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1 **Host-parasite relationships in invasive species: macroecological framework**

2

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18

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20

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26 All authors declare no competing interests.

27

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32

33 ***Authors' contributions***

34 V.L. conceived the idea, collected and analyzed data, and wrote and edited the manuscript. J.A.B
35 and S.M. designed the study. J.A.B, Y.D. and S.M. contributed to writing (review and editing).

36

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39

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45

46 **Abstract**

47 Despite considerable research effort, many aspects of the host-parasite relationships and parasite
48 spatial distribution in invasive hosts remain poorly understood due to complex and context-dependent
49 phenomena related to both the bioinvasions and the parasitism. Using macroecological patterns and
50 theory is a useful approach to analyzing parasitological observations, but in practice parasite ecology
51 and classical macroecology are disconnected. We propose a new framework that can use the
52 conventional parasitology sampling data much more effectively. The innovative concept combines
53 the data inferred from populations, infra- and component communities of parasites and the application
54 of a macroecological approach in the analysis of complex and frequently hidden relationships in host-
55 parasite systems. This comparative analysis draws on parasite data across regions and host species at

56 different organizational (population vs. community) and hierarchical (infra vs. component
57 community) levels of parasites. Our framework based on assessing and analysis of parasitological
58 and ecological indexes, including descriptors of parasite species richness (individual and total),
59 infection parameters, parasite aggregation (Taylor's power law) and macroecological models
60 (abundance-variance and abundance-occupancy relationships), can produce mechanistic explanations
61 of the Enemy Release Hypothesis and unravel host-parasite relationships of an invasive host and its
62 parasites. Moreover, abundance-variance and abundance-occupancy relationships, core-satellite
63 species hypothesis, patterns on the aggregation and the frequency distribution of prevalence,
64 infrapopulation size and individual parasite species richness provide useful tools to distinguish co-
65 introduced and acquired parasites in communities of the invasive host based on quantitative
66 descriptors. We hope that our framework becomes widely applied as it can potentially contribute to
67 enhance future practice and research in biodiversity conservation and control of invasive species.

68

69 **Keywords:** Abundance-occupancy and abundance-variance relationships, frequency distribution of
70 individual parasite species richness and number of parasite individual per host

71

72 **Why is it important to study parasites of invasive hosts?**

73 Increasing transport capacity and economic globalisation have accelerated the rate of species
74 translocation throughout the world (Saebi *et al.*, 2020; Alidoost Salimi *et al.*, 2021) and there are no
75 signs of slowing down (Seebens *et al.*, 2017). Thus, management and control of invasive species have
76 become a pressing issue (Tobin, 2018; Essl *et al.*, 2020). To tackle it effectively, an understanding of
77 the relationships between different components in the biological community in the invaded ecosystem
78 is required. These relationships are often difficult to uncover and must be filtered and analysed
79 carefully before being able to characterize the ecosystem.

80 The presence of certain species in ecosystems, or their abundance, may be entirely dependent
81 on the action of parasites (Mouritsen and Poulin, 2002). Invasive species may affect native
82 populations and communities through different mechanisms, including competition, predation,
83 habitat alteration, change in disease dynamics, etc., while parasites can play an important role in
84 mediating such effects (Lymbery *et al.*, 2014). The effect of parasites on hosts is difficult to unveil in
85 the field because dead hosts are rarely found and if they are, the cause of death can rarely be
86 unequivocally attributed to parasites (McCallum and Dobson, 1995). However, this effect can be
87 inferred from retrospective studies on the parasite infection dynamics, aggregation and spatial
88 distribution (Stanko, Krasnov and Morand, 2006; Sarabeev, 2015b, 2015a; Sarabeev, Balbuena and
89 Morand, 2017a, 2017b, 2018, 2019; Shvydka *et al.*, 2020). Despite considerable research effort, many
90 aspects of the host-parasite relationships and parasite spatial distribution in invasive hosts remain
91 poorly understood (Lymbery *et al.*, 2014; Sarabeev, 2015b; Keogh *et al.*, 2017; Sarabeev, Balbuena
92 and Morand, 2018). To fill this gap, we analyzed data from previous studies (Sarabeev, 2015a;
93 Sarabeev, Balbuena and Morand, 2017a, 2018, 2019) on native and invasive grey mullet fish (or
94 mugilids) using a macroecological framework that allows us to get new insights on how invasive
95 hosts integrate into new ecosystems.

96
97 **Why apply macroecological approach to parasites of invasive hosts?**

98 Macroecology emerged as a distinct field of research about three decades ago from the idea that
99 small-scale local processes alone are not able to fully explain the abundance and distribution of
100 species (Brown and Maurer, 1989; Gaston and Blackburn, 2000; Keith *et al.*, 2012). In other words,
101 macroecology aims at filling a knowledge gap by focusing on processes that emerge at large spatial
102 or temporal scales (Beck *et al.*, 2012). Unfortunately, there is a bias in the field towards
103 macroorganisms, whereas microorganisms have been largely ignored despite their important role in
104 ecosystem functioning (Shade *et al.*, 2018). The study of macroecological patterns and theory is a
105 useful approach for exploring parasite spatio-temporal distribution and disease dynamics in host
106 populations (Morand and Krasnov, 2008; Dallas *et al.*, 2018). In the context of invasion ecology,
107 macroecology is helpful to understand the abundance, distribution and diversity of alien host species
108 at regional and global scales (Pyšek *et al.*, 2020; Poulin, 2021), and their interspecific relationships
109 in a new environment (Sarabeev, Balbuena and Morand, 2017a, 2017b, 2018, 2019). There are several
110 reasons for developing a macroecological framework to the study of parasites of invasive hosts. First,
111 parasites are ubiquitous, occurring in every ecosystem on Earth (Wood and Johnson, 2015), virtually
112 every metazoan organism is infected by at least one parasite species (Poulin and Morand, 2000).
113 Second, parasite populations and communities are fragmented over space by host individuals, host
114 populations and host communities, thus supplying metadata to explore macroecological patterns
115 expressed by host-parasite systems. Third, it is often technically difficult to use observations of a
116 host-parasite system at individual or species levels to characterize the relationships of the invasive
117 species with their new biota, and to predict what will happen within an ecosystem. Thus, a large,
118 macro-level analysis is needed. Finally, the comparison of parasite populations and communities at a
119 large scale in an invasive context may provide fresh insights to investigate the enemy release
120 hypothesis (ERH) and offer a useful tool for the evaluation of the invasive species integration in new
121 ecosystems. The ERH is based on two key predictions (Torchin and Lafferty, 2009): 1) introduced
122 populations lack natural enemies (i.e. parasites) compared to populations within their original range;
123 and 2) invasive species benefit from parasite-mediated competitive advantages because they are less

124 likely to be infected than their native competitors (Torchin and Lafferty, 2009). Macroecological
125 methods allow quantitative evaluation of both predictions of the hypothesis using comparative
126 analysis at a large spatial scale, for instance to match parasites of the same host species across its
127 native and introduced range and/or populations of an introduced host species with populations of
128 native species coexisting in sympatry.

