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Advances and challenges in modelling the impacts of invasive alien species on aquatic ecosystems

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Advances and challenges in modelling the impacts of invasive alien

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24

25 **Abstract**

26 Invasive alien species (IAS) have become an important driver of biodiversity change
27 and have exerted severe pressure on natural ecosystems. The development of modelling
28 approaches to assess and predict their distributions and impacts, and evaluate
29 management options has increased substantially.

30 We reviewed these modelling approaches, applied in aquatic ecosystems, using a
31 systematic review approach in line with the Preferred Reporting Items for Systematic
32 Reviews and Meta-analyses (PRISMA). According to our results,
33 multispecies/ecosystem models dominated the applications, with dynamic and non-
34 spatial models being the most prevalent. Most of the models included an additional
35 stressor, mainly fisheries, climate change or nutrient loading. The impacts on biota
36 focused on predation, but also on competition and ecosystem functions, while the
37 impacts on ecosystem services focused on food provisions and water purification. At
38 species/population level, most of the studies reported negative impacts; while at
39 multispecies/ecosystem level, negative and both negative and positive impacts were
40 similarly represented.

41 We reflect on the ability of current models to assess different impacts of IAS
42 populations and highlight the need to advance their capabilities to predict future
43 impacts. Models that allow capturing the arrival, establishment and spread of IAS and
44 assess their impacts in an integrated way are still missing. Future development of
45 spatial-temporal modelling techniques bridging with novel analytical capabilities (such
46 as environmental DNA to investigate the presence of IAS and metabarcoding and
47 machine learning to predict future trophic behavior and distributions) may be the key
48 for future achievement and needed contributions to the development of scenarios of
49 global change and management alternatives.

50

51 **Keywords:** Invasive alien species; impacts; modelling; marine ecosystems; freshwater
52 ecosystems; PRISMA.

53

54

55 **Highlights**

56 • We reviewed past and state-of-the-art modelling approaches to assess impacts of
57 invasive alien species (IAS) in aquatic ecosystems.

58 • Multispecies/ecosystem models dominated, with dynamic and non-spatial
59 models being the most prevalent.

60 • We summarised the main features of available approaches and analysed their
61 capabilities and limitations.

62 • We highlighted the need to advance the capabilities of models to predict future
63 impacts of existing, emerging and potential new IAS.

64 1. Introduction

65 Biological invasions are currently one of the most important drivers of biodiversity
66 change and exert severe pressure on terrestrial, freshwater and marine ecosystems, with
67 both ecological and economic impacts ([Bax et al., 2003](#); [Simberloff et al., 2013](#);
68 [Gallardo et al., 2016](#)). Alien species (also known as exotic, introduced, allochthonous,
69 non-indigenous or non-native species) are any taxa crossing biogeographic barriers that
70 were introduced outside their natural past or present distribution by human agency,
71 including any part, gamete seeds, eggs, or propagules that might survive and
72 subsequently reproduce ([Essl et al., 2018](#)). Invasive alien species (IAS) are defined as
73 those alien species whose introduction or spread threaten biological diversity ([CBD,](#)
74 [2002](#)). Many organizations and states, e.g. the European Union (Regulation 1143/2014),
75 include in the definition of IAS not only impacts on biodiversity but also on ecosystem
76 services. The impacts of IAS can be detected at any biological level, ranging from
77 changes in the genetic diversity of native species to species extinction and alterations of
78 an entire ecosystem ([Grosholz, 2002](#); [Strayer, 2010](#); [Levin and Crooks, 2011](#)), and
79 include impacts on ecosystem services ([Pejchar and Mooney, 2009](#); [Katsanevakis et al.,](#)
80 [2014b](#); [Vilà and Hulme, 2017](#)).

81 Humans have traded and, intentionally or unintentionally, transported alien species for
82 millennia, but the rapid globalization and increases in trade and transport capacity in
83 recent decades have accelerated biological invasions, despite growing national and
84 international efforts to reduce invasion risk ([Hulme, 2009](#); [Katsanevakis et al., 2013b](#);
85 [Nunes et al., 2015](#); [Seebens et al., 2017](#)). In addition, biological invasions interact with
86 other stressors such as climate change, habitat degradation and loss, overexploitation
87 and pollution, which compromise the integrity of aquatic ecosystems ([Dudgeon et al.,](#)
88 [2006](#); [Halpern et al., 2015](#)). Because disturbance is generally thought to favour
89 invasions, stressed ecosystems may more easily be colonised by alien species
90 ([Occhipinti-Ambrogi and Savini, 2003](#); [Strayer, 2010](#)). Current levels of ecosystem
91 disturbance can explain the unprecedented rates of species extinctions and introductions
92 observed in aquatic ecosystems ([Miller et al., 1989](#); [Byrnes et al., 2007](#)). These
93 biodiversity changes, in turn, are leading to a general biotic homogenisation ([Rahel,](#)
94 [2002](#); [Sala and Knowlton, 2006](#)). Moreover, the impacts of IAS are projected to further
95 increase, especially due to climate change ([Walther et al., 2009](#); [Raitzos et al., 2010](#)).

96 There are many examples of large-scale and dramatic effects of IAS in aquatic
97 ecosystems. For example, 821 alien species have been recorded to date in the
98 Mediterranean Sea, of which more than half are considered established and spreading
99 ([Galil et al., 2014](#); [Katsanevakis et al., 2014a](#); [Zenetos et al., 2017](#)). The Mediterranean
100 Sea, in fact, is one of the most invaded regions in the world ([Molnar et al., 2008](#);
101 [Costello et al., 2010](#)) and its ecosystems have been significantly impacted, with declines
102 in abundance, modifications of biodiversity patterns and local extirpations concurrent
103 with IAS (e.g., [Galil, 2007](#); [Sala et al., 2011](#); [Edelist et al., 2013](#); [Katsanevakis et al.,](#)
104 [2014a](#)). The Laurentian Great Lakes, in North America, are among the most highly
105 invaded freshwater ecosystems in the world with over 180 IAS ([Ricciardi, 2006](#)). These
106 invasions have altered biodiversity, habitat structure, productivity, water quality,
107 contaminant cycling and ecosystem services ([Kelly et al., 2009](#)). The introduction of the
108 Nile perch (*Lates niloticus*) in Lake Victoria, Africa, to stimulate fisheries resulted in a
109 dramatic regime shift, where the very diverse and complex haplochromine-based
110 ecosystem was replaced by a system dominated by only a few species ([Goudswaard et](#)
111 [al., 2008](#)).

112 Studying the impacts of IAS in aquatic ecosystems is challenging due to: (1) the
113 dynamic and complex nature of natural ecosystems; (2) limitations of methodological
114 tools, which include uncertainties in field surveys ([Katsanevakis et al., 2012](#)) and
115 limitations of models (e.g. due to data available, complexity of models and how
116 processes are represented mathematically) ([Fulton et al., 2003](#); [Evans et al., 2013](#)); and
117 (3) a general lack of knowledge about IAS and their invading processes, which include,
118 the factors that affect the introduction and subsequent spread, a time lag between the
119 invasion and the discovery of IAS or between the invasion and its impacts, errors in
120 species inventories and alien status, environmental preferences and trophic interactions
121 (potential prey and predators) of IAS in the new environment ([Crooks, 2005](#); [McGeoch](#)
122 [et al., 2012](#); [Katsanevakis and Moustakas, 2018](#); [Moustakas and Katsanevakis, 2018](#)).
123 These have all led to great uncertainties in marine invasion science ([Katsanevakis and](#)
124 [Moustakas, 2018](#)).

125 However, our growing understanding of aquatic ecosystems and the improvement of
126 approaches has allowed the development of new insights into the ecological
127 consequences of IAS. Approaches range from documenting invaders and examining
128 interactions between invaders and native species to assess the ecological and economic

129 impacts of invasion by using a large variety of modelling techniques ([Wonham and](#)
130 [Lewis, 2009](#)). Humans have always used models, defined as a simplified representation
131 of some real-world entity, as tools to solve problems ([Levins, 1966](#); [Jørgensen and Fath,](#)
132 [2011](#); [Hannon and Ruth, 2014](#)). Modelling tools, in fact, can provide a means for
133 increasing understanding of processes, drivers and responses of organisms and
134 ecosystems to human pressures; identifying gaps in available knowledge and allowing
135 the development of predictions about possible future dynamics ([Jørgensen and Fath,](#)
136 [2011](#); [Hannon and Ruth, 2014](#)). Models will never be able to represent all the features
137 of the real system due to the complexity of ecosystems but they may contain qualitative
138 or quantitative descriptions of key components and processes of the system essential in
139 the context of the research questions ([Jørgensen and Fath, 2011](#); [Hannon and Ruth,](#)
140 [2014](#)). Intense research and our increasing understanding of aquatic ecosystems,
141 together with the development of computer technology, has allowed the development of
142 a large variety of model to assess the impact of invasive alien species ([Wonham and](#)
143 [Lewis, 2009](#)), as well as other drivers (e.g., [Hollwed et al., 2000](#); [Jørgensen, 2008](#);
144 [Pitcher, 2015](#); [Koenigstein et al., 2016](#)).

