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Habitat disruption and the identification and management of functional trait changes

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Abstract

32 Aquatic ecosystems are facing escalating threats from urbanization, habitat loss and

33 projected impacts of climate change, which both individually and in combination have

34 the potential to fundamentally alter ecosystem functioning. While it is well

35 established that habitat disturbances can affect the composition and diversity of

36 aquatic communities, only recently have studies considered whether such impacts

37 result in changes in species' functional traits. We consider how functional traits of

38 freshwater and marine fishes respond to environmental change, and how shifts in the

39 expression of these traits can impact community dynamics and key ecological

40 processes, including trophic interactions and nutrient transfer. We find that a

41 multitude of functional traits, including behavioural and sensory traits, are sensitive to

42 habitat disturbances. We demonstrate how these trait changes can be used to reveal

43 hidden "ecological diversity" as well as serving as early indicators of environmental

44 perturbation. We conclude that management strategies that consider the fundamental

45 biological responses of fishes to habitat disturbance will be particularly effective in

46 determining causal relationships within the ecological network. While detailed

47 information on trait function is often lacking, even some general understanding of

48 trait function and importance will facilitate targeted and efficient ecosystem

49 management. We urge fisheries biologists and aquatic ecosystem managers to

50 consider the role of functional traits in facilitating effective habitat restoration and

51 management.

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1. INTRODUCTION

Global biodiversity is facing significant threats due to both the individual and combined effects of habitat destruction, over exploitation, the introduction of non-native species, and the effects of climate change (Sala et al., 2000, Vorosmarty et al., 2010). The results of habitat disruption as a consequence of these processes often manifest through loss of species (Koh et al., 2004, Thomas et al., 2004), or changes in the abundance and distribution of populations or communities (Araújo and New, 2007). Observation of these impacts reveals that ecosystem-level responses have already occurred, which restricts the opportunities for mitigating and managing impacts to individual species or groups of species. However, the initial response of a species to habitat disruption is a change in the expression of phenotypic traits, such as those associated with individual performance or fitness (Alberti et al., 2017). Assessment of trait changes thus can not only act as an early warning signal for habitats under pressure, but can be useful in predicting how environmental perturbation may lead to subsequent population decline or loss of ecosystem function (Clements and Ozgul, 2016).

Functional traits are generally considered to determine the performance or the fitness of individuals, and include morphological, physiological, life history, behavioural and stoichiometric traits (McGill et al., 2006, Carmona et al., 2016). Identifying those traits that play a disproportionate role in ecosystem function is crucial for predicting the probability of species extinctions (e.g. Williams et al., 2005), invasions (e.g. Van Kleunen et al., 2010), and for identifying targets for habitat restoration (Laughlin,

100   2014). In the framework of environmental management, particularly of aquatic

101   ecosystems, we consider functional traits as those components of an individual's

102   phenotype that affect ecosystem level processes (Petchey and Gaston, 2006).

103   However, the task of determining which traits are functionally more important than

104   others is often problematic due to the challenges associated with linking changes in

105   individual traits to community assemblages and ecosystem functioning (Suding et al.,

106   2008). Furthermore, we currently have a limited understanding of the link between

107   both inter- and intraspecific variation in functional traits, particularly in animals, and

108   the role that these traits can play in determining ecosystem structure and services

109   (Gagic et al., 2015).

110

111   Anthropogenic disturbances to natural environments can alter patterns of intraspecific

112   trait variation *via* heritable evolutionary change and through phenotypic plasticity

113   (Hendry and Kinnison, 1999). Identifying the relative role of these two processes is

114   critical for mitigating and managing environmental disturbances and for predicting

115   how environmental disruption will impact individual fitness and population

116   persistence (Crispo et al., 2010, Ghalambor et al., 2007, Merilä and Hendry, 2014).

117   Phenotypic plasticity allows species to rapidly respond to environmental change, by

118   increasing individual fitness and facilitating persistence in altered environments (Price

119   et al., 2003). However phenotypic plasticity may also affect the rate of genetic

120   adaptation, depending on the strength of selection in the new environment (Price et al.,

121   2003). If the phenotypic response is optimal for the environmental conditions, the

122   population will persist but there will be limited evolutionary change (Ghalambor et al.,

123   2007). On the other hand, if the phenotypic response is suboptimal for the conditions,

124   there will be strong directional selection and rapid genetic adaptation (Ghalambor et

125   al., 2007). These broad evolutionary concepts apply to all species and are critical for

126   understanding how populations become established in new environments (Ghalambor

127   et al., 2007). Importantly, trait changes in fishes that result from both evolutionary

128   change and phenotypic plasticity can influence the outcome of species interactions

129   (Agrawal, 2001, Berg and Ellers, 2010) and affect ecosystem functioning (Harmon et

130   al., 2009). Understanding the relative contribution of these processes provides the

131   critical evolutionary link between functional trait changes and population responses to

132   habitat disruption, such as those resulting from climate change (Anderson and Gezon,

133   2015). While this approach is reasonably well established in evolutionary ecology

134 theory (e.g. Gienapp et al., 2008, Merilä and Hendry, 2014, Hendry et al., 2008,

135 Hoffmann and Sgrò, 2011) there have been limited attempts at integrating this theory

136 into ecosystem management practices.