129 Parasitology continues to suffer from the lack of large-scale comparative studies because of the
130 individually focused-research dimension (Guégan and de Magny, 2006) that is also true for studies
131 investigating alien species. Within the context of parasites from invasive hosts, three main phenomena
132 are usually considered: enemy release, parasite spillback and spillover (Kelly *et al.*, 2009; Peeler *et*
133 *al.*, 2011; Lymbery *et al.*, 2014; Chalkowski, Lepczyk and Zohdy, 2018). While testing the ERH
134 implies predominantly a comparative analysis of multispecies parasite data from different geographic
135 areas or host species (Bij de Vaate *et al.*, 2002; Ovcharenko *et al.*, 2009; Sarabeev, 2015a; Kvach *et*
136 *al.*, 2019; Ondračková *et al.*, 2019), studies on parasite spillback and spillover largely consider single
137 parasite species (Koops and Hartmann, 1989; Mo, 1994; Alderman, 1996; Tompkins *et al.*, 2000;
138 Daszak, Cunningham and Hyatt, 2003; Rauque, Viozzi and Semenas, 2003; Gozlan *et al.*, 2005;
139 Peeler *et al.*, 2011; Sarabeev, 2015b). Moreover, the analysis of parasite communities of invasive
140 hosts has been frequently limited to species richness, as it is the easiest metric to evaluate broad
141 patterns (Torchin and Mitchell, 2004; Torchin and Lafferty, 2009). Thus, studies of host-parasite
142 relationships in invasive species have largely focused on two main processes to investigate how a
143 particular co-introduced parasite can affect a native species or how the transmission of native
144 parasites can be enhanced by an introduced species. Although this approach is valuable, we propose
145 a new way to evaluate how invasive hosts integrate into new ecosystems by examining quantitative
146 parasite data derived from both populations and communities that emerge at a macroecological level.
147 Our *objective* is to enlarge the small-scale level (local and individual) on which the previous
148 investigations of parasites in invasive hosts have focused, and search for more general

149 macroecological patterns using recent dedicated methods, thus providing a new tool to assess and
150 manage bioinvasions.

151 Recently, researchers have shown an increased interest in using macroecological laws and
152 approaches in epidemiology and parasitology. The application of Taylor's power law to epidemiology
153 and evolutionary ecology of parasites have been discussed by Morand and Krasnov (2008). Based on
154 a thorough literature search, they argue that the values of slope b of Taylor's power law could reflect
155 regulation processes in host-parasite systems. Likewise, Pérez-del-Olmo et al. (2013) reviewed the
156 empirical findings of Rohde et al. (1995), Pérez-del-Olmo et al. (2011) and Thieltges et al. (2013)
157 about the spatial distribution of parasites, and proposed to use parasites' metapopulation structure and
158 dynamics as tools to evaluate the effects of anthropogenic disturbance. More recently, Stephens et al.
159 (2016) assessed macroecological tools in the light of understanding the ecology of global infectious
160 diseases. They demonstrated how emerging macroecological approaches can provide new insights
161 into scaling properties across all living taxa, and new strategies for mapping pathogen biodiversity
162 and infection risk. Thus, we believe this body of research together with our previous studies (Sarabeev
163 2015b; Sarabeev et al. 2017a, b, 2018, 2019) supply a basis to demonstrate how macroecological
164 tools can improve our understanding of the implications of the ERH and other host-parasite
165 relationships in invasive species.

166

167 **Shaping the parasite community of the invasive host**

168 Species translocation leads to a deep structural change in host's parasite fauna and disrupts the
169 equilibrium of the host-parasite system (Lymbery *et al.*, 2014; Chalkowski, Lepczyk and Zohdy,
170 2018; Llopis-Belenguer, Blasco-Costa, *et al.*, 2020). The parasite community of the invasive host can
171 be shaped by three main processes: release, co-introduction and acquisition of parasites (Fig. 1). The
172 ERH implies that parasite release is related to both resistance of the invasive host to native naïve
173 parasites in a new location and loss of its own parasites that occur in the area of origin. Loss and
174 resistance are not mutually exclusive and might be partial or total. The invasive host commonly brings

175 to the new region some of its parasite species, which can become co-introduced if they surmount
176 survival and reproductive barriers (Lymbery *et al.*, 2014). Note also that since parasite exchange
177 between sympatric host species is a common event, the invasive host may acquire local parasite
178 species in the invaded area (parasite spillover to the invasive host (Chalkowski, Lepczyk and Zohdy,
179 2018)). Then the invasive host can either transmit parasites back to native hosts (spillback) or can act
180 as a sink host in which parasite fitness is greatly reduced (Chalkowski, Lepczyk and Zohdy, 2018).

181

182 **Case Study**

183 *Studied hosts*

184 Our study system involves helminth parasites of the so-iuy mullet, *Planiliza haematocheila*
185 (Temminck & Schlegel), native to the Amur River estuary, Russia and the Sea of Japan, which was
186 deliberately introduced into the Azov-Black Seas in 70's of the last century (Occhipinti-Ambrogi and
187 Savini, 2003). In the Azov-Black Seas, its expansion corresponds to a sharp decline of native mugilid
188 species, which it replaces (Kottelat and Freyhof, 2007). Starushenko and Kazansky (1996) predicted
189 its movement towards the Mediterranean region, where it is recorded in the Aegean Sea since 1995
190 (Minos, Imsiridou and Economidis, 2010), but further expansion in the western direction has not been
191 reported (Minos's personal comments). Since one of the factors that confer resistance to invasions is
192 the native biodiversity of a recipient ecosystem (Miralles *et al.*, 2016), we assume that the further
193 expansion of the so-iuy mullet was stopped by the higher local biodiversity (of both free-living and
194 parasites (Surugiu *et al.*, 2010; Sarabeev, 2015a; Turan, 2016; Serena *et al.*, 2020)) and more
195 abundant schools of mugilids (author's personal observation) in the Mediterranean ecosystems when
196 compared with Azov-Black Seas.

197 In the new region of the Azov-Black Seas, this fish species co-occurs with the flathead mullet,
198 *Mugil cephalus* (L.). The Azov-Black Sea populations of the so-iuy and flathead mullets were
199 identified as potential competitors and formed mixed schools (Minos, Imsiridou and Economidis,
200 2010; Sarabeev, Balbuena and Morand, 2017a); these mugilid species display high trophic and niche

201 overlap and share most of their complex life cycle parasite species (Sarabeev, 2015a). Thus, we
202 compare data from helminth parasites of: (i) the same species (the so-iuy mullet) across native (in the
203 Japan Sea) and introduced (in the Azov-Black Seas) populations; and (ii) the population of an
204 introduced species (the so-iuy mullet) with a population of native species (the flathead mullet)
205 coexisting in sympatry in the Azov-Black Seas.

206

207 *Shaping helminth community of the so-iuy mullet in the Azov Sea*

208 The translocation of the so-iuy mullet has resulted in the co-introduction of six out of eight
209 strictly specific ectoparasitic monogenean species and in the acquisition of at least 19 endoparasitic
210 helminth species, including digeneans, acanthocephalans and nematodes (Sarabeev, 2015a).
211 Endoparasitic helminths include specific and nonspecific parasites with complex life cycles related
212 to the local fish community, mostly mullets (Sarabeev, Balbuena and Morand, 2017a). Thus, co-
213 introduced helminths with direct life cycle have surmounted survival and reproduction barriers,
214 whereas parasites with a complex life cycle did not and were completely lost in the new area.

215

216 *Database used*

217 We illustrate the methodological framework using a database of helminth parasites previously
218 collected from mugilids in two areas, the Sea of Japan and Azov-Black Seas (see Availability of data
219 and material), and described in Sarabeev (2015b). Parasites were collected according to a
220 standardized sampling protocol (Kostadinova *et al.*, 2004) across 12 localities and three seasons
221 (winter excluded) in 1998, 1999, 2004, 2005, 2009, 2011 and 2013 (Sarabeev, 2015a). All samples
222 were pooled together to comprise host-parasite information for: a) 204 and 427 individuals of *P.*
223 *haematocheila* and 21 and 25 helminth species from the Sea of Japan and Azov Sea, respectively;
224 and b) 185 individuals of *M. cephalus* and 20 helminth species in Azov-Black Seas. Although the
225 statistical hypotheses tested and the figures have been previously published (Sarabeev, 2015a;

226 Sarabeev, Balbuena and Morand, 2017a, 2018, 2019), all the figures presented here are rearranged or
227 regenerated to illustrate key patterns.