145 The principal aim of this study is to map and review available modelling approaches
146 used to evaluate the impacts of IAS in aquatic systems to date. We summarise the main
147 features of these applications and analyse their capabilities and limitations. Based on the
148 conclusions of this review, we reflect on future directions of development and
149 applications of suitable modelling tools.

150

151 **2. Methods**

152 We followed a systematic review approach in line with PRISMA (Preferred Reporting
153 Items for Systematic Reviews and Meta-Analyses) ([Moher et al., 2010](#)). This approach
154 consists of three steps: (1) systematic article selection using a search engine; (2) article
155 screening; and (3) a review of relevant articles and extraction of the information.

156 We performed the bibliographic search using Elsevier's Scopus database
157 (www.scopus.com). Eligibility criteria included any article, review, or book chapter
158 published between 1990 and the cut-off date, 8th February 2017, with the following
159 terms in the title, abstract or keywords:

- 160 1. "model" or "modelling" or "modeling"; and
- 161 2. "impact" or "impacts" or "effect" or "effects"; and
- 162 3. "invasive species" or "alien species" or "allochthonous species" or "introduced
163 species" or "non-indigenous species" or "non-native species" or "invasion" or
164 "exotic"; and
- 165 4. "marine" or "sea" or "coast" or "coastal" or "estuarine" or "bay" or "freshwater" or
166 "lake" or "river" or "reservoir" or "lagoon".

167 The search was limited to relevant subject areas (Agricultural and Biological Science,
168 Environmental Science, Earth and Planetary Sciences and multidisciplinary) and to
169 English and Spanish publications. The search resulted in 1306 publications.

170 Afterwards, we manually included additional relevant papers from other sources that
171 were not found in the main search as has been done previous studies ([Mačić et al.,
172 2018](#)). Additional papers included (1) an available bibliographic search ([Corrales et al.,
173 2014](#)) of the Ecopath with Ecosim modelling tool that assessed impacts of IAS (e.g.,
174 [Kitchell et al., 2000](#); [Downing et al., 2012](#); [Kao et al., 2016](#)); (2) papers cited in review
175 papers found in the initial search such as [Wonham and Lewis \(2009\)](#), [Thompson et al.
176 \(2013\)](#) and [Piroddi et al. \(2015\)](#); (3) papers from the personal files of the authors (e.g.,
177 [Padilla et al., 1996](#)); and (4) relevant papers found in selected articles during the third
178 step of the systematic review (extraction of the information). With these additional
179 articles, the total number of papers increased to 1382 (Fig. 1 in the Online
180 Supplementary Information A).

181 Article screening started with these 1382 articles and consisted of a two-stage process:
182 the first screening of articles was based on the title and the abstract, and the second on
183 the full article. During this process, articles were excluded if they: (1) did not apply or
184 develop a model to evaluate the impact of IAS, or (2) were related only to terrestrial
185 habitat/species. After the first selection process, 389 articles (28.3% of the original
186 papers) were selected. After the second selection process, 189 articles (see Online
187 Supplementary Information A for the final list of articles and their full references) were
188 included in the analysis (13.8% of the original papers). Species distribution models
189 (SDMs) and studies based on stable isotope analysis passed the first screening process
190 but were excluded in the second if they did not include, qualitatively or quantitatively,
191 the study of IAS impacts.

192 The following information was extracted from each selected article (see Online
193 Supplementary Information section B):

194 (1) Year of publication;

195 (2) Realm of the study (freshwater, estuarine or marine);

196 (3) Biogeographic region, based on [Olson et al. \(2001\)](#) (freshwater) and [Spalding et al.](#)
197 [\(2007\)](#) (marine);

198 (3) Ecosystem type (e.g., lake, river, bay);

199 (4) Information related to the IAS included in the model: number of IAS, scientific and
200 common name/s, type of organism/s (the groups were defined based on the detail of the
201 studies and the ecology of the organism) (e.g., fish, invertebrates), habitat/s (demersal or
202 pelagic) and trophic level/s (TL). The TL concept identifies the position of organisms
203 within food webs by identifying the source of energy of each organism, with TL 1 for
204 producers and higher values for consumers ([Lindeman, 1942](#)). We classified TL as low
205 ($TL < 3$), medium ($3 \leq TL \leq 3.5$) and high ($TL > 3.5$) based on outputs from models or
206 databases such as FishBase ([Froese and Pauly, 2017](#)) and SeaLifeBase ([Palomares and](#)
207 [Pauly, 2017](#));

208 (5) Information related to the model: modelling level (species/population or
209 multispecies/ecosystem level) ([Hollowed et al., 2000](#); [Jørgensen and Fath, 2011](#)), type
210 of model (statistical versus mechanistic) ([Levins, 1966](#); [Jørgensen, 2008](#)), model

211 category (e.g., bioenergetics and biogeochemical model), data type (time and spatial
212 scales) ([Jørgensen and Fath, 2011](#); [Hannon and Ruth, 2014](#)), if other external stressors
213 were included aside from IAS (for example, fisheries, climate change and nutrient
214 loading), if the model was validated and how it was validated, if uncertainty was
215 evaluated, and if the model was used to provide management recommendations; and

216 (6) Information related to the impacts of alien species: number and types of impacts on
217 ecosystem services (based on the classification by [Liquete et al. \(2013\)](#)) and/or on biota
218 (for example, predation, competition and ecosystem processes/function); if the impact
219 was positive (e.g. by providing a new food source for humans or other species or by
220 providing increased biofiltration) or negative (e.g. by causing the decline of native
221 populations due to predation, competition for resources or degradation of important
222 habitats) (see [Katsanevakis et al. \(2014b\)](#) for full classification of positive and negative
223 impacts); and which indicators were used to evaluate the impact (number of indicators,
224 type and units).

225 To summarise categorical variables and test pair-wise potential dependencies, we
226 applied a crosstabulation analysis and Chi-square test of independence ([Zar, 2013](#)),
227 using the statistical software Statgraphics ([Statgraphics-Centurion, 2009](#)). We tested the
228 hypothesis that the frequencies of occurrence in the various categories of one variable
229 are independent of the frequencies in the second variable.

230

231 3. Results

232 3.1. Temporal development, ecosystem coverage and species included

233 Since 1992, there has been an increase in the number of publications of models that
234 assessed the impacts of IAS in aquatic ecosystems (Fig. 1a). From 1992 to 2004 the
235 average rate of publications was 3.1 papers per year, while from 2005 to 2016 the rate
236 increased to 12.2 papers per year. Such temporal trends in the number of related
237 published articles were compared to the corresponding trends of published articles
238 (within the same subject areas) in the wider themes of (i) “aquatic” studies in general,
239 (ii) studies of biological invasions in the aquatic environment, and (iii) studies on the
240 impacts of biological invasions in the aquatic environment (see Online Supplementary
241 Information section C). The number of publications of models that assessed the impacts
242 of IAS in aquatic ecosystems increased at (i) a faster rate, (ii) the same rate, and (iii) a
243 lower rate, respectively. These trends indicate that although modelling studies of the
244 impacts of biological invasions in the aquatic environment have followed the general
245 trend of studies of aquatic biological invasions, which is much faster than general
246 aquatic-related papers, their relative importance in impact assessments of aquatic
247 biological invasions has been reduced with time. Most papers studied freshwater
248 ecosystems (75%), especially lakes, followed by marine (22%) and estuarine (3%)
249 ecosystems (Fig. 1b).

