson 2016). They will be taken here as the external parameters that

268   determine the social dynamics.

269   Given the three parameters and the number N of foragers, our goal is to compute the

270   forager's utility U, specified as their average rate of resource extraction (or total value gained

271   over a fixed time period), as a function of the adopted social strategy. An additional parameter

272   must be provided: c the fraction of time spent defending a territory, if the territorial strategy is

273   selected. Indeed, collective search naturally comes at the cost of sharing a patch, but territorial

274   exclusion would always be preferable over individualism unless it is made costly, here in terms

275   of lost exploitation time. It is then possible to abstract all spatial dynamics by simply

276   considering the "behavioural states" of the foragers, and their transition rates (see Box 1 for

277   details of the model). The state-based description can easily be extended to account for other

278   processes of interest. Spatial patterns are sufficiently captured by n, the expected number of

279   foragers exploiting the same patch, either due to voluntary sharing or scrambling, which can be

280   computed as a function of the three timescales and the social strategy. Despite this simplicity,

281   the mathematical model, previously implemented without consideration of territoriality, has

282   been shown to agree qualitatively and quantitatively with spatially-explicit agent-based

283   simulations (Barbier & Watson 2016). We thus present only the mathematical model outcomes

284   here.

285

286   **Results**

287   Figure 2 validates the outcomes of the qualitative analysis by demonstrating that

288   domains with distinct strategies corresponding to the quadrants of the qualitative Fig. 1 emerge

289   straightforwardly from the mathematical model. In the left panel of Fig. 2, the y-axis is

290   exploration difficulty and the x-axis exploitation potential, as defined from the key timescales in

291   the previous section. We focus here on collective optima: all foragers can either communicate

292   to a degree $\lambda \in [0,1]$ (yellow), or put an effort $\mu \in [0,1]$ (red) into excluding others from their

293   territory. The color pictured represents the one that maximizes the average intake of any

294   individual forager in the group, and therefore the best strategy for the population as a whole.

295

296   **Model 2: Evolutionary Lattice-model**

297   **Description**

298   We complement our mathematical modelling approach by introducing a simple, yet

299   generic, evolutionary simulation model of interacting agents, which compete for a temporally

300   variable finite resource that is spatially distributed on a lattice (see Box 1 for implementation

301   details and Table 2 for parameters). The model is computationally inexpensive and enables

302   simulations of large (evolving) agent populations. It focuses on competition among exploiters in

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303   terms of resource access and exploitation, as well as on collective searching via information

304   sharing. The evolutionary lattice-based model does not explicitly model individual search

305   strategy, but studies the selection operating on behavioural strategies. The evolutionary aspect

306   of this model accounts for the opportunity for learning, to transmit foraging strategies

307   culturally, or to transfer resources through inheritance. It thus applies to both animal and

308   human foragers.

309   We consider the exploitation of a resource, randomly distributed on a two-dimensional

310   discrete lattice, by a population of N agents. Each lattice site either contains a constant amount

311   of the resource or is empty. The spatial distribution of the resource is characterized by the area

312   fraction covered f_c. The average density of the resource in the environment is fixed, thus

313   depending on the area covered there exists either few high-yield sites given a low f_c or many

314   low-yield sites given a large f_c. In the simplest case considered here, there is no spatial

315   correlation in the resource distribution (see Supporting Information 1 for more details).

316   The distribution of the resource is assumed to have a finite life-time, T_r, setting a

317   characteristic time-scale, during which the agents may harvest the resources. Once the life-time

318   of the resource distribution is reached it is replaced by a new random distribution with the

319   same area covered. Thus, the resources can represent ephemeral stationary natural resources

320   or mobile ones.

321   All agents (i.e., foragers) may invest in three different strategies to try to maximize their

322   harvesting pay-off: 1) faster *exploitation* of the resources by increasing their harvest rate (c_{upt}),

323   2) *information sharing* via investing into their communicability (c_{sig}), and 3) effective *exclusion*

324   of competitors from resources by investing in their "repulsion" strength (c_{rep}). We distinguish

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325   three main strategies based on the primary investment of the respective agents: "Individualists"

326   with the main investment into increasing their harvesting rate, "Communicators" (or

327   "Information Sharers") who invest primarily in their communication ability, and "Territorial"

328   agents who invest most into excluding others from resource patches.

329   For computational simplicity we assume a sequential structure of a single competition

330   bout, consisting of the following steps: 1) random placement on a randomly generated resource

331   landscape (abstract search process), 2) signalling phase (communication) where agents on

332   resource patches may attract others based on their communication phenotype, 3) competition

333   phase with all agents at the same location performing pair-wise fights, where the losing agent is

334   displaced from the location to a neighbouring lattice site, and finally 4) exploitation phase,

335   where all agents remaining on the same resource patch harvest it in parallel constrained by the

336   finite life-time of the resource.