228

229 **Main concept**

230 Following Holmes and Price (1986) parasites can be studied at two levels, population and
231 communities. These in turn can be defined at the host individual and host population levels. In
232 ecological parasitology the prefix “infra-“ is used to refer to parasite populations or communities
233 studied at the host individual level, whereas “component” refers to populations or communities at
234 the host population level (Holmes and Price, 1986). Our concept relies on *the comparative analysis*
235 *of data sampled across regions and host species at different organizational (population vs.*
236 *community) and hierarchical (infra- vs. component community) levels of parasites* (Fig. 2). Such
237 an framework entails the use of a set of measurements, which are common in classical parasitology
238 and community ecology (Box I).

239

240 **Measures used**

241 The basic units characterising parasite quantity are infrapopulation size and infra-community
242 richness (Table I). Of these two parameters, the first one is more universal as it can be applied to
243 count both population and community characteristics of parasites, while the second one is used to
244 quantify communities. Prevalence, mean abundance and its variance are the basic descriptors of
245 parasites populations, which are also used as variables to evaluate their spatial and temporal
246 distribution. The local mean abundance of a given species is expected to be positively related to its
247 variance, and its probability of occurrence (i.e. prevalence) (Gaston *et al.*, 2006). These
248 intraspecific/interspecific abundance-occupancy (AOR) and abundance-variance (AVR)
249 relationships are used as two general macroecological patterns capturing essential fundamentals of
250 the structuring of species distributions (Morand and Guégan, 2000; Gaston *et al.*, 2006; Morand and
251 Krasnov, 2008; Pérez-del-Olmo *et al.*, 2011). The slope of the AVR is broadly accepted as a universal

252 parameter describing the aggregation of organisms (Wilson *et al.*, 2002; Morand and Krasnov, 2008;
253 Pérez-del-Olmo, Kostadinova and Morand, 2013; Ma, 2015) and comes from Taylor's (Taylor, 1961)
254 power law (Box 1). In its original interpretation (Taylor, 1961; Taylor and Taylor, 1977) the power
255 law characterizes the population abundance distribution within a single species, but it has been
256 recently extended to characterize the species abundance distribution within a community (Krasnov *et*
257 *al.*, 2006; Ma, 2015). Both the population and species abundance distribution of helminth parasites,
258 the latter at infra- and component community levels, were estimated and compared between native
259 and invasive host populations in our studies (Sarabeev, Balbuena and Morand, 2017a, 2019) (Fig.
260 3A-D and 4A-D; Table I). Parasite diversity was evaluated with the help of individual and total
261 species richness measured for a host individual or sample, respectively (Sarabeev, 2015a). The use
262 of alternative approaches describing the parasite community structure (e.g. analysis of beta-diversity)
263 to compare native and invasive host populations might be also useful (Llopis-Belenguer, Pavoine, *et*
264 *al.*, 2020), but has been not performed to date.

265 The findings of our studies (Sarabeev, 2015a; Sarabeev, Balbuena and Morand, 2017a, 2018,
266 2019) on infection parameters of the introduced so-iuy mullet are in agreement with the ERH except
267 for the total species richness. Although the introduced host appears to have accumulated a larger
268 number of new parasite species in the introduced range (Kostadinova, 2008; Sarabeev, 2015a), the
269 numbers of newly acquired species do not compensate for the number of parasite individuals that it
270 escaped. The introduced host was less heavily parasitized than its native counterpart and the sympatric
271 flathead mullet. This is clear from mean individual parasite species richness (Fig. 5C), mean
272 abundance and prevalence (Sarabeev, 2015a; Sarabeev, Balbuena and Morand, 2017a, 2018, 2019).
273 However, host translocation affects co-introduced and acquired groups of helminth parasites in a
274 different manner (Sarabeev, 2015a; Sarabeev, Balbuena and Morand, 2017a, 2018, 2019; Shvydka *et*
275 *al.*, 2020). Co-introduced parasites largely hold similar infection characteristics and distribution
276 patterns compared with their native area (Fig. 5B,D; Fig. 3A,C; Fig. 4B,D,F), while acquired
277 helminths sharply differ in these parameters when compared with the same taxonomic group of

278 parasites occurring in the native host populations (Fig. 5A,E; Fig. 3B,D; Fig. 4A,C,E). This similarity
279 in infection parameters and distribution patterns of monogeneans in the native and invasive host
280 populations was explained by the repeatability and identity of the host-parasite systems (Sarabeev,
281 Balbuena and Morand, 2018).

282

283 **Disentangling host-parasite relationships in the introduced host**

284 ***Frequency distributions***

285 The *frequency distribution of individual parasite species richness* (IPSR) can be a *first-line*
286 *indicator* of the antagonistic host-parasite relationships of the invasive host with acquired parasites.
287 The acquired parasites showed an aggregated (right-skewed) distribution for species number in infra-
288 communities (Fig. 5A). In contrast, random distribution of IPSR was found for co-introduced
289 monogeneans and in native populations of the so-iuy and flathead mullets (Fig. 5A and B). It is
290 commonly argued that infra-communities are random species assemblages if host individuals harbour
291 random samples of the parasites available in the environment (Poulin, 1997). Thus, the random
292 distribution of parasite species number in native host population may indicate that this host-parasite
293 system is in equilibrium and there are no effects of host on helminth species number or interspecific
294 parasite interactions in infra-communities, or parasite-induced host mortality (Shaw, Grenfell and
295 Dobson, 1998; Wilson *et al.*, 2002). In contrast, aggregated distribution may arise in new host-parasite
296 systems, in which the associations are imbalanced due to the absence of a common evolutionary
297 history. The most probable scenario is that native naïve helminth species are less able to infect the
298 new host and then tend to aggregate in a small portion of susceptible (or competent) host individuals,
299 while the largest portion of fish remain uninfected or infected by a few species (Sarabeev, 2015a).

300 Similarly, in the so-iuy mullet, *a unimodal, right-skewed frequency distribution of prevalence*
301 was common for the acquired higher level taxonomic groups of helminth parasites (digeneans,
302 acanthocephalans and nematodes) in the introduced range, whereas a bimodal distribution was more
303 common in the native range (Sarabeev, Balbuena and Morand, 2018). The right-skewed distribution

304 pattern of prevalence indicates that there are no species in the community able to infect the whole
305 host population (i.e. 90-100% host individuals in population). The bimodality was observed for
306 evolutionarily-established host-parasite systems, likely because of a strong rescue effect (Sarabeev,
307 Balbuena and Morand, 2018). Although frequency distribution of prevalence might be a useful
308 indicator for estimating the maturity of the establishment of an invader in an ecosystem, both bimodal
309 and unimodal patterns have been reported for metazoan parasites of native host populations (Poulin,
310 1999; Morand and Guégan, 2000; Šimková *et al.*, 2002; Pérez-del-Olmo *et al.*, 2011; Sarabeev,
311 Balbuena and Morand, 2018).