250 The studies covered several of the marine and freshwater biogeographic regions (Fig.
251 2). In the freshwater realm, most of the models were developed in the Nearctic
252 biogeographic region (75%), followed by the Palearctic (10%) and Afrotropical (8%).
253 We did not find studies in the Oceanian and Antarctic biogeographic regions. In the
254 marine realm, the Temperate Northern Atlantic (64%), the Tropical Atlantic (11%) and
255 the Temperate Northern Pacific (9%) biogeographic regions represented most of the
256 studies, while no studies were conducted in the Western and Central Indo-Pacific,
257 Tropical Eastern Indo-Pacific, Arctic and Southern Ocean biogeographic regions.

258 In freshwater and marine ecosystems, fishes (58 % and 31%, respectively) and molluscs
259 (mainly bivalves) (29% and 20%, respectively) were the most frequently studied groups
260 in the selected models, while in estuarine ecosystems, zooplankton (50%) and molluscs
261 (31%) were the main groups (Table 1). The frequency of occurrence of the three
262 categories of trophic level (low, medium and high) differed significantly among the

263 three environments (marine, freshwater and estuarine) (Chi-square test, $p < 0.005$).
264 Most of the studies focused on low trophic level species, especially in estuarine (71.4%
265 of the species) and freshwater (54.5% of the species) ecosystems, while in the marine
266 environment low and medium trophic level were equally represented (Fig. 3a). Pelagic
267 and demersal species were equally represented (48 and 52% respectively) (Fig 3b). The
268 frequency of occurrences of the two categories of habitat (pelagic and demersal) did not
269 significantly differed among the three environments (Chi-square test, $p = 0.16$) (Fig.
270 3b).

271 **3.2. Overview of the main modelling approaches**

272 Multispecies/ecosystem level models (77%) were more prevalent than
273 species/population level models (23%) in all ecosystem types (Fig. 4a). We found no
274 statistically significant difference in the frequencies of occurrence of the two modelling
275 levels among the three types of environment (Chi-square test, $p = 0.1$). The frequencies
276 of statistic or mechanistic models significantly differed between the two modelling
277 levels (species/population or multispecies/ecosystem) (Chi square test, $p < 0.005$). At
278 the species/population modelling level, we did not find large differences between the
279 number of studies that developed statistical ($n=18$) and mechanistic ($n=26$) models,
280 while at the multispecies/ecosystem level, most studies (129 out of 156) used
281 mechanistic models (Fig. 4b) . Of the statistical models, we found a similar diversity of
282 models at the species/population and multispecies/ecosystem levels (Table 2). On the
283 contrary, we found a higher diversity of mechanistic models at the
284 multispecies/ecosystem level (Table 2).

285 The average number of IAS included in the species/population level models was
286 significantly smaller (1.2 ± 0.4 SD), than the average number of IAS in
287 multispecies/ecosystem level models (2.9 ± 6.7 SD) (Mann-Whitney U test, $p = 0.03$)
288 (Fig. 4c). Some species/population level models encompassed two alien species but
289 their impacts were assessed together as they played the same ecological role, for
290 example, zebra mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*) filtering
291 phytoplankton (e.g., [Cha et al., 2013](#); [Rowe et al., 2015b](#)).

292 We found static studies that included a model representing a specific time period
293 (variables and parameters defining the system are time independent), static models
294 comparing different periods (comparative static), and dynamic models, which attempt to

295 capture the change in a simulated time period (variables and parameters defining the
296 system are time dependent). Dynamic models were more frequent than static models
297 and comparison between periods both at the single species and multispecies level (Fig.
298 5a), but we did not find significant differences in the frequencies of the model types
299 (static, dynamic and comparisons between periods) between the modelling levels (Chi-
300 square test, $p = 0.20$). Non-spatial models were more frequent than model comparisons
301 between study sites and fully spatial models (Fig. 5b) although differences were not
302 significant in the frequencies of non-spatial, fully spatial models or comparisons
303 between sites, between the two modelling levels (Chi-square test, $p = 0.47$).

304 Since 1992, there has been a progressive increase in the number of models that included
305 an additional stressor, especially since 2001. From 1992 to 2001, the average rate of
306 publications that included additional stressors aside from IAS was 1.1 papers per year,
307 while from 2002 to 2016 the rate increased to 6.3 papers per year (Fig. 6a). Most of the
308 multispecies/ecosystem models included additional stressors, while most of models at
309 the species level did not incorporate an additional stressor aside from the IAS (Fig 6b).
310 The frequencies of the inclusion or non-inclusion of other stressors significantly
311 differed between species/population and multispecies/ecosystem modelling levels (Chi-
312 square test, $p < 0.005$). The most frequently included additional stressors were fisheries
313 (commercial and recreational) (45%), followed by nutrient loading (25%) and climate
314 change (through changes in water temperature and primary production) (21%) (Fig. 6c).

315 Most studies (70%) did not evaluate uncertainty, with a similar percentage in
316 species/population and multispecies/ecosystem models (see Fig. 1 in the Online
317 Supplementary Information section D) (Chi-square test, $p = 0.37$). From those models
318 that assessed uncertainty we mainly found studies that manually changed different input
319 parameters using literature ranges (e.g., [Jiang et al., 2015](#)), estimated a degree of
320 increase or decrease based on expected changes ([Johnson et al., 2005](#); [Van Guilder and](#)
321 [Seefelt, 2013](#)), assessed effects of different initial IAS biomass values ([Zhang et al.,](#)
322 [2008](#); [Schwalb et al., 2014](#)) or used Monte Carlo routines ([Yurista and Schulz, 1995](#);
323 [Cha et al., 2011](#)).

324 **3.3. Modelling impacts of IAS**

325 **3.3.1. At the species/population level**

326 Several statistical models that focused on the species/population level were used to
327 assess the impact of IAS (Table 2). For example, [Onikura et al. \(2013\)](#) used a
328 generalised linear model to predict potential inter-sub-specific hybridisation and to
329 identify important areas of conservation. To evaluate the impact of competition for
330 resource, [Van Zuiden et al. \(2016\)](#) used multiple regression models to assess the impact
331 of smallmouth bass (*Micropterus dolomeiu*) and climate change on native walleye
332 (*Sander vitreus*). [Olden et al. \(2011\)](#) used a SDM to assess impacts of invasive rusty
333 crayfish (*Orconectes rusticus*) on two native congeners (*O. virilis* and *O. propinquus*),
334 while [Woodford et al. \(2011\)](#) used a GIS-based spatial model to predict whether two
335 invasive trout species (*Salmo trutta* and *Oncorhynchus mykiss*) would exclude the native
336 *Galaxias vulgaris* due to predation using a quantile limit function.

337 In addition, a variety of mechanistic models were used to assess the impact of IAS at the
338 species level. For example, [Liu et al. \(2014\)](#) developed a bioeconomic model to capture
339 the effects of invasive farmed fish on native stocks (growth and stock size) and harvest.
340 [Caldow et al. \(2007\)](#) developed an individual-based model to evaluate the positive
341 effects of the invasive Manila clam (*Tapes philippinarum*) on the Eurasian oystercatcher
342 (*Haematopus ostralegus*), which provided additional food and therefore reduced winter
343 mortality of the bird.

344 **3.3.2. At the multispecies/ecosystem level**

345 A large variety of statistical models that focused on the multispecies/ecosystem level
346 were used to assess the impact of IAS (Table 2). For example, [Bajer et al. \(2016\)](#) fitted
347 multivariate linear models to quantify the effects of the invasive common carp
348 (*Cyprinus carpio*) on plant cover and species richness, as well as additional effects of
349 water quality and total phosphorous. [De Amorim et al. \(2015\)](#) assessed the impacts of
350 the invasive African signalgrass (*Urochloa arrecta*) on a macrophyte community using
351 a generalised linear model, while [Knapp \(2005\)](#) used a generalised additive model to
352 assess the effects of invasive trout and habitat characteristics on lentic herpetofauna.
353 [Wenger et al. \(2011\)](#) assessed the effect of flow regime, temperature and biotic
354 interactions on the distribution of four trout species (of which three were IAS) under
355 climate change using a SDM.

356 A large variety of mechanistic models were used to assess the impact of IAS at the
357 multispecies/ecosystem level (Table 2). Within these model types, approaches ranged

358 from simple to more complex, including coupled models, where models were integrated
359 (with or without dynamic feedbacks) and outputs of one model provided inputs to the
360 other ([Travers et al., 2007](#)).