337   In the evolutionary lattice-model we employ a minimal search process: a random

338   placement of agents on the resource landscape. Here a key parameter is the probability that an

339   individual finds a resource patch, which equals the area fraction covered f_c. Reinterpreting this

340   probability as a rate of "landing" on a resource patch allows us to define a characteristic "search

341   time" in dimensionless units as the inverse probability, $T_s = 1/f_c$, which we then can use to

342   quantify the exploration difficulty (Fig. 3). The exploitation potential of the resource landscape

343   is quantified simply by the life-time of the resource T_r (Fig. 3). Note that in the lattice-model

344   there is no fixed time-scale associated with the resource exploitation, as the uptake rate is an

345   evolvable parameter. However, we can consider a corresponding handling time-scale set by the

346   base uptake rate $T_0 = 1/\alpha_0 = 1$.

347   **Results**

348   In Fig. 3 we summarize exemplary results for the evolved stationary strategies as a

349   function of the exploitation potential (resource life-time T_r) and exploration difficulty

350   (dimensionless search time). For long-lived and sparse resources $T_r \gg 1$, $T_s \gg 1$, the

351   predominant evolved strategy corresponds to 'Territoriality' with high investments in repulsion

352     $c_{rep} > c_{upt}, c_{sig}$, whereby the largest evolved c_{rep} corresponds to highest resource sparseness.

353   For short-lived resources ($T_r \ll 1$), and high exploration difficulty, the most frequent

354   behavioural phenotype is "Communicator", with the highest investments into signalling. Finally,

355   for low exploration difficulty the dominant strategy is "Individualism", with the highest

356   investments in increasing harvest rate for short resource lifetimes. The resulting strategy space

357   closely resembles the predictions of our qualitative framework and the general mathematical

358   model. Whereas this general structure is conserved for a wide range of model parameters (see

359   Table 2), the detailed shape and extension of the different regions will depend on specific

360   parameter choice (see Supporting Information 1 for details).

361   **Empirical Evidence in Fisheries and Aquatic Organisms as Case Studies**

362   We searched the literature (see Supporting Information 1 for methods) for empirical

363   cases in aquatic systems that describe the social behaviour of foragers ("harvesters" in the case

364   of fisheries) in response to the ecology of food patches or fish stocks and, in human cases,

365   technology. We focused on capture fisheries and aquatic systems as empirical cases because of

366   the relatively high uncertainty in outcomes and patterns of property rights formation in capture

367   fisheries systems (Acheson 2015) and the complementary wide behavioural diversity within

368 aquatic animal systems, particularly fish (Keenleyside 1979). We briefly touch on terrestrial

369 cases in the Discussion because we think the framework (Fig. 1) should apply generally. Our aim

370 was to gather examples across diverse systems to evaluate empirical support for our

371 framework and not to collect all known cases.

372 **Results**

373   We retained 84 empirical cases (33 from capture fisheries and 51 from aquatic

374 organisms; see Supporting Information 2). These cases covered a diversity of systems, from

375 small scale multi-species fisheries, to large scale commercial fishing fleets, targeting species

376 across trophic levels from urchins (*Strongylocentrotus* spp.) to lobsters (*Homarus americanus*),

377 to tuna (*Thunnus* spp.). Further, the cases examined animal populations in a range of ecological

378 conditions, including deep-sea abyssal plains, caves, lakes, reefs, rivers, and the marine pelagic.

379 We thus feel confident that our cases are sufficient to examine our framework's support.

380   The majority of evaluated fisheries systems corresponded primarily to collective

381 searching (n = 21 out of 33). Published cases with primarily territorial or individualistic

382 behaviour were less common in fisheries systems, with only five and seven cases respectively.

383 By contrast, cases specific to aquatic organisms corresponded primarily to territoriality (n = 35

384 out of 51), while nine cases and seven cases corresponded to collective searching and

385 individualism respectively.

386   When judging the social outcomes in each of the examined 84 cases against our

387 predictions, we found strong support that the forager's key social strategies — collective

388 searching, territoriality and individualism — followed our model predictions as a function of

389 exploitation potential and exploration difficulty (see Supporting Information 2). In fact, our

390   predictions were supported in 66 of 84 cases, partially supported in 15 cases and completely

391   unsupported in only three fish cases (Fig. 4). To our surprise, there were very few cases of

392   complete disagreement. A partially supported case included a mixture of the predicted and

393   unpredicted social behaviours existing within the same system, such as the glass shrimp,

394   *Pasiphaea japonica*, fishery in Toyama Bay, Japan where individualistic fishers fish on opposite

395   days to a group of cooperative, catch sharing fishers, despite targeting the exact same resource

396   with comparable fishing gear (Carpenter & Seki 2011). Ayu, *Plecoglossus altivelis,* are an

397   additional example from aquatic organism cases, where 30-50% of individuals defend rich algal

398   patches as predicted, while the remaining individuals of the population shoal and intrude the

399   defended patches (Kawanabe 1969).