137

138 The central aim of this review is to illustrate how the integration of ecological and

139 evolutionary theory with fisheries research can provide innovative outcomes for

140 conservation management. We reveal how the functional traits of fishes can be used

141 as a tool to evaluate and assess ecosystem vulnerability to environmental change.

142 Fishes are among the best-studied organisms for examining how environmental

143 pressures influence inter- and intraspecific trait variation and contribute to species

144 diversity (Schluter, 1996), and have also provided some of the most compelling

145 demonstrations of human-induced trait changes in animals (Walsh et al., 2006). We

146 incorporate methodologies from evolutionary ecology and quantitative genetics to

147 review the available methods for evaluating and predicting trait changes in impacted

148 populations, and for identifying the genetic and environmental contributors to trait

149 divergence. Scaling from individual trait changes to ecosystem responses is

150 notoriously challenging for ecologists and environmental managers; here, we

151 highlight several studies that have demonstrated how functional trait changes can

152 affect trophic interactions and ecosystem structure.

153

154 **2. PRE-DISTURBANCE MODELLING AND ASSESSMENT**

155

156 2.1 Use of functional traits to determine ecosystem vulnerability to disturbance

157

158 While biodiversity analyses are most frequently derived from taxonomic parameters,

159 assessment of functional traits can be a particularly effective approach for identifying

160 regions or habitats that require heightened protection, or to identify regions or

161 communities that are particularly at risk from environmental perturbations. For

162 example, a global analysis of six traits of coral reef fishes (body size, mobility,

163 activity, grouping, etc.) revealed that in regions where multiple species performed

164 similar functions, species also had fewer unique combinations of traits (Mouillot et al.,

165 2014). Thus, areas of high taxonomic richness previously considered to be buffered

166 from the negative effects of habitat disturbances, may not be as protected from species

167 loss as previously thought (Mouillot et al., 2014). Coupling abundance data with the

168   range of functional traits present in a community is an ideal approach, which has also

169   revealed new hotspots of reef fish diversity which were not evident based only on

170   species richness (Stuart-Smith et al., 2013). These examples illustrate the importance

171   of considering the functional contribution of species to ecosystem processes when

172   studying ecological diversity and when developing habitat protection policies. Thus

173   management programs that aim to conserve species richness alone may inadvertently

174   reduce community functional diversity and consequently impede ecosystem function

175   (Cadotte, 2011).

176

177   2.2 Nutrient elements as predictive traits

178

179   For effective habitat management, it is important to identify those species that play a

180   disproportionate role in driving ecosystem function. One approach is to assess the

181   ecological stoichiometry (Sterner and Elser, 2002), which refers to the distribution

182   and balance of energy and elements in ecosystem interactions. There is considerable

183   variation among fishes in body composition and excretion rates of elements such as

184   nitrogen (N) and phosphorus (P), causing some species to play a more important role

185   in nutrient cycling than others. For example, an analysis of fish excretion rates in four

186   lowland streams in Costa Rica found that banded tetra (*Astyanax aeneus*, Characidae)

187   has relatively higher rates of P excretion than other fishes in the community; this

188   species has thus been described as a keystone nutrient recycler (Small et al., 2011).

189   Stoichiometric traits can also be used to predict how invasive species might alter

190   ecosystem processes. For example, the introduction of sailfin catfish

191   (*Pterygoplichthys* spp., Loricariidae), into an oligotrophic river in Mexico resulted in

192   significant shifts in the biogeochemical processing of N and P. These catfish excrete

193   around 25 times more N than native fishes and also sequester P in their body tissues

194   resulting in major shifts in carbon to nutrient and N: P ratios in other ecosystem

195   components (Capps and Flecker, 2013). This example illustrates how ecological

196   stoichiometry might be used to predict how invasive species alter patterns of nutrient

197   cycling in freshwater ecosystems (Capps and Flecker, 2013).

198

199   2.3 Methods for predicting trait change in impacted populations

200

201 Predicting the ecological impact of a planned disturbance (for example, infrastructure

202 developments or resource extraction projects) is challenging but is nevertheless

203 generally a key requirement of the approval process and to comply with particular

204 local, national or even international environmental regulations. In the context of this

205 review, a first step to assessing how individuals are likely to respond to a planned

206 environmental disturbance is to examine current patterns of trait variation across the

207 species' range (both within and among communities) or, ideally, the distribution of

208 functional traits among multiple and interacting species (Fig. 1). Importantly,

209 establishing collaborations among industry, government and research organisations is

210 a cost effective way to collect pre-disturbance data (e.g. through data sharing) and to

211 experimentally test some of the predicted impacts, particularly where there are long-

212 term monitoring systems in place. Several ecological and evolutionary methods (e.g.