312 The frequency distribution of the total numbers of parasite individuals in infra-communities
313 also provides an informative pattern of host-parasite relationships in the invasive host (Fig. 5D,E)?.
314 The groups of helminths acquired in the invasive population of the so-iuy mullet display a **higher**
315 **number of uninfected hosts and a shorter distribution tail** compared with its native counterpart and
316 the flathead mullet with which it co-occurs in the new region (Sarabeev, Balbuena and Morand,
317 2017a). The proportion of susceptible individuals to parasite-related diseases is expected to be lower
318 in the invasive host because of a shorter distribution tail of parasite abundance (i.e. lower number of
319 heavily infected hosts).

320

321 *Macroecological models*

322 The slope b of AVRs as a measure of aggregation is also helpful to characterize host-parasite
323 relationships in the invasive host. This parameter estimated for the parasite population and species
324 abundance distributions revealed similar and paradoxical results when the native and introduced
325 helminth populations of the so-iuy mullet were compared. The absence of significant differences in
326 b between monogeneans in both regions was confirmed at the population and community levels (Fig.
327 3A,C and 4B,D). It is explained by the repeatable infection and aggregation parameters for the same
328 host-parasite system (Sarabeev, Balbuena and Morand, 2018, 2019). The **acquired endoparasitic**
329 **helminths showed a general tendency to be more aggregated in populations and less aggregated in**

330 **communities** when compared with parasites of native hosts (Fig. 3B,D vs. 4A,C) (Sarabeev, Balbuena
331 and Morand, 2017a, 2019). Since b values estimated for populations and communities actually
332 represent different types of sampling data, their parameters have different biological interpretations
333 (Ma, 2015). Sarabeev et al. (Sarabeev, Balbuena and Morand, 2017a, 2019) propose two reasons for
334 this pattern: (i) Because acquired parasite species commonly show extremely low infection
335 parameters, the invasive host individual has an approximately equal negative effect on any
336 encountered species; (ii) highly infected individuals could be removed from the population due to
337 parasite-induced host mortality (Sarabeev, 2015b). Assumptions inferred from different types of
338 sampling data agree well with each other and support the suggestion that a large part of the introduced
339 host population remains uninfected due to host resistance to parasites of the invaded range. This
340 contention is further supported by AORs. The **regression line of AORs move along the abundance**
341 **axis and the slope b is lower** for the acquired groups of helminths compared with parasites from
342 native hosts (Fig. 4E). This indicates a tendency of helminths to accumulate in infra-communities of
343 a small portion of susceptible host individuals. Furthermore, the study of macroecological patterns of
344 helminths distribution leads to the conclusion that encounter an infected hosts with (i) the same
345 parasite species will increase infra-population size, increasing population aggregation as an
346 adaptation to mating opportunities; and with (ii) another parasite species may not result in new
347 infection due to interspecific competition, strongly mediated by the host defence system, thus
348 decreasing community aggregation (Sarabeev, Balbuena and Morand, 2019).

349

350 ***Distinguishing co-introduced and acquired parasites***

351 The variety of measurements for populations, infra- and component communities of parasites
352 offers an opportunity to identify the **set of indicators** to distinguish the origin of parasite species.
353 First, since co-introduced and acquired helminths occupy different spatial distribution scales, they are
354 detectable on both macroecological models, AVRs and AORs. The charts of both relationships show
355 that populations of acquired helminths are mainly aggregated in the lower left quadrant as opposed

356 to co-introduced monogeneans and those from the native host, which stretch across the entire plot
357 area or allocated in its upper right quadrant (Fig. 3 and 4). Second, the core-satellite species
358 hypothesis on parasites of invasive host suggests that co-introduced ectoparasitic monogeneans are
359 the only core species in the introduced range, while acquired endoparasitic helminths (digeneans,
360 acanthocephalans and nematodes) infect a small portion of the introduced host population with low
361 mean abundance and are satellite (Sarabeev, Balbuena and Morand, 2018). The recently proposed
362 “Fuzzy Quantification of Common and Rare Species in Ecological Communities” (Balbuena *et al.*,
363 2021) is a useful tool to categorize communities and to reveal co-introduced parasites. Third, as it has
364 been shown above, co-introduced parasites may demonstrate the abundance distribution tail, which
365 is much longer than for acquired parasites (Fig. 5D,E). Finally, the frequency distribution of the IPSR
366 of acquired parasites is characterized as right-skewed, while it is random for co-introduced species
367 (Fig. 5A,B) (Sarabeev, 2015a). To summarize, the macroecological models, core-satellite species
368 hypothesis, patterns of frequency distribution of the number of parasite individuals in a host and IPSR
369 provide tools to distinguish co-introduced and acquired parasites in communities of an invasive host
370 based on quantitative descriptors.

371

372 **Concluding remarks and future perspectives**

373 Understanding the relationships between the structure and function of biological communities
374 is crucial for monitoring and control bioinvasions. Although the ERH is a very prominent and
375 synthetic theory (Chalkowski, Lepczyk and Zohdy, 2018), it overlooks processes acting in host-
376 parasite systems at the population and individual level, which are important to identify the role of
377 parasites in the invasion process. *The innovative concept presented here combines the data inferred*
378 *from populations, infra- and component communities of parasites and the application of a*
379 *macroecological approach in the analysis of complex and frequently hidden relationships in host-*
380 *parasite systems*. Our framework can produce mechanistic explanations of the ERH and unravel host-
381 parasite relationships of an invasive host and its parasites at the population level. Our basic

382 assumption is that in the invaded community a mature or evolutionary established host-parasite
383 system of the invasive host and acquired native parasites will display the same infection and
384 distribution patterns as other co-occurring hosts inhabiting an ecosystem. In addition, considering the
385 nature of parasite origin and distinct patterns of their spatial distribution, AVRs and AORs, core-
386 satellite species hypothesis, patterns on the aggregation and the frequency distribution of prevalence,
387 infrapopulation size and individual parasite species richness represent indicators for the quantitative
388 differentiation of co-introduced and acquired parasites. ***The proposed framework can be used to***
389 ***assess how invasive hosts integrate new ecosystems.*** In this regard, we think that network analysis
390 of the host-parasite system opens an avenue of further research, providing a tool to study host-parasite
391 interactions and to predict the possible impact of biological invasions on ecosystems (Llopis-
392 Belenguer, Blasco-Costa, *et al.*, 2020; Llaberia-Robledillo *et al.*, 2021).

393 Despite these encouraging findings, the current study is limited to a single invasive host and
394 encompassing ectoparasitic and endoparasitic subsets of species. Therefore, future research should
395 address other host-parasite systems to ***evaluate the recurrence of specific patterns*** described here.
396 Moreover, by considering parasite subsets according to transmission mode, we can obtain additional
397 insights into understanding host-parasite relationships of invasive hosts (e.g. Llopis-Belenguer *et al.*
398 2020a; Llaberia-Robledillo *et al.* 2021). The key objective of both the researchers and stakeholders
399 is a search for effective and safe methods to control invasive species in an ecosystem, while the
400 framework described here can be used as a tool to assess the suppressive effect of parasites on host
401 populations. In macroparasites, host mortality and morbidity display dose-dependent relationships
402 and thus parasites have the greatest effect on individuals in the tail of the parasite distribution (Wilson
403 *et al.*, 2002). The indicators proposed herein, such as AVRs and AORs, aggregation indices and the
404 frequency distribution of prevalence and abundance, are helpful to measure the proportion of
405 susceptible host individuals in this tail. This approach has been partially implemented to evaluate the
406 effect of native naïve parasites on juveniles of the invasive so-iuy mullet in the Sea of Azov. It has
407 been shown that larval digeneans are associated with the mortality of juvenile *P. haematocheila*. Fish

408 loss due to parasites was estimated to be over 50% for the first-year cohort born in the Molochny
409 Estuary (Sarabeev, 2015b). In this context, future research should concentrate on the evaluation of a
410 *suppressive spillover effect of parasites* on invasive species. This concept, recently introduced by
411 (Chalkowski, Lepczyk and Zohdy, 2018), assumes that parasites could suppress the ability of
412 introduced species to expand and hence become invasive. This is because they may affect host fitness,
413 fecundity and survival rate (Bittner, Rothhaupt and Ebert, 2002; Sarabeev, 2015b; Flink, Behrens and
414 Svensson, 2017; Chalkowski, Lepczyk and Zohdy, 2018) and thus reduce the abundance of invasive
415 species in an ecosystem. Finally, we hope that our framework becomes widely applied as it can
416 potentially contribute to enhance future practice and research in biodiversity conservation and control
417 of invasive species.