400   Collectively, our case studies indicate — in agreement with our qualitative framework

401   and two quantitative models — that key ecological and social properties subsumed in the

402   exploration-exploitation trade-off lead to the emergence of characteristic behavioural

403   strategies of the average forager. For example, in fisheries systems, pot and trap fisheries,

404   targeting lobsters and crayfish tended to show territoriality, and were characterized by medium

405   to high exploration difficulty and high exploitation potential (Acheson 1975; Levine 1984;

406   Wagner & Davis 2004; Acheson & Gardner 2005; Turner *et al.* 2013, 2014). By contrast, shellfish

407   fisheries which target molluscs such as cockles and scallops and also sea urchins, were

408   characterised by low to high exploitation potential and low exploration difficulty and thus

409   tended to show individualism (Murray *et al.* 2011; Johnson *et al.* 2012; Beitl 2014, 2015;

410   Lynham 2017). Moreover, large-scale commercial pelagic fishing fleets, targeting mobile, and

411   sparse (high exploration difficulty and low exploitation potential) pelagic species such as tuna

412   and billfish with trawls or long-lines, showed high degrees of collective searching (Mangel &

413   Clark 1983; Dreyfus-Leon & Kleiber 2001; Curtis & McConnell 2004; Gaertner & Dreyfus-Leon

414   2004; Dreyfus-Leon & Gaertner 2006; Girardin *et al.* 2016).

415   Cases of aquatic organisms also mostly showed characteristic social behaviours

416   according to our framework. We found territoriality in river and stream dwelling fish feeding on

417   drifting invertebrates (e.g. Slaney & Northcote 1974; Grant & Noakes 1987; Blanchet *et al.*

418   2006; Steingrímsson & Grant 2008) and in reef fish exploiting algal patches (e.g. Brawley & Adey

419   1977; Roberts & Ormond 1992; Letourneur 2000; Hamilton & Dill 2003) as both environments

420   are characterized by sparse, yet rich patches of small prey, which relates to a high exploration

421   difficulty and exploitation potential. Collective searching tended to occur in organisms hunting

422   mobile shoaling pelagic prey as predicted by our framework (e.g. Schmitt & Strand 1982;

423   Parrish 1993), but counter to the fisheries cases, collective search was commonly paired with

424   other social strategies, such as collective hunting and anti-predator behaviour, suggesting

425   differences between animal and human foragers. Finally, individualism was recorded in deep-

426   sea scavengers (Priede *et al.* 1990a) and pelagic filter feeders (Sims & Quayle 1998; Sims 2008),

427   which is understandable because deep-sea food falls are scarcely, but randomly distributed and

428   consumed quickly (i.e. scramble competition), and pelagic plankton blooms are relatively easily

429   found (low exploration potential) and have high exploitation potential. The resemblance of

430   various case studies from similar, but geographically separate aquatic systems and fisheries

431   overall supported our proposition that the properties of finding and harvesting a given resource

432   systematically relate to the emergence of specific social behavioural patterns of the foragers.

433   Importantly, we found three cases, all examples of foraging fish, in complete

434   disagreement with our qualitative framework. Firstly, in experiments within drainable ponds,

435   group-foraging adult Eurasian perch, *Perca fluviatilis*, captured more prey and grew faster

436   compared to solitary perch (Eklöv 1992). Perch are known to be social foragers and group

437   naturally in the wild even when prey fish are abundant and widely distributed (Nakayama *et al.*

438   2018), which we predict fosters individualism bordering territoriality depending on spatial

439   patchiness. Adult northern pike, *Esox lucius*, by contrast, forage on the same prey species in the

440   same habitats as perch, but showed agonistic reactions and avoidance behaviour and were

441   most successful when foraging alone (Eklöv 1992), as predicted by our framework. Telemetry

442   studies show pike are usually solitary, forming home ranges, and do not like to feed in the

443   presence of conspecifics (Nilsson *et al.* 2006; Kobler *et al.* 2009; Rosten *et al.* 2016). Secondly,

444   several surgeonfish species (*Acanthurus* spp.), feeding on algal patches and expected to behave

445   territorially, were unable to dominate individual damselfish (*Stegastes* spp.) defending algal

446   patches in reef systems and therefore, counter to predictions, surgeonfish either formed

447   groups to overwhelm the damselfish and access preferred patches, or foraged individually and

448   suffered from increased damselfish attacks (Foster 1985; Reinthal & Lewis 1986). Lastly, Parrish

449   (1993) found green jacks, *Caranx caballus,* and black skipjacks, *Euthynnus lineatus*, foraged for

450   herring alone; however, in agreement with our framework, the most efficient foraging strategy

451   was found to be collective searching. The low number of cases in complete disagreement

452   indicates exceptions to our framework may be rare, but the causes of such exceptions appear

453   to be variable and often involve a survival risk from predation or threatening interspecific

454   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 social-ecological systems. 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

477   appears to consistently tend towards private property systems (i.e. territorial behaviour)

478   (Acheson 2015).