213 comparative approaches, habitat modeling, model selection analyses) are available to

214 identify the most important environmental variables, or combinations of

215 environmental variables, that explain trait variation (within a species) and functional

216 trait diversity (in the community). This information, in combination with knowledge

217 of trait function, could provide a basis from which to make *a priori* predictions of trait

218 divergence under different disturbance scenarios. Another approach is to collate

219 available trait data (e.g. from academic sources, online databases such as FishBase

220 and unpublished databases developed through long-term monitoring programs) and

221 perform computational modeling of the response of virtual species to particular

222 environmental stressors. This approach has recently revealed that dispersal distance

223 and annual survival best explain the rate of population spread of terrestrial mammals

224 under projected climate change models (Santini et al., 2016). Such modeling methods

225 are particularly suited to cases in which species data are limiting and can be useful for

226 identifying species or habitats that are particularly at risk (Santini et al., 2016).

227

228 A more hands on experimental approach to determine how traits will respond to

229 environmental disturbance(s) is to expose ancestral individuals to novel habitats that

230 vary in the level of the environmental or ecological factor that is considered most

231 important (Ghalambor et al., 2007). For example, a number of studies have revealed

232 that morphological responses of fishes are phenotypically plastic and can be readily

233 induced in the laboratory in response to factors such as predation risk, water flow,

234 habitat structure, and food presentation (Robinson and Wilson, 1995). Thus if a

235 planned disturbance is expected to change the natural flow regime, it would be

236 advisable to compare each species' morphological and behavioural responses to the

237 anticipated range of flow conditions. The field of quantitative genetics has a number

238 of powerful experimental tools for evaluating and predicting how functional traits

239 respond to selection (Hill, 2010, Roff, 2007). For example, the genetic variance-

240 covariance matrix (G matrix) summarizes the additive genetic variation of traits and

241 describes the levels of genetic covariance among these traits. The G matrix also

242 determines how traits responds to selection, while the matrix of non-linear selection

243 gradients (γ) provides information on changes in an individual's fitness (Blows,

244 2007). However, these experiments can be logistically challenging and many

245 quantitative genetic studies are conducted in the laboratory on organisms with fast

246 generation times; thus the direction and strength of selection is unlikely to replicate

247 that observed in nature. Nonetheless, quantitative genetics has been used to examine

248 the consequences of size specific harvesting in salmonids (reviewed by Naish and

249 Hard, 2008), and with the declining costs of molecular technologies (e.g. eDNA,

250 transcriptome sequencing), is likely to become an increasingly important conservation

251 and management tool.

252

253 **3. IDENTIFYING TRAIT CHANGES TO INFORM MANAGEMENT**

254 **DECISIONS**

255 If we consider that species respond to habitat disruption in a stepwise fashion, starting

256 with the ability of individuals to detect and respond to changes in the environment,

257 and ending in the alteration of ecosystem processes and biodiversity (Fig. 2)

258 (Tuomainen and Candolin, 2011), then it is possible to identify the early stages of

259 environmental change and implement appropriate strategies for management. In the

260 following section, we consider the key functional traits of fishes that are affected by

261 habitat disruptions, and we examine some of the subtle indicators of environmental

262 change that may have been overlooked.

263

264 3.1 Changes in body size, growth rate and age at maturity

265

266 Body size is one of the most fundamental functional traits of fishes, and one that is

267 relatively easy to measure. Body size plays an important role in influencing trophic

268   interactions in fishes, because body length is a strong predictor of gape size and thus

269   feeding behaviours and predator-prey interactions (Persson et al., 1996). Since body

270   size also varies predictably with metabolic activities, such as consumption and

271   excretion, this can affect ecosystem processes (Woodward et al., 2005). Introduced

272   species in freshwater ecosystems worldwide display consistently larger median body

273   sizes than native fishes (Blanchet et al., 2010). This size differentiation also occurs on

274   small spatial scales but depends on trophic guild. For example, a detailed assessment

275   of species assemblages in a dryland river in the USA found that introduced species

276   tend to have smaller size distributions than native species, but in fish members of the

277   invertivore and piscivore guilds, non-native fishes are overall larger (Fritschie and

278   Olden, 2016). Although size structuring is not influenced by predatory or competitive

279   interactions between native and introduced fishes in this system, it is likely that a

280   variety of ecological and evolutionary mechanisms influence community dynamics

281   and ecosystem processes (Fritschie and Olden, 2016). Regular evaluation of the

282   population size structure may provide a cheap and simple way of monitoring food

283   web structure, since body size is usually positively (Romanuk et al., 2011), but

284   sometimes negatively (Burress et al., 2016) correlated with a species' trophic position.

285   Importantly, quantifying both intra- and interspecific variation in body size can serve

286   as an important indicator of niche overlap and the functional variation (or

287   redundancy) present in a community (Micheli and Halpern, 2005, Guillemot et al.,

288   2011). In some scenarios, such as fish communities inhabiting European lakes, body

289   size diversity can be a better predictor of functional variation than species diversity

290   (Brucet et al., 2017).