418

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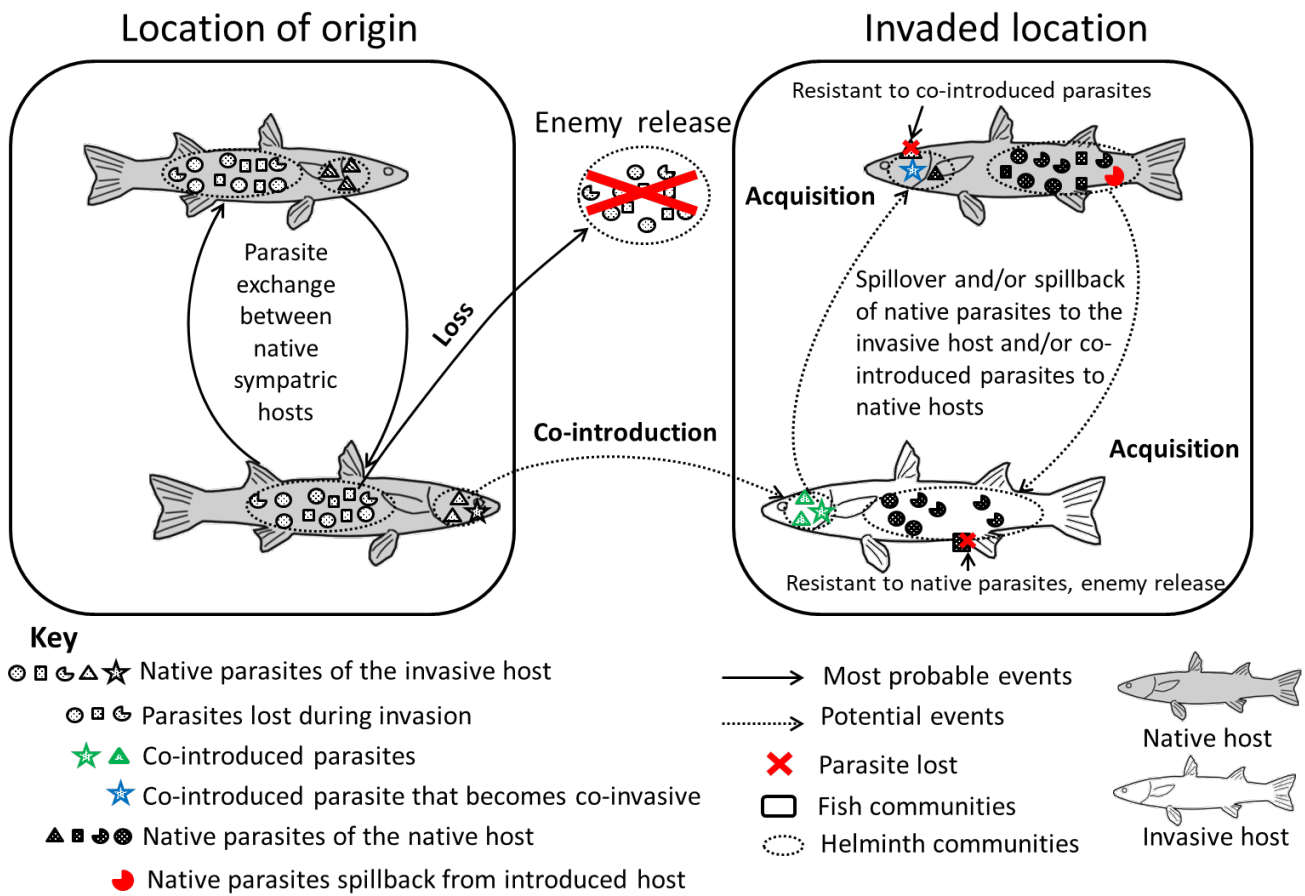
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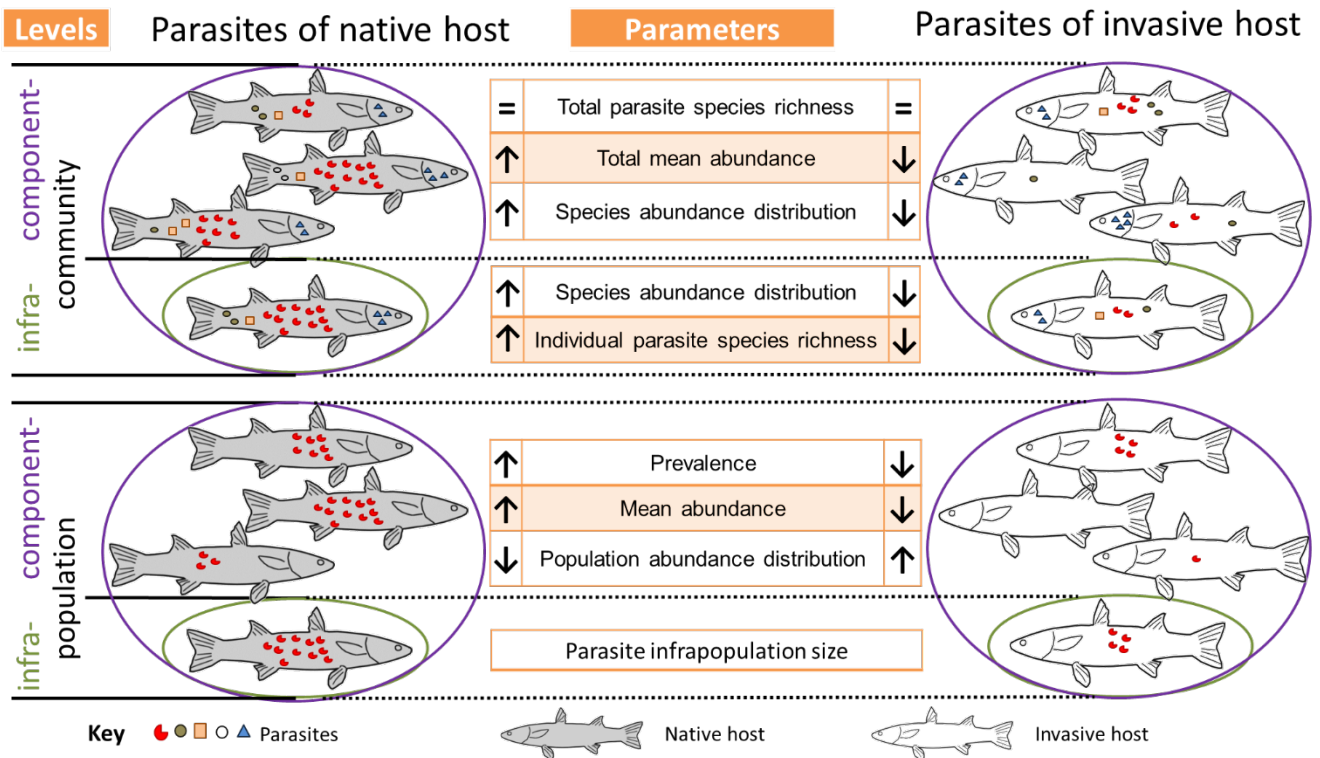
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643