479   There is also much support for our predictions in terrestrial animals. Increased

480   clumping, or increased predictability of food patches tends to result in territoriality across a

481   variety of taxa as expected (see Maher & Lott 2000 for a comprehensive review of vertebrate

482   territoriality). Information sharing has been observed in patchy resource environments, where

483   food cannot be consumed completely alone (Stevens & Gilby 2004) (i.e. high exploration

484   difficulty and low exploitation potential). For example, Elgar (1986) showed that when

485   presented food was divisible, house sparrows, *Passer domesticus*, were more likely to recruit

486   conspecifics to the food source. Further, in mesic habitats with abundant, evenly distributed,

487   long-lasting, quickly regenerated food sources (low exploration difficulty, high exploitation

488   potential), family groups of Plains zebras, *Equus burchelli*, show overlapping homeranges and

489   no territoriality, as predicted (Rubenstein 2010). By comparison, in nearby xeric habitats, where

490   food is patchy and long-lasting (high exploration difficulty and exploitation potential), Grevy's

491   zebras, *Equus grevyi*, show characteristic territorial behaviour (Rubenstein 2010)

492   Our combined results of conceptual theorizing, quantitative modelling and empirical

493   cases suggest it may indeed be possible to identify characteristic social behaviours within

494   specific SES types or animal populations on average across empirical systems. Hence, it may be

495   possible to make generalisations about broad groups of SESs regarding how they exploit natural

496   resources of given ecological properties (see types of fisheries placed on Fig. S12). We suggest

497   the consistent highly communicative behaviour of pelagic fishing fleets, territoriality of trap

498   fishers, stream-dwelling juvenile salmonids or herbivorous reef fish, and the independence of

499 shellfish divers and trawlers and of many recreational fisheries found in our case studies can

500 largely be caused by the ecological properties of the targeted natural resources, specifically in

501 terms of exploration difficulty and exploitation potential, in light of biological or technological

502 foraging constraints.

503 Although our qualitative framework predicts one dominant social strategy, a number of

504 empirical cases showed multiple behavioural strategies co-existing within the same system. A

505 stable co-existence of multiple social strategies is a possible outcome according to the lattice-

506 model (see Supporting Information 1, Fig. S4) and is commonly reported in natural populations

507 in terms of animal personalities (Kobler *et al.* 2009; Spiegel *et al.* 2017). Hence, mixed strategies

508 may naturally emerge. For example, in two SESs dominated by individualism (diving for urchins

509 and bottom trawling for hoki, *Macruronus novaezelandiae*) tracking the movement of other

510 boats without explicit communication was common (Vignaux 1996; Lynham 2017). Similarly,

511 abyssal grenadiers, *Coryphaenoides* spp., foraging on deep-sea food falls behave

512 individualistically, but may also minimize turbulence while swimming to avoid the risk of

513 alerting other individuals to potential food sources (Priede *et al.* 1990b, 1991). These cases with

514 multiple coexisting strategies are likely positioned closer to boundaries between qualitative

515 framework's quadrants (Fig. 1).

516 Other mixed strategy cases can be better explained through mechanisms unaccounted

517 for in our framework. In some SES cases the ability to defend a territory or search collectively

518 related to membership in an exclusive group requiring strong social ties (Gatewood 1984;

519 Carpenter & Seki 2011; Beitl 2014, 2015) or to a historical separation of communities (Krause &

520 Ramos 2015), stressing the relevance of social norms, social and personal capital, social

521   identity, the need for repeated interactions and path dependencies of property rights.

522   Additionally, mixed strategies may be the result of different top-down governmental controls

523   emerging from development of a fishery under different political systems (e.g., socialist to

524   democratic political systems, Daedlow *et al.* 2011), or biological constraints such as the threat

525   of predation pressure (James 1987; Hoare *et al.* 2004). These processes, in addition to the three

526   empirical cases in complete disagreement with our predictions, emphasize limitations to our

527   qualitative framework and quantitative modelling.

528

529   **Framework and Model Limitations**

530   Our model is based on a number of assumptions, notably that foragers maximize their

531   fitness through resource exploitation and natural selection or cultural evolution has guided

532   foragers towards optimal behaviour (Pyke 1984). In reality, behaviour, even of commercial

533   fishers, is guided by multiple factors, some of which are unrelated to the expected utility

534   derived from resource intake (Dall *et al.* 2005; Arlinghaus 2006; Girardin *et al.* 2016). For

535   example, recreational anglers frequently cite non-catch related benefits, such as experiencing

536   nature or social experiences, as more important than catch related ones for determining

537   whether, when and where to fish (Fedler & Ditton 1994; Beardmore *et al.* 2011; Hunt *et al.*

538   2011). If the currency on which foraging decisions are based is misidentified, then predictions

539   from our framework will collapse. Accordingly, we expect our models will be most appropriate

540   in contexts where behaviour is mainly harvest-oriented, such as in top predators, or commercial

541   fisheries where mortality risk is relatively low.