361 A common method for assessing the impacts of IAS at the multispecies/ecosystem level
362 was the development of bioenergetics models (24.8% of the mechanistic
363 multispecies/ecosystem models). For example, [Walrath et al. \(2015\)](#) used a
364 bioenergetics model to estimate predation of the invasive northern Pike (*Esox lucius*) on
365 westslope cutthroat trout (*Oncorhynchus clarkia lewisi*) and other prey taxa. [Reed-
366 Andersen et al. \(2000\)](#) coupled a zebra mussel bioenergetics model with an empirical
367 phytoplankton growth model to predict the impacts of zebra mussels on water clarity.

368 Some ecological models were coupled with economic models (5.4% of the mechanistic
369 multispecies/ecosystem models). For example, [Knowler \(2005\)](#) assessed the economic
370 consequences of the invasive comb jelly (*Mnemiopsis leidy*) on the Black Sea anchovy
371 (*Engraulis encrasicolus*) fishery using an integrated ecological-economic approach.
372 This model combined a Ricker stock-recruitment model of the anchovy population with
373 a balance model of *Mnemiopsis* biomass and an economic model. [Grosholz et al. \(2011\)](#)
374 assessed the economic impacts of the invasive European green crab (*Carcinus maenas*)
375 on commercial shell-fisheries along the West Coast of the United States using a
376 combination of ecological and economic models. They first estimated the probability of
377 spread using information of the potential northern and southern boundaries and a
378 multiple logistic regression approach. Then they calculated the impacts on shellfish
379 population due to predation using a regression analysis. Finally, the economic analysis
380 used the losses from the second ecological model to estimate the overall economic
381 consequences of these reductions in commercial shellfish harvest on shellfish producers
382 and consumers, via market demand and supply relationships ([Grosholz et al., 2011](#)).

383 Biochemical models, which were mainly developed to represent chemical fluxes
384 (mainly nitrogen and phosphorus) affecting low trophic level groups (e.g.
385 phytoplankton and zooplankton), were also used to assess impacts of IAS (8.5% of the
386 mechanistic multispecies/ecosystem models). For example, [Magnea et al. \(2013\)](#)
387 developed a dynamic model for 12 alpine lake ecosystems to describe the dynamics of
388 phosphorous (the limiting nutrient), phytoplankton, three zooplankton compartments
389 and fish abundance (in 6 lakes they included the invasive brook trout *Salvelinus*

390 *fontinales*). [Bierman et al. \(2005\)](#) used an ecosystem model in Saginaw Bay (Lake
391 Huron, US) in which zebra mussel bioenergetics were integrated with an eutrophication
392 model that represented nutrients and multiple functional groups of phytoplankton and
393 zooplankton.

394 The coupling of biogeochemical models with hydrodynamic models (19.4% of the
395 mechanistic multispecies/ecosystem models) allowed the inclusion of spatial and
396 temporal variability of the environment, mainly represented by variables such as
397 temperature, irradiance, salinity and currents. For example, [Schwalb et al. \(2014\)](#) and
398 [Bocaniov et al. \(2014\)](#) used a three-dimensional (3D) hydrodynamic model (ELCOM)
399 coupled with a biogeochemical model (CAEDYM). The CAEDYM included a mussel
400 sub-model that allowed the authors to assess impacts of invasive dreissenids on
401 phytoplankton. [Isaev et al. \(2016\)](#) used a 3D ecosystem model (SPBEM), that coupled a
402 transport module with a biogeochemical module, to assess the impact of bioirrigation
403 activity of the invasive alien polychaetes *Marenzelleria* spp. in the Gulf of Finland. In
404 addition, [Zhang et al. \(2011\)](#) used a coupled 2D-hydrodynamic model and a water
405 quality model (CE-QUAL-W2) to evaluate effects of invasive dreissenids and
406 zooplankton on phytoplankton in Lake Erie, USA.

407 Food-web models, which include a description of species interactions within the
408 ecosystem, were also frequently used (37.9% of the mechanistic multispecies/ecosystem
409 models). These models ranged from those that included only some species or functional
410 groups to the inclusion of the entire food web. For example, [Blamey et al. \(2014\)](#) used a
411 Model of Intermediate Complexity for Ecosystem assessments (MICE) (also called
412 Minimally Realistic Model or MRM), to evaluate if overfishing of predatory fish may
413 have caused a regime shift following the invasion of West Coast rock lobster (*Jasus*
414 *lalandii*). [Miehls et al. \(2009\)](#) used an Ecological Network Analysis (ENA) to assess the
415 effects of the invasive zebra mussel within and between two invaded ecosystems and
416 compare food web characteristics before and after the invasion. The Ecopath with
417 Ecosim (EwE) approach ([Christensen and Walters, 2004](#); [Heymans et al., 2016](#)) was
418 frequently used to assess impacts of IAS. For example, [Lercari and Bergamino \(2011\)](#)
419 quantified the impacts of two IAS (the gastropod, *Rapana venosa*, and the bivalve,
420 *Corbicula fluminea*) in Río de la Plata estuary (Argentina and Uruguay) during a
421 specific time period by developing an Ecopath model, while [Downing et al. \(2012\)](#)
422 assessed impacts of IAS and fishing in Lake Victoria through three Ecopath models

423 representing the before, during and after periods of the Nile perch bloom. In addition,
424 [Kao et al. \(2014\)](#) developed a time dynamic (Ecosim) model to evaluate relative impacts
425 of changes in nutrient loads, fishing and two invasive groups (dreissenids and the
426 alewife *Alosa pseudoharengus*).

427 Other types of multispecies models were employed to assess impacts of IAS. For
428 example, [Cook et al. \(2014\)](#) used an integrated conceptual ecosystem model (Driver-
429 Pressure-State-Ecosystem Service-Response or DPSE) to explore the direct and
430 indirect relative impact of 12 ecosystem pressures on 11 ecosystem state variables and
431 11 ecosystem services in southern Florida. [Ortiz and Stotz \(2007\)](#) used qualitative
432 (loop) models of ecological and socio-economic systems to analyse and predict the
433 impact of a possible accidental introduction of the abalone (*Haliotis discus hannai*)
434 into the benthic community of north-central Chile. A conservative additive model was
435 developed to assess the spatial cumulative impacts of IAS on marine habitats in the
436 Mediterranean Sea ([Katsanevakis et al., 2016](#)).

437 Finally, we found a growing interest in recent years to develop models that attempt to
438 represent an entire ecosystem. These models are called end-to-end (E2E) or whole-of-
439 system models and represent ecosystem components from nutrients, biogeochemical
440 cycling and primary producers to top predators (including human and socio-economic
441 components) linked through trophic interactions and the associated abiotic environment
442 (e.g., currents and water column properties such as temperature and salinity) ([Travers et](#)
443 [al., 2007](#); [Fulton, 2010](#)). However, only one example of end-to-end models dealing with
444 IAS was found (0.8% of the mechanistic multispecies/ecosystem models). [Nyamweya](#)
445 [et al. \(2016\)](#) developed an Atlantis model for Lake Victoria to assess impacts of
446 overfishing, IAS such as Nile perch and Nile tilapia (*Oreochromis niloticus*),
447 eutrophication and climate change.

448 **3.4. Predicted impacts of IAS at species and ecosystem levels and the utility of** 449 **models in impact management**

450 The frequency of the types of impacts reported (positive, negative or both) significantly
451 differed between the type of model used (Chi-square test, $p < 0.005$) (Fig. 7a). At the
452 species/population level, 84.1% of the studies reported negative impacts of the IAS on
453 ecosystem compartments and/or ecosystem services, while at the
454 multispecies/ecosystem level, negative (51.4% of the studies) and both negative and

455 positive (47.1% of the studies) impacts were similarly represented (Fig. 7a). We found
456 only a limited number of cases of positive impacts in the results of single species and
457 multispecies models (Fig. 7a).

458 Most studies reported impacts on biota rather than on ecosystem services, and on
459 multiple-species than single-species (Fig. 7b and c). Most of these impacts (single and
460 multispecies) were due to ecological interactions of IAS involving predation and/or
461 competition for resources. In addition, some models were used to assess impacts on
462 ecosystem processes and function (Fig. 7b), such as biodiversity, biogeochemical
463 fluxes, energy flows and ecosystem stability, and impacts on other ecosystem services
464 (Fig. 7c). Water purification (39%) and food provision (from fisheries or aquaculture)
465 (36%) were the most assessed ecosystem services, followed by recreation and tourism
466 (for example, recreational fisheries) (15.8%) (Fig. 7c).