291

292   Anthropogenic activities that result in selection for individuals with a particular body

293   size, as is often the practice in commercial fisheries, provide a classic example of how

294   such trait changes can serve as indicators of imminent population decline or collapse

295   (reviewed by Kuparinen and Festa-Bianchet, 2016). The collapse of the Atlantic cod

296   (*Gadus morhua*, Gadidae) fishery in the late 1990's was preceded by rapid evolution

297   of early maturation at small body sizes, that if identified at the time, may have been

298   used to inform fisheries management and avoid fishery collapse (Olsen et al., 2004).

299   The identification of evolutionary changes in growth rate (encompassing selection for

300   both slow-growing fish and fast-growing fish, due to high fishery mortality of

301   intermediate length fish) in harvested populations provides a potential explanation for

302   the slow recovery of Atlantic cod populations (Swain et al., 2007), and can result in

303   the permanent loss of adaptive genetic variation (Kuparinen and Merilä, 2007).

304   Nonetheless, experimental studies that have observed changes in body size and

305   growth rate in response to size-specific harvesting, have also revealed that populations

306   can revert back to their original state, once selection is relaxed (Conover et al., 2009).

307

308   Importantly, exploitation, such as harvesting, exerts selection on other traits besides

309   body size and age at maturity, but the impacts of these effects are only recently

310   coming to light (Tillotson and Quinn, 2017). For example, the creation of marine

311   reserves may generate selection on fish home range size (and correlated traits, such as

312   personality) if individuals with small home ranges remain inside the reserve, while

313   those with large home ranges spend more time outside the reserve (Villegas-Rios et

314   al., 2017). An observed change in the distribution of species' traits (in this case, home

315   range size) could be used to refine management decisions, for example, by increasing

316   the size of the reserve to account for species with relatively large home ranges

317   (Villegas-Rios et al., 2017). Management of traits such as home range size has

318   important consequences for ecosystem function, because fish biomass tends to decline

319   with increasing distance from the reserve (Kramer and Chapman, 1999).

320

321   3.2 Changes in body shape

322

323   In freshwater ecosystems, a number of studies have revealed that anthropogenic

324   disruption of flow regimes can result in changes in fish morphology because of the

325   tight coupling between water flow rates, fish morphology and fitness-correlated traits

326   (reviewed in Langerhans, 2008, Langerhans and Reznick, 2010). Impoundment of

327   streams for the construction of reservoirs is one of the most common forms of

328   anthropogenic habitat alteration causing a shift in the morphology of fishes (Franssen,

329   2011, Franssen et al., 2012, Franssen et al., 2013, Cureton and Broughton, 2014, Haas

330   et al., 2010). For example, red shiners (*Cyprinella lutrensis*, Cyprinidae) collected

331   from reservoirs have deeper bodies and smaller heads relative to those collected from

332   nearby streams (Franssen, 2011). Red shiners reared in the laboratory from stream and

333   reservoir populations maintain their morphological characteristics suggesting that

334   impoundments have resulted in adaptive phenotypic divergence (Franssen, 2011). The

335   well-known link between body shape and traits such as foraging habit can be used by

336   managers to predict how these morphological shifts will lead to divergence in the

337   trophic structure of food webs in natural and impacted habitats. However, the link

338   between morphological variation and functional traits can be species-specific, thus

339   this approach may often be hampered by lack of information on the focal community.

340

341   3.3 Changes in behaviour

342

343   Behaviour is an important component of phenotypic plasticity and one of the foremost

344   traits that is affected by a change in environmental conditions. Individuals in

345   disrupted habitats often display changes in a large variety of behaviours, including

346   habitat choice, foraging preferences, social behaviour, and mate choice (Tuomainen

347   and Candolin, 2011, Wong and Candolin, 2015). For example, increased turbidity is

348   known to disrupt mechanisms of mate choice in sheepshead swordtails (*Xiphophorus*

349   *birchmanni*, Poeciliidae) (Fisher et al., 2006), reduce female preferences for males in

350   threespine sticklebacks (*Gasterosteus aculeatus*, Gasterosteidae) (Engström-Öst and

351   Candolin, 2007) and increase female assessment time in broadnosed pipefish

352   (*Syngnathus typhle*, Syngnathidae) (Sundin et al., 2010). These changes in

353   reproductive behaviours can have huge implications for biodiversity conservation; in

354   cichlids from Lake Victoria (Africa), for example, increased turbidity has constrained

355   mate choice, resulting in relaxed sexual selection and loss of species diversity

356   (Seehausen et al., 1997).

357

358   Impacts to aquatic habitats can also exert strong directional selection on particular

359   behaviours. For example, survival analysis of an intensively harvested population of

360   pearly razorfish (*Xyrichthys novacula*, Labridae) revealed that captured individuals

361   were more exploratory, foraged over larger areas, and had higher swimming speeds

362   than those that survived (Alós et al., 2016). Thus the selection pressures imposed by

363   passive fishing gear tend to first target behavioural traits, rather than morphological

364   traits such as body size, and may lead to changes in correlated traits such as growth

365   and reproduction (Alós et al., 2016, Arlinghaus et al., 2017, Diaz Pauli and Sih, 2017).