542   Further, we expect our framework will be more accurate when applied to social-

543   ecological systems than to animal populations. Studies of optimal foraging in animal

544   populations frequently observe deviations from predictions because behaviours are

545   constrained by unaccounted factors, such as predation risk, sensory or memory limitations or

546   incomplete information (Perry & Pianka 1997; Matsumura *et al.* 2010). An enduring mortality

547   threat is a critical factor in an animal's behavioural decisions (Werner *et al.* 1983; Boutin 1990;

548   Laundré *et al.* 2010), which does not exist to the same extent in human foragers. Accordingly,

549   because shoaling has multiple advantages for fish against predation risks (Pitcher 1986),

550   foraging in groups to combat predation threats regardless of resource distribution or

551   exploitability may be more common in fish populations (e.g. James 1987; Hoare *et al.* 2004).

552   However, human foragers will also experience constraints on social behaviour such as harvest

553   regulations or other institutions (e.g. Acheson & Gardner 2005). Our framework cannot

554   represent such transitory institutional influences on social behaviour.

555   Our case studies highlight additional important differences between fish and fisher

556   behaviour, further challenging whether our framework can be similarly applied to animal

557   populations and SESs. Animals often lack the sophisticated communication technology of

558   modern humans, which allows instant and complex information sharing across long distances.

559   However, differences in communication range and ability between human and animal foragers

560   may be rectified by adjusting the scale of patch and patch lifetime definitions, which are

561   context dependent (Wu & Loucks 1995; Marceau 1999). Human foragers are additionally

562   affected by strong social norms (Tavoni *et al.* 2012; Kinzig *et al.* 2013; Tilman *et al.* 2016),

563   cultural values (Manfredo *et al.* 2017), governance systems and associated institutions (Branch

564   *et al.* 2006; Ostrom 2007; Lubchenco *et al.* 2016), market mechanisms and associated

565   prosociality (Basurto *et al.* 2016) and historical path-dependencies (Levin *et al.* 2013);

566   phenomena which may not translate directly into animal populations. Although some of these

567   factors are conceptually integrated in the two axes of our framework, others are not,

568   specifically the overwhelming importance of social norms and culture. Experimental and

569   empirical studies are needed to analyse how well our framework approaches behavioural

570   reality in a range of contextual conditions.

571

572   **Empirical Measurement**

573   A critical step forward is to translate exploration difficulty and exploitation potential

574   into empirical measurements in real systems. Specifically, three factors must be measured to

575   test our framework: the relative exploration difficulty of a resource, the relative exploitation

576   potential of a resource and the social behaviour of the foragers. The three factors must be

577   measured according to the correct currency (e.g. net energy gain, or monetary gain) of patch

578   value and defence costs (Higginson & Ruxton 2015). To measure exploration difficulty, one may

579   measure the time (or cost) of the average search investment (e.g., during a fishing trip or

580   foraging bout) or the investment into attractants, such as fish-chum, to discover the targeted

581   resource. To measure exploitation potential, one must be able to measure the proportion of a

582   patch/resource unit harvested before it is lost. In animal populations the individual

583   consumption rate relates to the functional response (Holling 1959). In fisheries the harvest rate

584   relates to the catchability coefficient q, the fraction of the resource unit harvested per unit

585   effort (Arreguín-Sánchez 1996). If the typical resource patch life-span is known (e.g., how fast a

586   fish school leaves an area), and the individual-specific (or gear-specific) functional response or

587   *q*, is also known, then an individual's effort to exploit a full patch can be calculated. The effort

588   exerted before the patch disappears can then be divided by the effort to exploit a full patch as

589   an indication of the exploitation potential. If the definition of a patch is unclear, or the ability to

590   measure the full amount of a resource within a patch is impossible before resource exploitation

591   can begin, then the functional response, or *q* alone, can provide a reasonable relative

592   approximation when comparing foragers exploiting environments with identical resource

593   properties. To estimate the foragers' social behaviour one can use bio-logging techniques when

594   possible (Krause *et al.* 2013; Lennox *et al.* 2017) or more standard methods such as surveys,

595   participant observation and semi-structured interviews (Acheson 1975; Neis *et al.* 1999;

596   Acheson & Gardner 2005; Mueller *et al.* 2008). We suggest experimental and observational

597   tracking studies where both foragers and resources are followed in real-time (Hussey *et al.*

598   2015; Monk & Arlinghaus 2017; Stowers *et al.* 2017) as direct measurements of forager-

599   resource interactions, uptake rate and other parameters key to empirical tests of our

600   framework.

601

Implications for Policy and Management

603   Our framework offers some implications for governance and management systems as

604   they may emerge from the behavioural patterns shown by humans in response to spatio-

605   temporal natural resource variability or technological change (Wilson *et al.* 2013). Depending

606   on whether local and regional outcomes are judged as desirable or not, institutions could be

607   tuned to incentivize certain social behavioural strategies for improved biological and

608   socioeconomic outcomes (Lubchenco *et al.* 2016). These policy options will strongly differ

609   depending on whether exploiters' behaviour is individualistic, collective searching or territorial.