467 Most of the studies (90.4%) did not provide management recommendations based on
468 their findings. No significant differences were found in the frequencies of occurrence of
469 studies that reported management recommendations between single and multispecies
470 models (Chi-square test, $p = 0.64$) (see Fig. 2 in the Online Supplementary Information
471 section D) or among the three types of environment (Chi-square test, $p = 0.72$) (see Fig.
472 2 in the Online Supplementary Information section D). In studies that provided
473 management recommendations, these were mostly of a general nature and no specific
474 management actions were listed (Online Supplementary Information B). However,
475 some studies provided management advice. For example, [Stapp and Hayward \(2002\)](#),
476 based on a stage-structured matrix model, suggested the development of control
477 programs to reduce survival of all age classes of lake trout (*Salvelinus namaycush*).
478 Using an EwE model, [Arias-González et al. \(2011\)](#) and [Pine et al. \(2007\)](#) assessed,
479 through different scenarios of fishing exploitation, how to eradicate invasive alien top
480 predators.

481

482 4. Discussion

483 4.1. Making progress in modelling impacts of IAS on aquatic ecosystems

484 In recent decades, the rate of human-mediated introductions have increased ([Hulme,](#)
485 [2009](#); [Seebens et al., 2017](#)) and some have had great impact on native species and
486 recipient ecosystems and their services ([Simberloff et al., 2013](#); [Gallardo et al., 2016](#)).
487 In parallel, considerable research has been conducted to understand and predict
488 invasions and assess their ecological impacts ([Ricciardi et al., 2013](#); [Chan and Briski,](#)
489 [2017](#)), highlighting the growing concern over this issue. Therefore, evaluating IAS
490 impacts is essential to developing strategies to prevent and manage their effects ([Pyšek](#)
491 [and Richardson, 2010](#); [Ojaveer et al., 2015](#)).

492 According to our results, while there has been an important growth of modelling
493 approaches, this growth has not been consistent across ecosystem and biogeographic
494 regions. Most of the studies were concentrated in freshwater ecosystems, followed by
495 marine and estuarine ecosystems. This is in line with a review of hypotheses for causes
496 of biological invasions and their impacts, which showed that most studies were carried
497 out in terrestrial ecosystems, followed by freshwater, marine and estuarine ecosystems
498 ([Lowry et al., 2013](#)). Such a higher publication rate of freshwater studies does not
499 reflect the number of alien species in the two environments as there is more marine than
500 freshwater alien species. For example, in Europe 1369 marine ([Katsanevakis et al.,](#)
501 [2013a](#)) vs 756 freshwater ([Nunes et al., 2015](#)) alien species have been estimated.
502 However, it may reflect the fact that the freshwater environments have been the most
503 impacted and highly modified because of biological invasions

504 Our results highlight geographic differences in IAS modelling efforts. While models
505 have been developed for most biogeographic regions (freshwater and marine realms)
506 they have mainly focused on particular areas, namely North America but also Europe, in
507 agreement with [Lowry et al. \(2013\)](#), [Pyšek et al. \(2008\)](#) and [Buchadas et al. \(2017\)](#).
508 This geographic distribution of models can be largely explained by different availability
509 of data and funding opportunities for research ([UNESCO, 2017](#)), although there may
510 have been some bias in our findings due to the exclusion of non-English and non-
511 Spanish publications in our review.

512 According to our results, most available studies focused on species occupying low
513 trophic levels. [Lowry et al. \(2013\)](#) and [Pyšek et al. \(2008\)](#) also found that most of the
514 research on biological invasions focused on low trophic levels. However, in their
515 reviews most of the species were primary producers (mainly terrestrial plants), while
516 most of the species we identified were fishes and molluscs (mainly bivalves). It is likely
517 that this taxonomic composition indicates research priorities over the last few decades
518 and, in some regions, also reflects the proportion of IAS in the studied ecosystems. In
519 fact, impacts have been described for a small proportion of IAS, which tend to be those
520 with the greatest impact on organisms and ecosystems and their services ([Vilà et al.,
521 2009](#); [Pyšek and Richardson, 2010](#)). For example, dreissenids (freshwater mussels) have
522 been largely studied and modelled due to their wide distribution and dramatic ecological
523 and economic impacts, especially in North America ([Pyšek et al., 2008](#); [Higgins and
524 Vander Zanden, 2010](#)).

525 Most models were used to assess the detrimental effects of IAS ([Pyšek et al., 2008](#);
526 [Katsanevakis et al., 2014b](#)). However, IAS can have positive effects on native species
527 and ecosystems, as well (e.g., [Caldow et al., 2007](#); [Norkko et al., 2012](#)). This is
528 highlighted in multispecies/ecosystem level models, which incorporate interactions
529 among many species, and therefore indirect effects that can cause both positive and
530 negative impacts. Most of the reported impacts are related to the effect of an invasive
531 alien predator on native preys, but research has also focused on competition for
532 resources and ecosystem processes and function. Effects of invasive alien prey on native
533 predators have been less studied ([Carlsson et al., 2009](#)), and according to the trophic
534 position hypothesis, we could expect negative impacts of IAS on biodiversity within a
535 trophic level but positive effects on the biodiversity of higher trophic levels through
536 community-wide antagonism (competition and consumption) and facilitation (habitat
537 and food provisioning) interactions, respectively ([Thomsen et al., 2014](#)).

538 Ecological processes operate at a wide range of spatial and temporal scales, and thus the
539 choice of these scales in model development is very important ([Jørgensen and Fath,
540 2011](#)). These choices affect model complexity, as finer temporal and spatial resolution
541 need more detailed data and require increased computation power and effort, while
542 exacerbating uncertainty ([Rose et al., 2010](#); [Plagányi et al., 2014](#)). Therefore, the spatial
543 and temporal scales should be modelled to the degree required to address the question
544 under consideration ([FAO, 2008](#); [Fulton, 2010](#)). In the context of modelling the impacts

545 of IAS in highly invaded aquatic ecosystems and within an Ecosystem-based
546 management, suitable modelling frameworks may need to allow the incorporation of
547 several IAS with different ecological and trophic roles and, therefore, with different
548 temporal and spatial requirements. Connecting these parts of the model or even “sub-
549 models” is a challenging task ([Rose et al., 2010](#)).

550 Dynamic models were the most frequently developed, followed by static and
551 comparative static models. This is likely due to the fact that assessing the impact of IAS
552 in aquatic ecosystems requires a dynamic view of the process, which is time dependent.
553 It may also be due to the need for novel tools to manage aquatic ecosystems
554 ([Cuddington et al., 2013](#); [Buchadas et al., 2017](#)). Model comparison between periods
555 provides a means of assessing the impact over time. This modelling technique presents
556 some advantages over developing a single static model, especially if comparison
557 includes models before and after invasion, as it allows the assessment of the overall
558 impact of IAS on the invaded ecosystem with a temporal baseline (the ecosystem before
559 the invasion). Non-spatial models were more frequent than spatial ones. This is due to
560 the challenges of spatial modelling of IAS and associated data requirements ([Fulton et
561 al., 2004b](#); [Jørgensen, 2008](#)). In non-spatial models, comparisons between invaded and
562 non-invaded areas are interesting and have provided insights into the impacts of IAS
563 (e.g., [Rowe, 2007](#); [Blamey et al., 2013](#)) while fully spatial models allow to represent
564 important dynamics observed in nature such as distribution, movement, and dispersal
565 ([Jørgensen and Fath, 2011](#)). Spatial-temporal models allow a more realistic
566 representations of the ecosystem and provide advantages in modelling impacts of IAS
567 (e.g., [Zhang et al., 2011](#); [Norkko et al., 2012](#)).

568 **4.2. Advantages and disadvantages of existing modelling approaches**

569 A desirable model is one that maximizes generality (the applicability of a model to
570 different ecosystems, data sets and questions), realism (the model includes detailed
571 processes through mathematical equations) and precision (the degree of exactness in
572 measurement or predictions) ([Levins, 1966](#)). However, in practice, modelling is
573 essentially a trade-off among these desirable attributes ([Levins, 1966](#)). A main
574 difference between statistical and mechanistic models is related to their internal
575 structure. In mechanistic models, relationships among variables are specified in terms of
576 the biological process, while statistical models look for patterns and relationships in the

577 observed data, regardless of the causative processes involved ([Hilborn and Mangel,](#)
578 [1997](#); [Robson, 2014](#)).