644 **Fig. 1.** Potential changes in parasite community structure in an introduced host. The most probable
 645 scenario is the enemy release, where the invasive host is resistant to parasites in the invaded location
 646 and/or loses its own parasites from the location of origin. The invasive host commonly colonise a
 647 new region with some of its parasite species, which can become co-introduced or co-invasive. Co-
 648 introduced parasites turn into co-invasive if they surmount dispersal barriers and colonise new host
 649 species (Lymbery *et al.*, 2014) (parasite spillover to native host (Chalkowski, Lepczyk and Zohdy,
 650 2018)). In the invaded region invasive host may acquire new parasite species as a result of parasite
 651 exchange between sympatric hosts (parasite spillover to invasive host (Chalkowski, Lepczyk and
 652 Zohdy, 2018)). Invasive host infected with native parasites expanding their host range may transmit
 653 back these parasites to native hosts (parasite spillback) or not, then becoming a sink host (Chalkowski,
 654 Lepczyk and Zohdy, 2018)

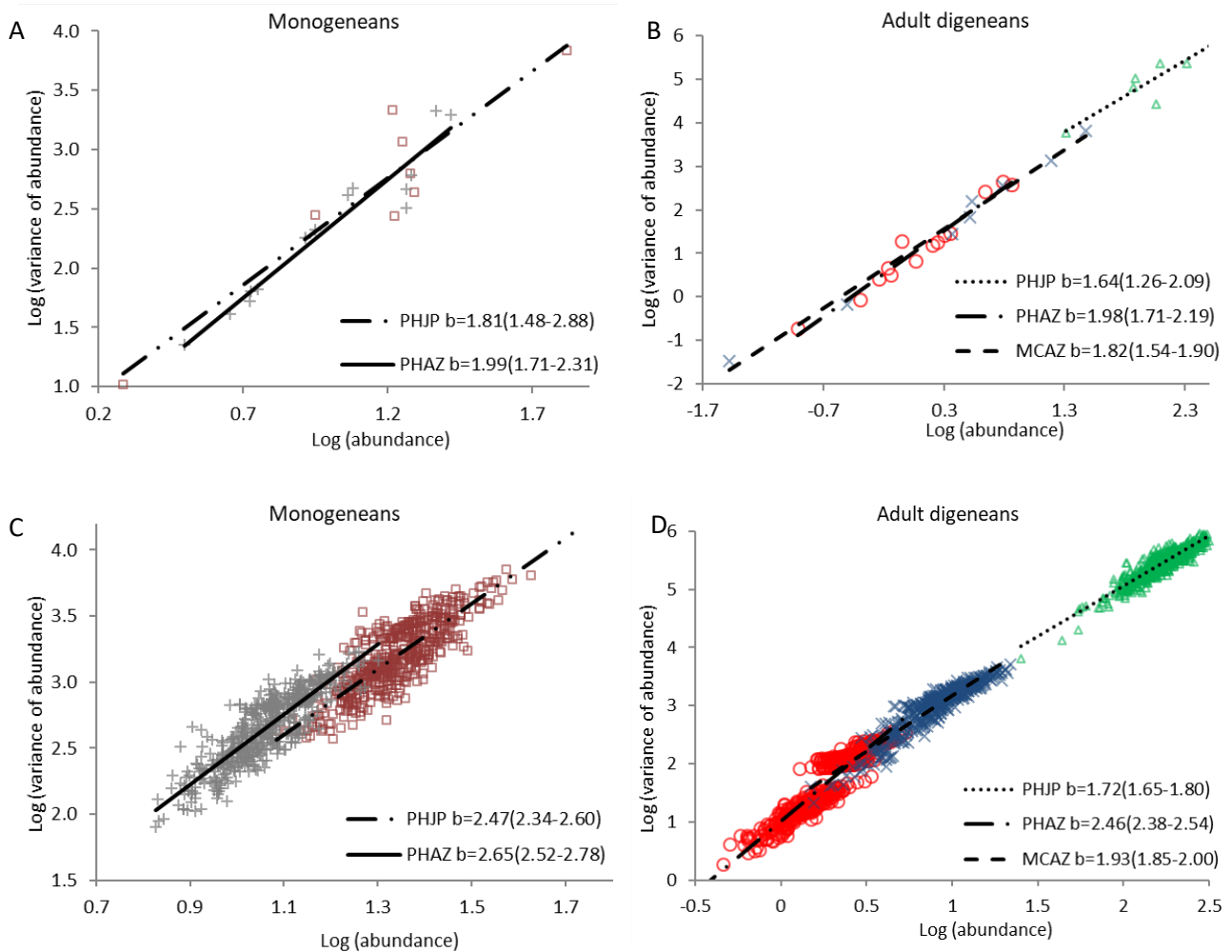
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656

657 **Fig. 2.** Diagram summarizing the main findings obtained with the framework proposed. The
 658 framework is based on the comparative analysis of epidemiological and ecological parameters of
 659 parasite populations and communities from native and invasive species at host individual and
 660 population levels (indicated herein as infra- and component- levels following Holmes and Price
 661 (1986)). Parasite infrapopulation size as the basic unit was used to obtain various parameters. In
 662 agreement with the Enemy Release Hypothesis, introduced mullets were less heavily parasitized than
 663 their native counterparts both in terms of prevalence and abundance at community and population
 664 levels. In contrast, parasites in invasive hosts tended to be more aggregated in populations and less
 665 aggregated in communities than parasites in native hosts. Similarly, patterns of parasite species
 666 richness at the component and infra-community levels differed. Thus, the same parameters estimated
 667 at different organizational levels may indicate opposite trends because they convey information at the
 668 specific level considered. This comparative approach can therefore provide a more complete picture
 669 of host-parasite relationships in invasive and native hosts that can ultimately improve our
 670 understanding of the success of an invasive species in a new area.