610   Individualistic behaviours tend to be associated with the race-for-fish, with overexploitation in

611   open access systems being a likely outcome (Hardin 1968). In particular, individualistic

612   behaviour may be associated with scrambling behaviour to collect resources before others,

613   which creates excess and wasteful investment into new technologies required to keep up with

614   competitors (Homans & Wilen 1997). Such situations are particularly hard to manage, and

615   building proper incentives usually means forceful implementation of harvest regulations (e.g.,

616   effort controls, licensing, individual quotas in fisheries). Under these situations, incentivising

617   proper behaviour could be improved by implementation of some form of access or harvest

618   rights, e.g., individual transferable quotas (Copes 1986; Costello *et al.* 2008), which often

619   promotes efficiency and long-term planning. With respect to territoriality, the primary

620   management issues may be antisocial behaviours related to territory defence and possibly

621   equity. Explicitly acknowledging and legally enforcing the emerging territories through

622   traditional user rights to fishing (TURFs) could reduce conflicts (Acheson & Gardner 2005) and

623   split the costs of territory enforcement evenly among all foragers. Shared costs may increase

624   the economic rent from the resource (Humphries *et al.* 2012), but also introduces the

625   substantial equity based issue of defining who is entitled to become a territory member. There

626   are few panaceas: depending on the context, even community-based management may lead to

627   resource overuse, for instance when there are abundant actors, few alternatives to fishing and

628   good access to markets (Cinner *et al.* 2012). Finally, systems where collective searching

629   behaviour is prominent fall somewhere in-between individualistic and territorial systems in

630   terms of biological and socioeconomic sustainability. Collective search improves a management

631   body's monitoring capabilities and improves the ability to feed information into the fleet or

632   community, but may also contribute to inequalities in success among foragers under certain

633   conditions (Klein *et al.* 2017). In this context, it would be important to detect leaders in the

634   social network and to work proactively with these individuals (Gutiérrez *et al.* 2011; Barnes *et*

635   *al.* 2016). Lastly, collective information sharing increases the likelihood informal institutions,

636   such as agreed-upon rules of proper behaviour through self-enforcement, will develop (Ostrom

637   2007).

638   The ability to identify characteristic social behaviours within animal populations can also

639   inform management decisions. For example territorial defence of high quality patches could

640   lead to range contraction as territorial individuals are harvested and replaced, which can

641   facilitate overharvesting (Post *et al.* 2002; Burgess *et al.* 2017). When range contractions cannot

642   be directly observed, the foraging ecology of a target species could provide early indications of

643   potential overharvesting. Changes in social behaviour may also alter the exposure of individuals

644   to predation risk and increase the natural mortality rate (Huey & Pianka 1981; Werner *et al.*

645   1983; Brown *et al.* 1999). Anticipating changes in natural mortality rates would help fine tune

646   population assessments, and adjust conservation measures, or harvest rates accordingly (Clark

647   1999; Laundré *et al.* 2010). Importantly, our framework highlights that social behaviour is

648   dynamic and changes in the social behaviour of the predators and prey feedback to one

649   another through changes in space use, resource depletion or consumer rarefaction (See Fig S4).

650   Therefore if these dynamics do not stabilize, policy implementations may require temporal

651   updates or re-evaluations.

652 **Conclusions**

653   We have developed a novel framework for predicting social forager behaviour,

654 demonstrating that the exploration difficulty and exploitation potential of a given social-

655 ecological system gives rise to three social strategies – territoriality, collective search and

656 individualism. Our framework received substantial empirical support when judged against a set

657 of cases from fisheries and aquatic organisms. Going forward, it is important that the

658 framework be tested with a range of new empirical and experimental studies, to systematically

659 understand whether the predictions we offer are accurate. To that end, we proposed measures

660 that could be used to quantify the exploration difficulty and exploitation potential. In the case

661 of fisheries, novel Global Positioning System technology can be used to study the spatial

662 behaviour of fish and fishers in almost real-time, which is particularly useful to advance the

663 empirical understanding of how the ecology of renewable natural resources interfaces with

664 human factors to determine outcomes of harvesting patterns. If the amount of empirical

665 support for our framework continues to grow, it may advance context-specific governance and

666 management solutions and help support sustainable fisheries and other natural resource

667 systems.