366   Indeed, selective targeting of large individuals by commercial fishers has the result of

367   indirectly selecting on growth rate because individuals of the same size can be of

368   variable age (Biro and Post, 2008). Behavioural traits can thus have important and

369   indirect consequences for ecosystem level responses, for example, by affecting

370   nutrient transport via fish movement patterns, but these indirect effects are less well-

371   studied (Wong and Candolin, 2015).

372

373   3.4 Sensory systems

374

375   Sensory traits are an important but less recognised determinant of species' responses

376   to habitat disruption, because they provide the critical link between an animal's

377   environment and its behaviour. While it has long been known that chemical pollutants

378   can directly block senses such as the olfactory systems (e.g. Hara and Thompson,

379   1978), recent research has revealed that sensory impairment can have more subtle

380   affects on behaviour. In marine fishes, the projected effects of climate change,

381   specifically ocean acidification, have been shown to impair visual (Chung et al.,

382   2014), auditory (Simpson et al., 2011) and olfactory (Munday et al., 2009) systems

383   and lead to a reduction in behaviours such as predator recognition (Dixson et al.,

384   2010) and homing ability (Devine et al., 2012). These effects are likely to impact

385   patterns of recruitment on coral reefs because larval fishes exposed to high levels of

386   CO_2 exhibit diminished predator avoidance behaviours and consequently have higher

387   mortality rates than those exposed to control levels of CO_2 (Munday et al., 2010).

388

389   In freshwater fishes, sensory system responses to environmental change are less well

390   studied, but intraspecific variation in the mechanosensory lateral line in threespine

391   stickleback has been linked with individual differences in the rheotactic response

392   (swimming response in flowing water) (Jiang et al., 2017). Intriguingly, these

393   differential responses potentially explain lake/stream divergence in dispersal

394   behaviours in this species (Bolnick et al., 2009, Jiang et al., 2017, Jiang et al., 2015).

395   Surprisingly few studies have investigated intraspecific variation in the sensory

396   system, yet such variability is likely linked with behavioural function, fitness and

397   population ecology. For example, a recent study of an Australian dryland fish, the

398   western rainbowfish (*Melanotaenia australis*, Melanotaeniidae) revealed that within-

399   species variation in the lateral line system is associated with environmental variables

400   such as habitat structure and invertebrate prey availability, revealing that populations

401   exhibit habitat-specific sensory specializations (Spiller et al., 2017). Furthermore,

402   while some studies have demonstrated that this intraspecific sensory variation has a

403   genetic basis (Wark et al., 2012), senses such as vision (Fuller et al., 2010) and the

404 lateral line (Fischer et al., 2013, Kelley et al., 2017) can exhibit developmental

405 plasticity. The potential impact of human activities on the sensory systems of fishes

406 urgently warrants further attention, particularly in freshwater ecosystems.

407

408 3.5 Identifying genetic and environmental contributors to trait divergence

409

410 Where it is evident that fitness-associated traits have diverged between ancestral and

411 disturbed populations, an important step is to identify the genetic and environmental

412 contributors to this divergence, so that the response of the population and the rate of

413 adaptation to the changed environment can be predicted. This is important because

414 management procedures often require an estimate of population size, as well as the

415 factors contributing to inter-annual variation in abundance (Crozier et al., 2011). One

416 approach is to perform a common garden experiment, or a reciprocal transplant

417 experiment, whereby individuals from the ancestral population are raised in the new

418 environment (revealing early plasticity) and animals inhabiting the novel or disturbed

419 site are reared in the ancestral environment (revealing the evolution of plasticity)

420 (Ghalambor et al., 2007). Identifying the genetic or plastic basis of trait changes is

421 important for predicting how commercially valuable species, such as salmonids, will

422 respond to climate change. Most studies to date have been correlative, linking changes

423 in environmental drivers such as water temperature with plasticity in traits such as the

424 timing of migration, body size, fecundity and timing of spawning (Crozier and

425 Hutchings, 2014). Studies demonstrating genetic responses to factors such as climate

426 change are less common, because of a lack of suitable methodologies. However, time

427 series models have been used to explain changes in migration of sockeye salmon

428 (*Oncorhynchus nerka*, Salmonidae) in response to water temperature, revealing that

429 an evolutionary response explained up to two-thirds of the observed change in

430 migratory behaviour (Crozier et al., 2011). While intraspecific trait variance may be

431 eroded over time due to random drift (particularly in small populations), relaxed

432 selection is more likely to increase trait variance due to mutation and recombination.

433 Best management practices should be reviewed throughout the disturbance period to

434 ensure that ecosystem requirements are met. To initiate habitat restoration, knowledge

435 of the time-scale of functional trait responses is essential and will inform the time

436 taken to reach the target habitat conditions. Ideally, this would be evaluated at a

437   species-specific level and on a case-by-case basis to account for intraspecific variation

438   in species' responses to disturbances.