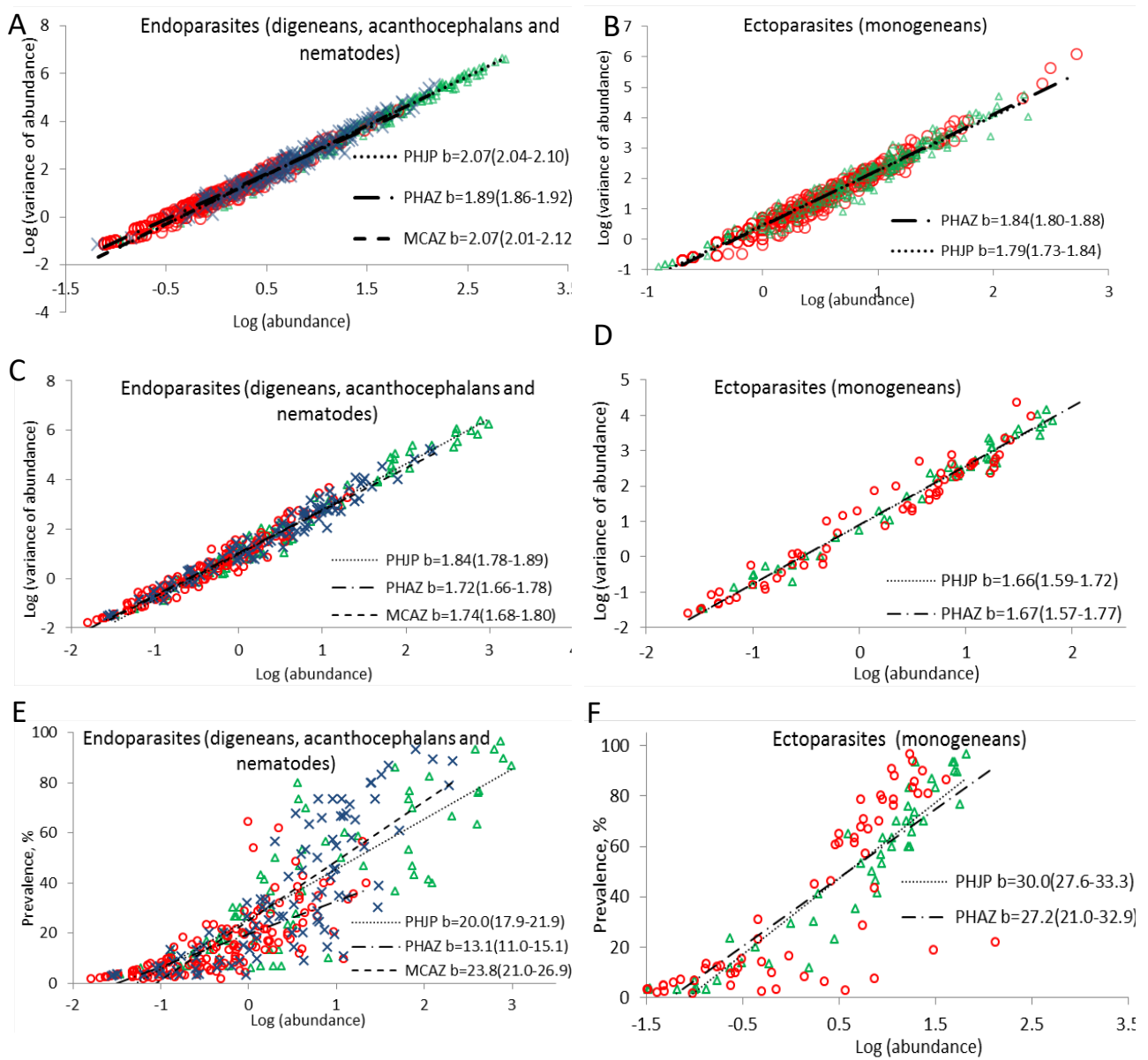
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672

673 **Fig. 3.** Abundance-variance relationships (AVR) of parasite population fitted to a power function (A-
 674 D). Charts and b values are obtained directly from empirical (A and B) and bootstrapped datasets (C
 675 and D) (Sarabeev, Balbuena and Morand, 2019). Values of the slope b and 95% bootstrap confidence
 676 intervals are shown in the legend. A and C AVRs of the ectoparasitic monogeneans *Ligophorus*
 677 *pilengas* from *Planiliza haematocheilus* across its native (PHJP, brown square, double-dotted-dashed
 678 line) and invaded locations (PHAZ, grey cross, solid line) in the Sea of Japan and Azov Sea,
 679 respectively. B and D AVRs of the endoparasitic digeneans *Pseudohapladena mugili* from *P.*
 680 *haematocheilus* in the native range, the Sea of Japan (PHJP, green triangle, dotted line), and
 681 *Saccocoelium tensum* from native *Mugil cephalus* (MCAZ, blue cross, dashed line) and invasive *P.*
 682 *haematocheilus* (JPAZ, red open point, dotted-dashed line) host species in the Azov Sea.

683



684 **Fig. 4.** Relationships between the abundance-variance (A-D) and abundance-occupancy
 685 (prevalence) (E and F) of species in infra- (A and B) and component (mixed population-species data)
 686 communities of parasites (C-F). Datasets are fitted to a linear function for endo- (A, C and E) and
 687 ectoparasitic helminths (B, D and F) occurring in the invasive *Planiliza haematocheila* from the Azov
 688 Sea (PHAZ, red open point, dotted-dashed line), the native population of the same host from the Sea
 689 of Japan (PHJP, green triangle, dotted line) and the native *Mugil cephalus* from the Azov-Black Seas
 690 (MCAZ, blue cross, dashed line). Values of the slope b and 95% bootstrap confidence intervals are
 691 shown in the legend.