579 Statistical and single-species models offer a simplistic view of the ecosystem, ignoring
580 processes and interactions, but they are easily constructed and can highlight ecosystem
581 characteristics. Large complex models, on the other hand, can provide a more
582 comprehensive picture of the ecosystem but they have large data demands, can
583 represent processes poorly and can have a large degree of uncertainty due to errors in
584 model structure and parameter values ([Fulton et al., 2003](#); [Link et al., 2012](#); [Gal et al.,](#)
585 [2014](#)). Therefore, it has been recommended to include essential processes and
586 components in a balanced way to address the question under consideration while
587 capturing the complexity of aquatic systems ([FAO, 2008](#); [Hannon and Ruth, 2014](#)).

588 Statistical models have been widely used to study the impacts of IAS in aquatic
589 ecosystems. These models have been shown to be useful to assess impacts of IAS on
590 native species (e.g., [Stapanian et al., 2009](#); [De Amorim et al., 2015](#)) and also to predict
591 potential spatial exclusion (e.g., [Sharma et al., 2011](#); [Wenger et al., 2011](#)). In addition,
592 they are used to disentangle the relative importance of IAS and other stressors in native
593 species declines (e.g., [Light and Marchetti, 2007](#); [Hermoso et al., 2011](#); [Bajer et al.,](#)
594 [2016](#)), as well as changes in abiotic factors (e.g., [Macdonald et al., 2012](#); [Pagnucco and](#)
595 [Ricciardi, 2015](#)). Such analyses can improve our understanding of broad patterns in
596 biodiversity changes and provide insight into processes that may be responsible for the
597 patterns observed in the data ([Whipple et al., 2000](#); [Light and Marchetti, 2007](#)).
598 However, statistical models incorporate low levels of realism as they indirectly capture
599 the ecological processes that generate them ([Levins, 1966](#); [Jørgensen and Fath, 2011](#)).

600 A large number of mechanistic models have been used to study the impacts of IAS,
601 ranging from simple to very complex. At the species level, models assess impacts of
602 IAS on populations. These impacts include effects on growth ([Liu et al., 2014](#); [Crane](#)
603 [and Einhouse, 2016](#)), catchability ([Kateregga and Sterner, 2009a](#)), mortality ([Caldow et](#)
604 [al., 2007](#)), predation ([Green et al., 2014](#); [Rowe et al., 2015b](#)) and competition ([Liu et al.,](#)
605 [2014](#)), as well as economic impacts on property values ([Olden and Tamayo, 2014a](#)) and
606 fisheries ([Liu et al., 2014](#)). However, aquatic ecosystems are dynamic and complex,
607 with interactions between species (trophic and non-trophic) which generally involve
608 competition and predation, and interactions with the environment and human stressors

609 ([Garcia et al., 2003](#); [Thoms, 2006](#)). An understanding of the functional interactions and
610 processes in aquatic ecosystems, as well as the cumulative impacts of human activities,
611 requires a more comprehensive analysis, as is emphasized by ecosystem-based
612 management ([Rosenberg and McLeod, 2005](#)).

613 Most of the mechanistic models at the multispecies/ecosystem level that we found were
614 quantitative, with only one qualitative model (loop analysis) found applied to the study
615 of the impacts of IAS on aquatic ecosystems ([Ortiz and Stotz, 2007](#)). Within the context
616 of modelling impacts of IAS, with data limitations in many cases, loop analysis could
617 become a valuable tool ([Metcalf, 2010](#)), as precise model predictions and estimates of
618 the magnitude of the impacts are not always necessary to inform management questions
619 ([Ramsey and Veltman, 2005](#)).

620 The development and application of bioenergetics models have increased in recent years
621 ([Chipps and Wahl, 2008](#); [Hartman and Kitchell, 2008](#)) due to their user-friendly
622 software, reasonable time and effort to develop, ease of interpretation and ability to
623 make predictions ([Chipps and Wahl, 2008](#); [Jørgensen, 2008](#)). In invasion ecology, these
624 models are particularly useful because they provide a means of evaluating the trophic
625 impacts (e.g., the amount of prey eaten) of IAS and assessing the suitability of an
626 ecosystem for invasion considering their energy requirements and food availability
627 (e.g., [Anderson et al., 2015](#); [Foley et al., 2017](#)). However, the use of these models
628 presents some disadvantages, including the requirement of good data, associated with
629 intense sampling, and the difficulties to calibrate them ([Chipps and Wahl, 2008](#);
630 [Hartman and Kitchell, 2008](#); [Jørgensen, 2008](#))

631 Biogeochemical models (which may or may not be coupled with hydrodynamic models)
632 have been widely used over the last few decades as a research and management tool due
633 to the increasing power of computers, the development of more robust and detailed
634 processes and increasing data availability, and user-friendly software ([Jørgensen, 2008](#);
635 [Fulton, 2010](#); [Ganju et al., 2016](#)). Coupling biogeochemical models with hydrodynamic
636 models represented an important and necessary step, and considerable progress has been
637 made in the spatial resolution of the hydrodynamic models ([Ganju et al., 2016](#)). In
638 invasion ecology, these models (coupled or not) have proved to be a useful tool to
639 assess: (1) the role of top-down (grazing by native species, i.e. zooplankton, and IAS,
640 i.e. dreissenids) and bottom-up (nutrient availability) forces on primary productivity and

641 changes to energy pathways due to IAS ([Higgins et al., 2014](#)), (2) the competition
642 between native and invasive alien grazers ([Zhang et al., 2011](#)), (3) the role of IAS (i.e.
643 dreissenids) on nutrient (i.e. phosphorous) and native community (i.e. macrophytes)
644 dynamics ([Gudimov et al., 2015](#)), (4) the role of IAS in the proliferation of toxic algae
645 blooms ([Bierman et al., 2005](#)), and (5) the role of IAS in the recovery of hypoxic
646 regions due to the impacts of bioirrigation on biogeochemical cycles within sediments
647 ([Norkko et al., 2012](#)). Despite these advantages and applications, hydrodynamic-
648 biogeochemical models are time consuming, and can be difficult to calibrate and
649 validate with independent data due to the large amount of data needed and processes
650 included ([Fulton et al., 2003](#); [Arhonditsis and Brett, 2004](#); [Jørgensen and Fath, 2011](#)).

651 Food-web models have been increasingly used over the last few decades, and one
652 example is the wide application of the Ecopath with Ecosim (EwE) approach ([Heymans
653 et al., 2014](#); [Colléter et al., 2015](#)). Assessing the impacts of IAS in a food web including
654 the temporal dynamic context is challenging, especially for species that invaded the
655 ecosystem after the baseline model ([Langseth et al., 2012](#)). Therefore, some applications
656 have addressed this challenge by developing two Ecopath models, one representing the
657 food web before the invasion and one after the invasion (e.g., [Downing et al., 2012](#);
658 [Corrales et al., 2017b](#)). However, this approach impedes the study of the expansion
659 process and their impact over time. Several strategies have been successfully applied to
660 simulate IAS and their temporal impacts using the temporal dynamic model of EwE,
661 Ecosim (e.g., [Langseth et al., 2012](#); [Kao et al., 2016](#); [Corrales et al., 2017a](#)). In addition,
662 Ecosim has been used to evaluate the eradication and resilience of IAS and the potential
663 effects of its removal on the ecosystem within a management context (e.g., [Pine et al.,
664 2007](#); [Arias-González et al., 2011](#)), as well as the possible impacts that a new IAS might
665 have on the ecosystem ([Pinnegar et al., 2014](#)). At the same time, there has been a
666 growing interest in MICE ([Plagányi et al., 2014](#)), which, unlike whole food-web models
667 (e.g., EwE), represents a limited number of species believed to have the most important
668 interactions with target species. MICE can be an especially valuable tool for areas
669 where available data for the whole ecosystem are lacking.

670 Despite the growing development of a variety of end-to-end models in aquatic
671 ecosystems ([Fulton, 2010](#); [Rose et al., 2010](#)), we only found one study using end-to-end
672 modelling (within the Atlantis framework ([Fulton et al., 2004a](#))) to study impacts of
673 IAS on aquatic ecosystems. This may reflect the current challenges of implementing

674 end-to-end modelling within the context of invasion ecology due to the lack of process
675 knowledge, data restrictions and computational limitations.