439

440   **4. USING FUNCTIONAL TRAITS TO PREDICT CHANGES IN SPECIES**

441   **INTERACTIONS**

442

443   4.1 Changes in trophic interactions

444   Functional traits can be used to predict whether species interactions, such as predator-

445   prey relationships, may be altered as a result of habitat disturbances such as the spread

446   of invasive species. For example, the vulnerability of coral reef fishes to predation by

447   invasive Indo-Pacific lionfish (*Pterois volitans* and *P. miles*, Scorpaenidae) was

448   affected by a combination of morphological and behavioural traits (Green and Côté,

449   2014). Fish that were small, solitary, shallow-bodied and not engaged in cleaning

450   behaviour were more likely to be targeted than species not displaying these traits

451   (Green and Côté, 2014). The study by Green and Côté (2014) demonstrates how

452   combined knowledge of predator diets and prey traits, in combination with a model

453   selection approach that considers multiple and interacting variables, can be used to

454   predict how environmental impacts alter interactions between species.

455

456

457   A decline in the body size of top predators can have significant impacts on the trophic

458   structure of aquatic ecosystems (Heithaus et al., 2008). An analysis of fish

459   communities in the Northwest Atlantic has revealed a reduction in the average body

460   size of top predators, which is associated with poor physiological condition, reduced

461   predation efficiency and a corresponding increase in prey biomass (Shackell et al.,

462   2010). An experimental study using medaka (*Oryzias latipes*, Adrianichthyidae) as a

463   top predator revealed that reducing predator body size had a stronger effect than

464   predator removal, because the reduced predation on water fleas (*Daphnia* spp.)

465   resulted in an increase in phytoplankton abundance (Renneville et al., 2016). This

466   example demonstrates how size-specific harvesting can have a strong effect on

467   ecosystem structure by relaxing predation on the trophic levels below (Table 1).

468

469   Increasing numbers of studies are considering how changes in body shape as a result

470   of anthropogenic activities subsequently affect ecosystem-level processes (Table 1;

471   Harmon et al., 2009, Palkovacs et al., 2011, Bassar et al., 2010). An excellent

472   example is provided by examining zooplankton communities that coexist with alewife

473   (*Alosa pseudoharengus*, Clupeidae*)* predators that diverge in foraging morphology

474   (gape size and gill raker spacing), depending on whether they are anadromous or

475   inhabit lakes that have become landlocked due to dam construction (Palkovacs et al.,

476   2008, Palkovacs and Post, 2008). During summer, anadromous alewives (i.e. that

477   migrate upriver to spawn) prey on the largest zooplankton, while landlocked alewives

478   target the most abundant species of zooplankton (Palkovacs and Post, 2009). Thus,

479   habitat alterations such as impoundment can promote within-species trait divergence

480   that has knock-on affects for trophic interactions within the community (Post et al.,

481   2008). Interestingly, the phenotypic differentiation of alewives is also observed in a

482   competing species, bluegill sunfish (*Lepomis macrochirus*, Centrarchidae).

483   Specifically, predation by landlocked alewives has resulted in a change in plankton

484   community structure, which has caused corresponding adaptations in gill raker

485   morphology, growth rate and prey size selection in bluegill sunfish in these lakes

486   (Huss et al., 2014). This study illustrates how the effects of impoundment on

487   zooplankton predation by alewife are ramified across the food web (Huss et al., 2014).

488

489   4.2 Functional diversity and ecological networks

490

491   There is increasing realization that the functional diversity of traits, which describes

492   the diversity of traits among organisms, is a more important determinant of ecosystem

493   function than species diversity (Cadotte et al., 2011). Indeed, modeling a species'

494   single trait responses to environmental variation, such as temperature variation

495   associated with climatic change, can lead to erroneous and simplistic predictions of

496   species' responses (Davis et al., 1998). More recently, ecologists have sought to

497   understand the functional role of a species, or groups of functionally related species,

498   within an ecological network (Coux et al., 2016, Pigot et al., 2016). For example, a

499   simulated extinction of Amazon rainforest fishes found that the decline of functional

500   richness, functional specialization and functional originality was faster when rare

501   species were removed than when species removal was random (Leitao et al., 2016).

502   While this is an important step forward, such an approach is often hampered by a

503   limited understanding of the functional roles of different species within the ecological

504   network, along with the common assumption that intraspecific trait variation is less

505   important than interspecific trait variation (Violle et al., 2012). For example, an

506   analysis of morphological traits related to feeding ecology in marine fishes was

507   accurate in broadly classifying species according to trophic guild, but was a poor

508   predictor of diet overlap and resource partitioning, probably due to intraspecific

509   variation in fish foraging preferences (Albouy et al., 2011).

510

511

512   5. CONCLUSIONS AND SUMMARY

513

514   Traditional measures of biodiversity based on species diversity and abundance are

515   poor predictors of ecosystem function compared with trait-based measures that

516   incorporate functional diversity (Gagic et al., 2015). Indeed, it is becoming apparent

517   that functional traits play a critical role as ecosystem drivers and are major

518   contributors to global biodiversity (Stuart-Smith et al., 2013). While functional traits

519   potentially provide environmental managers with a powerful tool for predicting the

520   ecological consequences of trait changes resulting from habitat disruption, detailed

521   knowledge of the functional role of phenotypic traits is often lacking. In particular,

522   while there are considerable links between the functional traits of plants (as primary

523   producers) and key ecosystem processes, these relationships are indirect, and thus less

524   easily observed, in animal communities.