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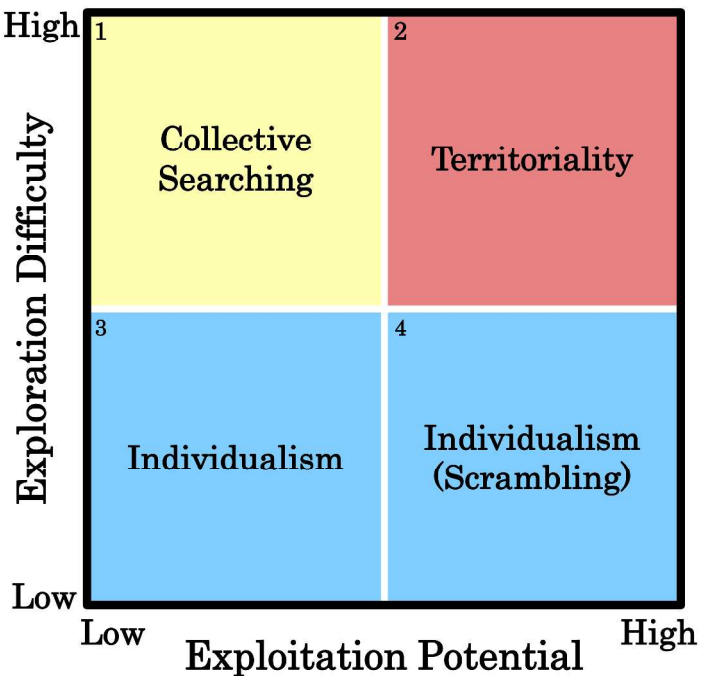
1170 **Figure Captions**

1171

1172 Figure 1. Conceptual model of how exploitation potential and exploration difficulty in natural
1173 resources should select for particular social behaviour by foragers.

1174

1175 Figure 2: Results of the general mathematical model for N = 30 users. Optimal behaviour versus
1176 exploitation potential $log_{10} T_r/T_h$ and exploration difficulty $log_{10} T_s/T_h$. For clarity, investment
1177 into territorial exclusion (red, μ) and communication (yellow, λ) are made mutually exclusive
1178 here. The cost of exclusion is set to $c = 0.3$, meaning that agents must spend 30% of their
1179 time on a patch defending it to guarantee full exclusivity. Three domains are made apparent:
1180 territorial (*T*), collective searching (*C*) and individualistic (*I*) agents.

1181

1182 Figure 3: Evolutionary lattice model: (a) Behavioural map obtained from the evolutionary
1183 simulations distinguishing three regimes based on most frequent strategy in the population:
1184 Communication (C) with $c_{sig} > c_{rep}, c_{upt}$, Territoriality (T) with $c_{rep} > c_{sig}, c_{upt}$ and
1185 Individualism (I) with $c_{upt} > c_{sig}, c_{rep}$. The red dots show parameter values corresponding to
1186 the ternary plots (b,c,d) of the evolved phenotype distribution for different regimes: (b)
1187 Communication, (c) Territorial, (d) Individualistic.

1188

1189 Figure 4. Placement of empirical case studies within the qualitative framework, based on
1190 agreement with predictions. Panel (a) shows placement for fisheries case studies, and panel (b)
1191 shows placement for aquatic organism cases.
1192

Boxes
1194 Box 1, Evolutionary Lattice Model Details; Box1.pdf
1195

Figures
1197 See separate files
1198 Figure 1: Figure 1.png
1199 Figure 2: Figure 2.eps
1200 Figure 3: Figure 3.png
1201 Figure 4: Figure 4.png
1202

Tables
1204 See separate files
1205 **Table 1:** General mathematical model parameters; Table 1.pdf
1206 **Table 2:** Evolutionary lattice-model parameters and variables; Table 2.pdf