676 **4.3. Moving forward**

677 Some of the main limitations in model development are data availability, accessibility
678 and quality. Within the context of IAS, this is even more important since there is an
679 urgent need to deal with uncertainties in IAS inventories and species information
680 ([McGeoch et al., 2012](#); [Katsanevakis and Moustakas, 2018](#)). For example, there is a
681 general lack of knowledge of IAS population dynamics, biological traits, basic ecology
682 such as trophism and behavior, and environmental affinities. This knowledge is
683 essential for model parameterization and calibration due to the permanent change of
684 IAS dynamics when they invade an ecosystem and the fact that climate change may
685 favor the establishment and spread of IAS depending on ecological and environmental
686 factors of potential invading ecosystems and species, while native species may be
687 forced out of their tolerance limits ([Walther et al., 2009](#); [Rilov, 2016](#)). The improvement
688 of data availability and better collaboration among data collectors and modelers is
689 needed to enhance model development validation and interpretation of model results.

690 Calibration (defined as the attempt to find the best agreement between the computed
691 and observed data by changing selected parameters), validation (defined as an objective
692 test to reflect how well model outputs fit observed data through the comparison of
693 model results with independent data) and uncertainty analyses are critical processes for
694 evaluating model performance and testing the validity of the assumptions included in
695 the models ([FAO, 2008](#); [Jørgensen and Fath, 2011](#); [Grüss et al., 2017](#)). Our review
696 highlights that most models used to evaluate impacts of IAS on aquatic systems did not
697 assess uncertainties, in line with previous research ([Katsanevakis and Moustakas, 2018](#);
698 [Stelzenmüller et al., 2018](#)) and validation procedures were also scarce. This is an
699 important shortcoming that needs further research and development in the field.

700 Our study illustrated the capabilities of models to assess the impacts of already
701 established IAS. However, IAS are increasing in aquatic ecosystems and this increase is
702 likely to continue into the future and expand to new ecosystems. Therefore, there is a
703 need for predictive methodologies that allow the forecasting of plausible scenarios that
704 include existing, emerging and potential new IAS ([Dick et al., 2014](#)). Making
705 predictions about future impacts of IAS presents several obstacles linked to the high

706 uncertainties of ecological forecasting ([Maris et al., 2017](#)), in addition to intrinsic
707 features of IAS and the lack of data ([Havel et al., 2015](#)), especially related to the
708 unknown population dynamics in current and future invaded ecosystems. The invasion
709 process includes the phases of arrival, establishment and naturalisation and, therefore,
710 depends on the combination of dynamic interspecific relationships (with native species
711 or even other IAS), habitats, environmental effects and other anthropogenic activities.
712 We did not find one single model that deals with the three phases in an integrative way,
713 which demonstrates a profound gap in IAS modelling. A modelling approach dealing
714 with these phases fully may require coupling different models that are able to predict the
715 probability of a species to arrive and, once it is established and invades the ecosystem,
716 to model species interactions, its impacts and the effect of multiple environmental
717 factors and human activities.

718 Several tools are available to predict potential IAS and their spread ([Kolar and Lodge,
719 2001](#); [Wonham and Lewis, 2009](#)), such as risk assessments ([Kolar and Lodge, 2002](#);
720 [Townhill et al., 2017](#)), vector-based models ([Seebens et al., 2016](#)), species distribution
721 models (SDMs) ([Jiménez-Valverde et al., 2011](#); [Larson et al., 2014](#)), or studies that
722 identify characteristics of species likely to invade, such as environmental affinity and
723 ecological traits ([Belmaker et al., 2013](#)). Within this context, [Romanuk et al. \(2009\)](#)
724 simulated invasions by integrating models of network structure and nonlinear
725 population dynamics. In addition, SDMs are increasingly used to forecast potential
726 distributions of species, although the climate niche could be different between the native
727 and invaded ecosystem ([Mainali et al., 2015](#); [Parravicini et al., 2015](#)) and despite
728 dispersal limitations ([Václavík and Meentemeyer, 2009](#)). Current research of SDM is
729 focusing on incorporating the effects of species interactions ([Wisz et al., 2013](#); [Albouy
730 et al., 2014](#)) while environmental DNA is a novel method that may be useful to improve
731 SDM (data about presence/absence) and for early detection of IAS and predict their
732 future distribution through SDM ([Muha et al., 2017](#); [Bourne et al., 2018](#)). Within this
733 context, the new habitat foraging capacity (HFC) model and the spatial-temporal
734 module of EwE, Ecospace ([Steenbeek et al., 2013](#); [Christensen et al., 2014](#)), provides a
735 step forward for temporal-spatial modelling, as it combines food-web modelling with
736 SDMs and could be a valuable tool for predicting the future spread of IAS within an
737 ecosystem context. Current developments of the HFC model include the integration of

738 Bayesian SDM results within a food web model either using response functions to
739 model species distributions or driving niche preferences directly ([Coll et al., Submitted](#)).

740 Future scenarios of biological invasions are rarely available in the literature due to the
741 complexity of invasion biology ([Courchamp et al., 2017](#)), which as previously
742 highlighted include a general lack of knowledge about IAS and invading processes,
743 dynamic relationships between species, dynamic anthropogenic stressors and dynamic
744 abiotic effects. Despite these constraints, there have been attempts to predict impacts of
745 already established IAS, particularly in aquatic ecosystems ([Ricciardi, 2003](#)) but also on
746 marine ecosystems ([Corrales et al., 2018](#)). For example, [Pinnegar et al. \(2014\)](#) used a
747 Rank Proportion Algorithm (RPA) ([Link, 2004](#)) to predict the diet composition of a
748 potential new IAS in the Western Mediterranean Sea based on its diet on an already
749 invaded ecosystem in the Eastern Mediterranean Sea. The authors of this study used this
750 new diet as input to an EwE model representing an ecosystem of the Western
751 Mediterranean Sea. Finally, [Pinnegar et al. \(2014\)](#) used the EwE model to assess
752 possible impacts of the IAS on the new ecosystem assuming different expansion rates.
753 In fact, the RPA model, or similar approaches, developed using machine learning
754 techniques could be keys tools to predict potential new trophic behavior for recent or
755 future invaders. The bridge and integration of novel capabilities with current spatial-
756 temporal multispecies models may bring a new growth of modelling development and
757 application in the future, and a promising future development to enable the inclusion of
758 IAS in future scenarios of global change.

759 Models, especially multi-species/ecosystem models, have become an essential decision-
760 making tool ([Collie et al., 2014](#)). However, they are generally not used to manage
761 ecosystems, mainly due to ecosystem complexity and large uncertainties and the
762 challenge of translating complex results to management decisions ([Fogarty, 2013](#);
763 [Collie et al., 2014](#); [Lehuta et al., 2016](#)). Within IAS management, models are even more
764 rarely used to provide management recommendations. A possible reason is that there is
765 a mismatch between research outputs and decision-makers priorities ([N'Guyen et al.,](#)
766 [2016](#); [Piria et al., 2017](#)). While researcher outputs have focused on IAS impacts,
767 decision-makers have prioritized IAS prevention. In fact, prevention of new
768 introductions through managing vectors and pathways has been a priority for decision-
769 makers in the development of effective policies ([CBD, 2002](#)) and as such, risk
770 assessment has been widely used in IAS management ([Pyšek and Richardson, 2010](#)).

771 Future collaboration between researchers, decision-makers and other stakeholders is
772 essential to make the use of modelling techniques fully operational within the
773 management context of biological invasions and the likely future use of these tools to
774 test management alternative of IAS eradication and control ([N’Guyen et al., 2016](#);
775 [Novoa et al., 2018](#)).

776 **4.4. Concluding remarks**

777 Our review has highlighted that current modelling approaches are useful tools to assess
778 different impacts of already established IAS and have provided insights into their
779 ecological consequences. Many modelling techniques have been applied to investigate
780 IAS in aquatic ecosystems, but there are several challenges that need to be addressed in
781 the near future. Due to uncertainties in invasion science, one of the main limitations in
782 model development (data availability, accessibility and quality) is even more
783 considerable in IAS modelling. As new invasions are expected in the future, there is a
784 need for predictive methodologies to forecast existing, emerging and potential IAS and
785 their impacts. Within this context, different tools are available to predict potential new
786 IAS and their spread. However, models that allow capturing the arrival, establishment
787 and spread of IAS and assess their impacts in an integrated way are still missing and
788 highlight a profound gap in IAS modelling despite recent developments. The
789 development of spatial-temporal methodologies that integrate the arrival, establishment
790 and spread of IAS and their impacts within an ecosystem context is needed to inform
791 management advice and contribute to the analyses of future scenarios of global change.
792 Integrating and bridging novel techniques and disciplines such as environmental DNA
793 to investigate the presence of IAS, metabarcoding and machine learning techniques to
794 predict future trophic behavior and distributions with novel spatial-temporal model
795 capabilities may further advance IAS modelling.