525

526   The functional response of fish communities to habitat disruption will depend on how

527   much the disturbed environment deviates from the recent ecological history of the

528   system, and the extent to which the ecosystem is already impacted by human activities

529   such as urbanization (Poff, 2002). While much of our review has highlighted the

530   consequences of human-induced, or experimental changes in, fish body size,

531   including the consequent restructuring of trophic cascades, this approach does not

532   account for other sources of variation among similar-sized species, such as differences

533   in diet, morphology and behaviour (Rudolf et al., 2014). Importantly, selection on

534   body size (and other phenotypic traits) is likely to be preceded by more subtle

535   indicators of environmental perturbation, such as changes associated with exploration

536   behaviour and boldness of individuals (Uusi-Heikkilä et al., 2015, Diaz Pauli and Sih,

537   2017). Indeed, our review finds that little attention has been paid to the physiological,

538   morphological, sensory and behavioural traits of individuals that likely have

539   important, but indirect effects on interspecific interactions and ecosystem processes.

540

541   Finally, there is an incomplete understanding of the consequences of trait changes on

542   ecosystem structure and function, and an overestimation of the importance of

543   plasticity in driving these processes (Forsman, 2015). Research to date (Table 1) has

544   been restricted to only a few traits with known functional significance, or traits that

545   are known to exhibit phenotypic plasticity. Functional traits reflect the combination of

546   both genetic and environmental factors, but the rate and overall pattern of phenotypic

547   change is of primary importance when considering the evolutionary consequences of

548   human activities (Palkovacs et al., 2011, Alberti, 2015). Because the environment has

549   an important effect on population divergence and gene flow, human-induced habitat

550   alterations can potentially facilitate or constrain speciation processes (Seehausen et al.,

551   1997). However, evolutionary processes can also shape ecosystem structure and

552   function. For example, mesocosm experiments have revealed that recent (within

553   10,000 years) diversification of threespine sticklebacks into benthic and limnetic

554   forms causes rapid divergence in prey community structure and ecosystem

555   productivity (Harmon et al., 2009). This finding implies that if human disturbances

556   result in the collapse of species that have recently undergone adaptive radiation, then

557   the consequences for ecosystem function may be severe (Seehausen, 2009).

558

559   It is important to consider that selection acts on multiple traits, which can make

560   patterns of phenotypic divergence difficult to predict (Fischer et al., 2016). We

561   suggest that a trait-based approach is important for understanding evolutionary

562   responses to disturbances and that traits that are highly sensitive to environmental

563   variation and can respond rapidly will confer some level of resilience to the

564   population, but at the potential cost of genetic diversity. The identification and

565   management of trait changes in aquatic communities requires an interdisciplinary

566   approach; we stress that collaboration among aquatic managers, ecologists and

567   evolutionary biologists is likely to be particularly fruitful in generating novel and

568   innovative conservation solutions.

569

570   Acknowledgments

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579   References

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1004

1005   Table 1. Morphological and behavioural trait changes in fishes that are associated

1006   with altered community processes and a change in ecological functioning.

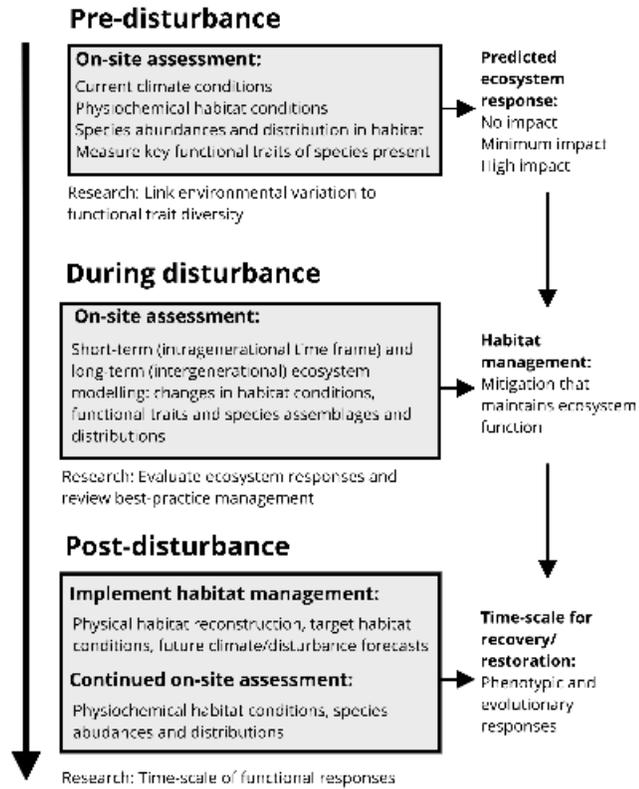| Trait	Disturbance	Ecological effect	Species	References
Body size	Fishing	Trophic cascade	Various	Shackell et al., 2010
	Introduction of invasive species	None detected	Various	Fritschie and Olden, 2016
	Loss of top predators	Trophic cascade	Medaka	Renneville et al., 2016
Body shape morphology	Impoundment	Change in zooplankton biomass, primary productivity, respiration and dissolved oxygen concentration	Threespine sticklebacks	Harmon et al., 2009
		Algal standing stock, primary productivity, chironomid biomass, decomposition rates	Guppies (*Poecilia reticulate*, Poeciliidae)	Bassar et al., 2010
Feeding morphology and migratory behaviour	Impoundment	Zooplankton community structure, algal biomass, total phosphorus (P)	Alewives (*Alosa pseudoharengus*, Clupeidae*)*	Post et al., 2008
		Zooplankton biomass, body size and species richness	Alewives	Howeth et al., 2013; Palkovacs and Post, 2009
		Daphnia sp. life history	Alewives	Walsh and Post, 2011