692

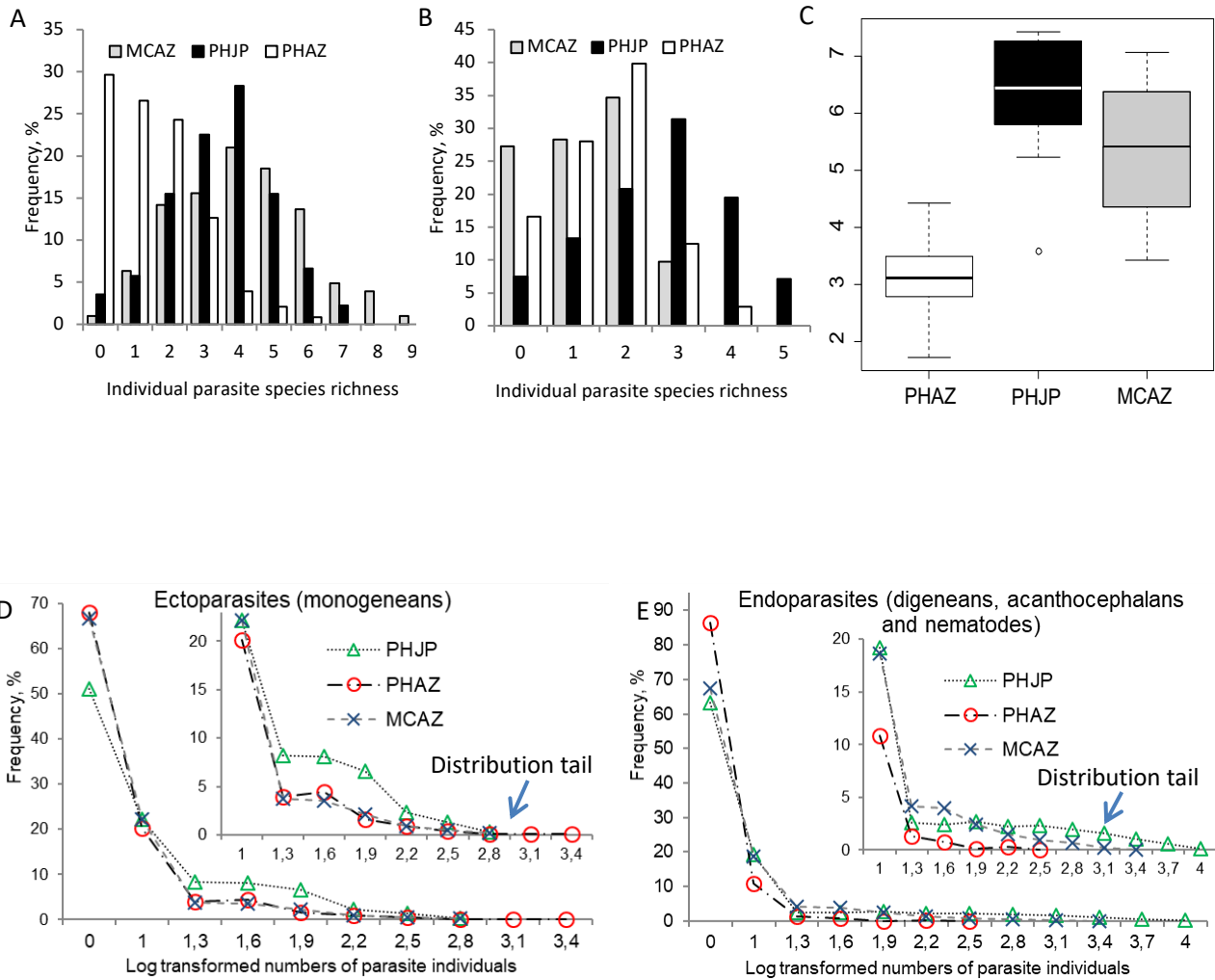


Fig. 5. Frequency distribution of the individual parasite species richness (**A** and **B**) and the total numbers of parasite individuals in infra-communities (**D** and **E**) of endoparasitic taxa (digeneans, acanthocephalans and nematodes) (**A** and **E**) and ectoparasitic monogeneans (**B** and **D**); and boxplot of mean individual parasite species richness of the whole helminth community (**C**) in populations of grey mullet fish. The inserts in **D** and **E** display the frequency distributions of parasite abundance excluding zero observations. Legend: parasites of *Planiliza haematocheila* in the invasive area of the Azov Sea (PHAZ), and in the location of origin of the Sea of Japan (PHJP); parasites of native *Mugil cephalus* from the Azov-Black Seas (MCAZ).

695 **Box 1. Descriptors of parasite populations and communities**

696 *Populations (Table I, green strip):*

697 Prevalence, intensity and mean abundance (see Bush et al. (Bush *et al.*, 1997)) are the main
698 infection parameters for assessing parasite burden on host population and testing the Enemy Release
699 Hypothesis.

700 Among a number of available parameters describing the aggregation (for review see Wilson et
701 al. (Wilson *et al.*, 2002)), the slope b of the Taylor's power law is considered as being the most
702 reliable measure (Wilson *et al.*, 2002; Morand and Krasnov, 2008; Pérez-del-Olmo, Kostadinova and
703 Morand, 2013; Ma, 2015). This parameter can be derived from the Taylor's power law relationship,
704 $V=am^b$, where m is the temporal or spatial mean abundance of population and V its variance.
705 Abundance and variance values are often fitted to a linear regression to estimate b after a *log-log*
706 transformation (Morand and Krasnov, 2008). The classical approach proposed by Taylor (Taylor,
707 1961) requires different samples to calculate b for a single species. However, the bootstrapping
708 technique proposed by Boag et al. (Boag *et al.*, 2001) and further developed by Sarabeev et al.
709 (Sarabeev, Balbuena and Morand, 2019) allows estimating b empirically from abundance data of a
710 single parasite population (Fig. 3).

711

712 *Infra-communities (Table I, yellow strip):*

713 Individual parasite species richness (IPSR) is counted as the sum of helminth species per
714 individual fish. This parameter is evaluated as its mean and frequency distribution in comparative
715 analysis (Sarabeev, 2015a) (Fig. 5A-C). The mean of IPSR is counted for a given sample including
716 both infected and uninfected host individuals.

717 Relative mean abundance and its variance are counted for the species infra-population size of
718 each host individual in a sample regardless of whether or not the parasite species is present in the
719 given host. The slope b is estimated from pairs of the relative mean abundance and its variance

720 regressed across the host sample to characterise species abundance distribution in infra-communities
721 (Fig. 4A, B).

722

723 *Component communities (Table I, orange strip):*

724 Total mean abundance was proposed to distinguish total parasite abundance estimated per
725 sample from relative abundance counted for a single host individual (Sarabeev, Balbuena and
726 Morand, 2017a). The total mean abundance is the number of individuals of all parasites species in a
727 community per sample divided by the total number of host individuals examined in that sample
728 (including both infected and uninfected hosts). Total parasite species richness is the number of
729 parasite species present in the community (Walther and Morand, 1998).

730 The slope b is estimated from $m-V$ pairs characterizing the parasite population regressed across
731 species in a given sample, then representing mixed species-population data of parasites (Fig. 4C, D).
732 Similarly, the mixed species-population data of the mean and prevalence across samples for a given
733 host species and geographic location is used to obtain the slope b for the abundance-occupancy
734 relationships (Fig. 4E, F).

735

736 **Table I.** Set of metrics and indicators used to compare infection and dispersion patterns of parasites in native
 737 and invasive hosts

	PS1 ²	PS2	PS3	...	PS _i		
	PICR ³					Characteristics of infra-communities	*Individual parasite species richness, its mean and frequency distribution
HI1 ¹	4	0	109	PIPS ⁴	0		Relative mean abundance
HI2	3	0	0	PIPS	0		Relative variance of the mean
HI3	0	16	1	PIPS	0		Species abundance distribution in infra-communities
...	PIPS	PIPS	PIPS	PIPS	PIPS		
HI _i	0	0	5	PIPS	37		
Characteristics of populations	Prevalence					Characteristics of meta/component communities	Total parasite species richness
	Mean abundance						Total mean abundance
	Variance of the mean abundance						Species abundance distribution in component communities
	Population abundance distribution						*Abundance-occupancy and abundance-variance relationships of component communities
	*Abundance-occupancy and abundance-variance relationships of species						*Core/satellite species classification
						*Frequency distribution of the total numbers of parasite individuals in infra-communities	

738 Footnote: ¹HI, host individual; ²PS, parasite species; ³PICR parasite infra-community richness; ⁴PIPS, parasite
 739 infrapopulation size; *the proposed set of indicators to distinguish the origin of parasite species (see the text for
 740 details.

742 **Glossary**

743 **Parasite abundance:** number of individuals of a particular parasite in a single host whether or not
 744 the host is infected (Bush *et al.*, 1997).

745 **Co-introduced parasite:** applies to a parasite transported with an introduced host to a new location,
 746 outside its natural range (Lymbery *et al.*, 2014).

747 **Co-invasive parasite:** a parasite which was co-introduced and then spread to a new, native host
 748 (Lymbery *et al.*, 2014).

749 **Component community:** all infrapopulations of parasites associated with a host sample at a
 750 particular time/locality (Bush *et al.*, 1997).

751 **Infra-community:** a community of parasite infrapopulations in a single host (Bush *et al.*, 1997).

752 **Infrapopulation:** includes all individuals of a species in an individual host at a particular
 753 time/locality (Bush *et al.*, 1997).

754 **Invasive:** an introduced species which become established in a new geographic area and expanded
755 its range (Lymbery *et al.*, 2014).

756 **Native naïve:** parasite or host species which lacks coevolutionary adaptations and therefore more
757 likely suffers greater immunologic or pathogenic consequences, respectively, from infection
758 (Allison, 1982; Lymbery *et al.*, 2014).

759 **Native:** parasite or host species occurring within its natural range, independent of human activity
760 (Lymbery *et al.*, 2014).

761 **Parasite infrapopulation:** includes all individuals of a species in an individual host at a particular
762 time.

763 **Prevalence (occupancy):** number of hosts infected divided by the number of hosts examined for a
764 given parasite species in a sample an expressed as a percentage

765 **Spillback:** occurs when the introduced host becomes infected with a parasite species from the native
766 hosts, followed by subsequent transmission back to native hosts (Kelly *et al.*, 2009;
767 Chalkowski, Lepczyk and Zohdy, 2018).

768 **Spillover:** occurs when a parasite typical for one host species becomes also infective for a new host
769 when geographical barriers are removed (Chalkowski, Lepczyk and Zohdy, 2018).

770 **Suppressive spillover:** when a parasite infects an introduced host species and the range of the
771 introduced host species is suppressed as a result of this interaction (Chalkowski, Lepczyk and
772 Zohdy, 2018).

773