Figure 1. Conceptual model of how exploitation potential and exploration difficulty in natural resources should select for particular social behaviour by foragers.
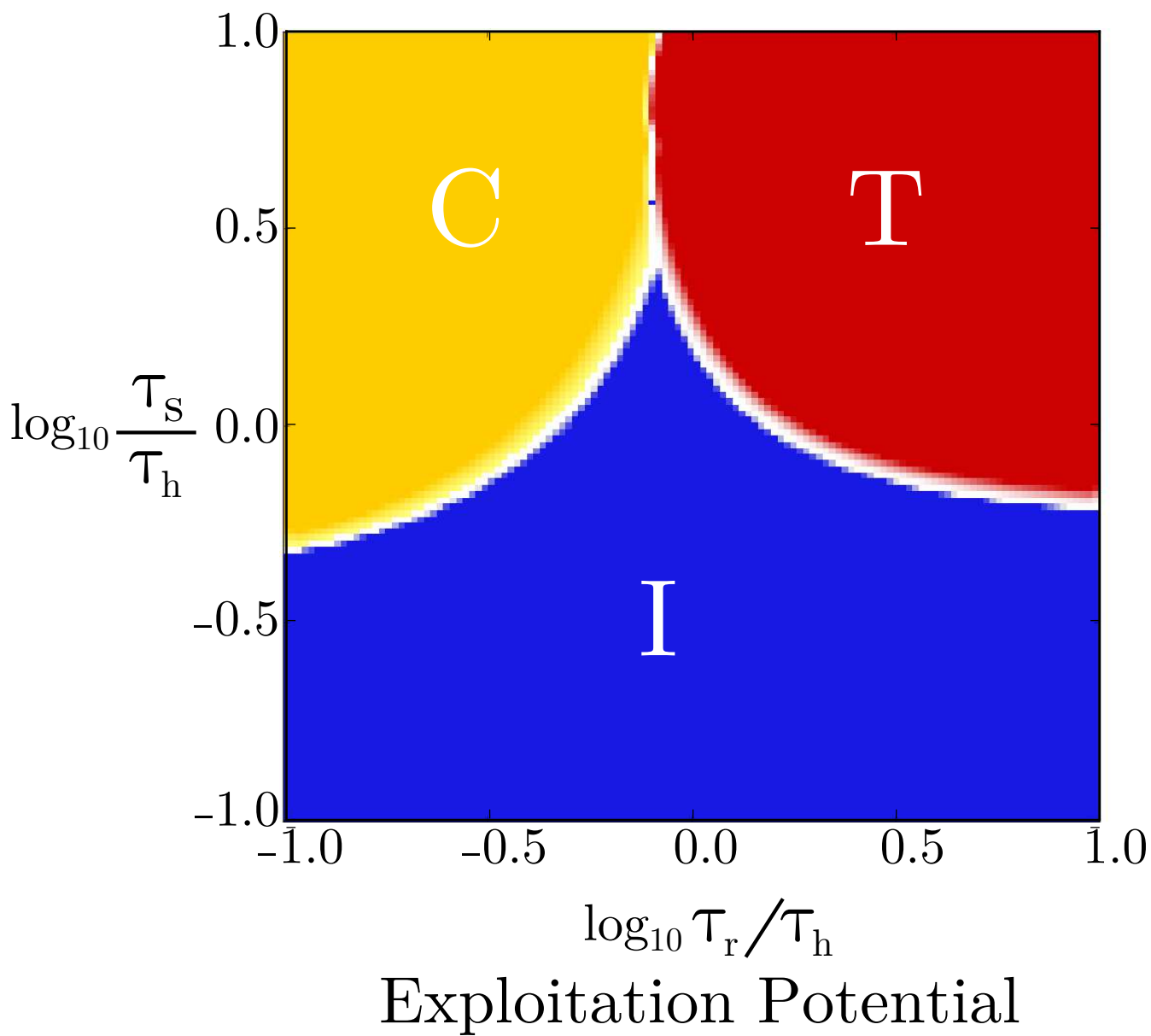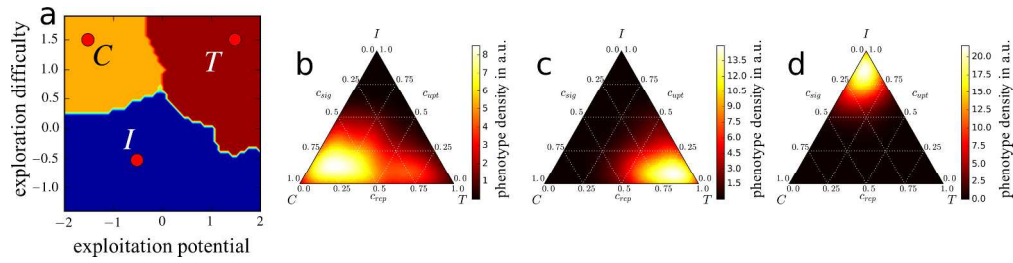
Figure 3: Evolutionary lattice model: (a) Behavioural map obtained from the evolutionary simulations distinguishing three regimes based on most frequent strategy in the population: Communication (C) with c_sig>c_rep,c_upt, Territoriality (T) with c_rep>c_sig,c_upt and Individualism (I) with c_upt>c_sig,c_rep. The red dots show parameter values corresponding to the ternary plots (b,c,d) of the evolved phenotype distribution for different regimes: (b) Communication, (c) Territorial, (d) Individualistic.
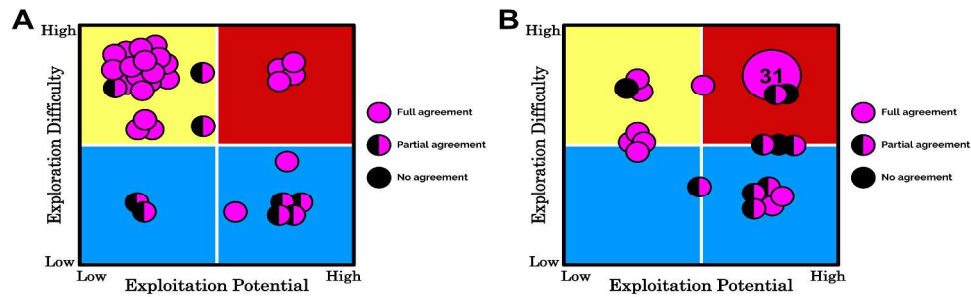
Figure 4. Placement of empirical case studies within the qualitative framework, based on agreement with predictions. Panel (a) shows placement for fisheries case studies, and panel (b) shows placement for aquatic organism cases.