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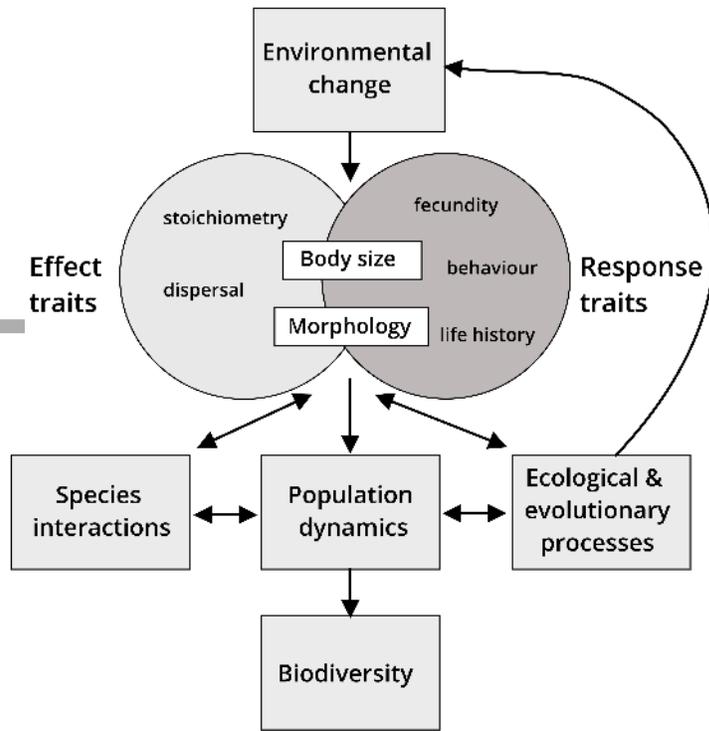1010   Figure captions

1011

1012   Figure 1. Diagrammatic illustration of a three-stage guidance plan for managing

1013   functional trait responses to environmental disturbances. Prior to disturbance, field

1014   assessments combined with a detailed desktop review of species' functional traits and

1015   abundances are required to predict and assess the impact of environmental change.

1016   During the disturbance, key habitat changes should be evaluated in combination with

1017   an assessment of trait changes and community interactions. Planning for habitat

1018   restoration should involve extensive review of evolutionary and plastic responses to

1019   environmental variables, allowing management plans to be implemented at an

1020   appropriate time-scale for recovery.

1021

1022   Figure 2. Pathways linking environmental change with alterations in functional traits

1023   that ultimately influence biodiversity. Human-induced habitat alterations act on top of

1024   natural environmental variation to influence effect traits such stoichiometry, sensory

1025   systems, physiology and dispersal. Changes in response traits, such as fecundity,

1026   dispersal and a variety of behaviours (e.g. foraging, habitat selection) can serve as

1027   early indicators of environmental disturbance. Effect and response traits are

1028   determined by an individual's body size and morphology and in practice, traits may

1029   serve both these functions. Trait changes have knock-on effects on species

1030   interactions, population dynamics and ecological and evolutionary processes, all of

1031   which influence biodiversity. Ecological and evolutionary processes also affect

1032   ecosystem function causing changes in growth rates, productivity and trophic

1033   interactions.

Pre-disturbance

On-site assessment:
Current climate conditions
Physiochemical habitat conditions
Species abundances and distribution in habitat
Measure key functional traits of species present

Research: Link environmental variation to functional trait diversity

Predicted ecosystem response:
No impact
Minimum impact
High impact

During disturbance

On-site assessment:

Short-term (intragenerational time frame) and long-term (intergenerational) ecosystem modelling: changes in habitat conditions, functional traits and species assemblages and distributions

Research: Evaluate ecosystem responses and review best-practice management

Habitat management:
Mitigation that maintains ecosystem function

Post-disturbance

Implement habitat management:
Physical habitat reconstruction, target habitat conditions, future climate/disturbance forecasts

Continued on-site assessment:
Physiochemical habitat conditions, species abundances and distributions

Research: Time-scale of functional responses

Time-scale for recovery/ restoration:
Phenotypic and evolutionary responses

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