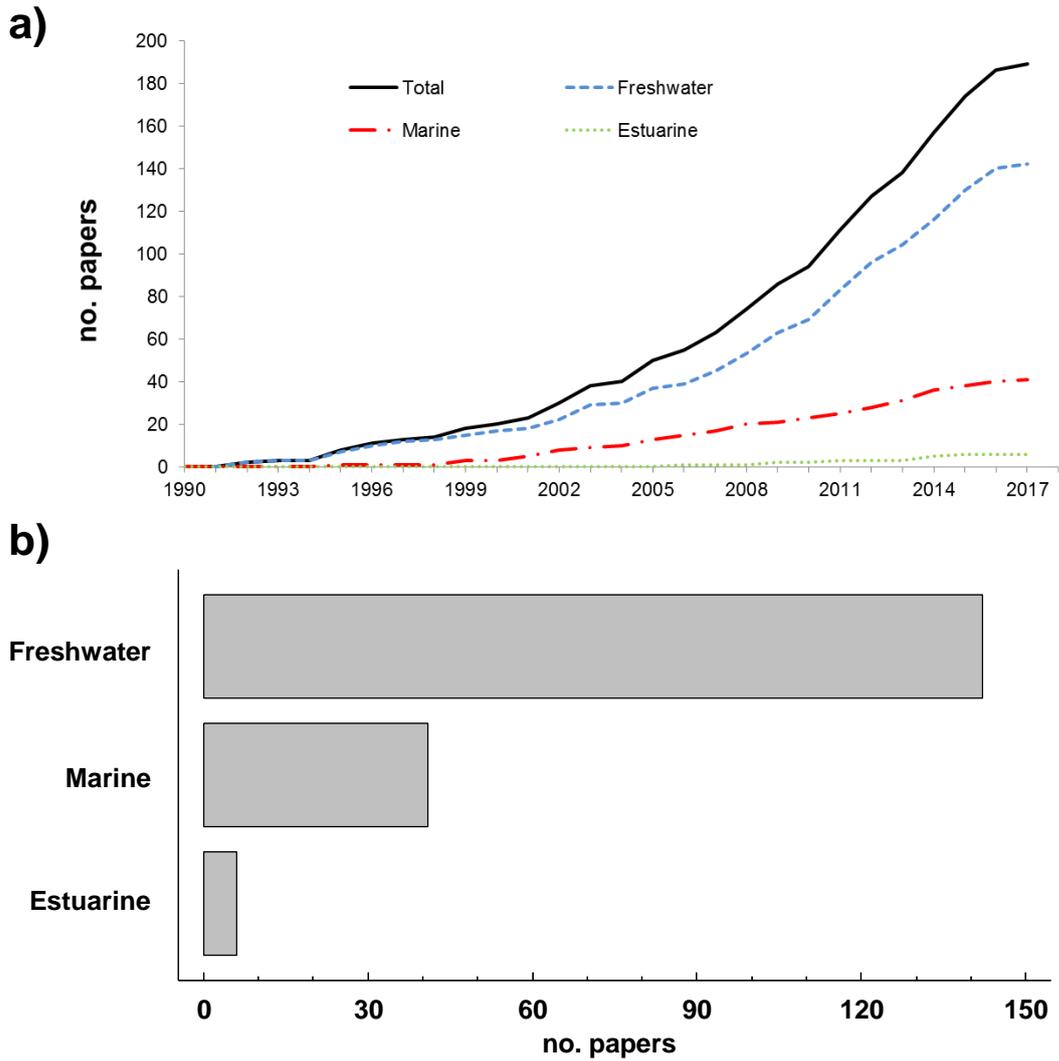
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811 **Figure 1.** (a) Cumulative number of publications over time found in the systematic
 812 review (the year 2017 covers January 1st to 8th February); and (b) number of
 813 publications per ecosystem type.

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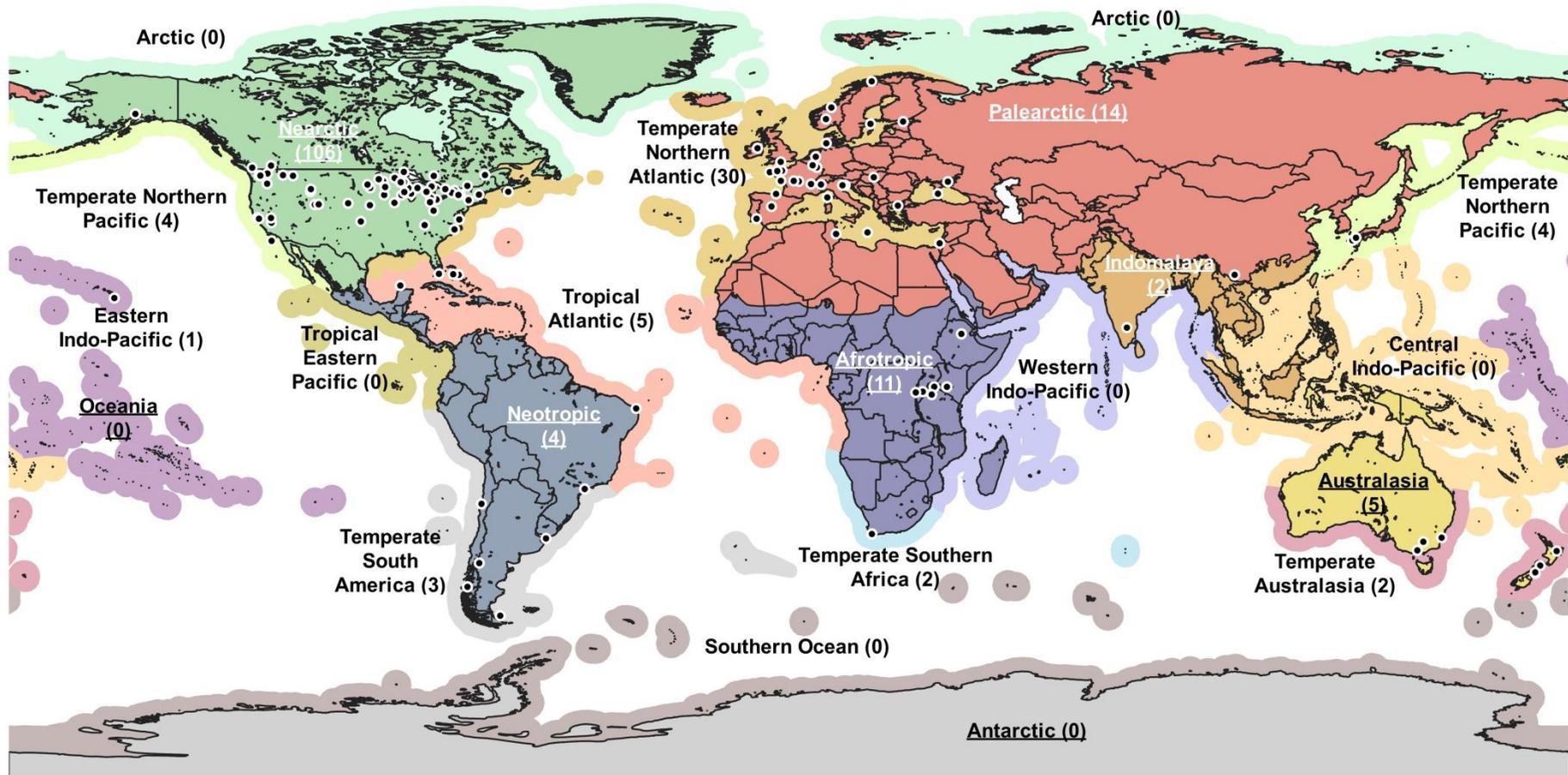


Figure 2. Distribution of the studies included in the systematic review. Different realms (marine and terrestrial biogeographic regions) are presented with different colours. Realms were based on [Spalding et al. \(2007\)](#) and [Olson et al. \(2001\)](#). Numbers in brackets indicate the total number of studies for each biogeographic region.

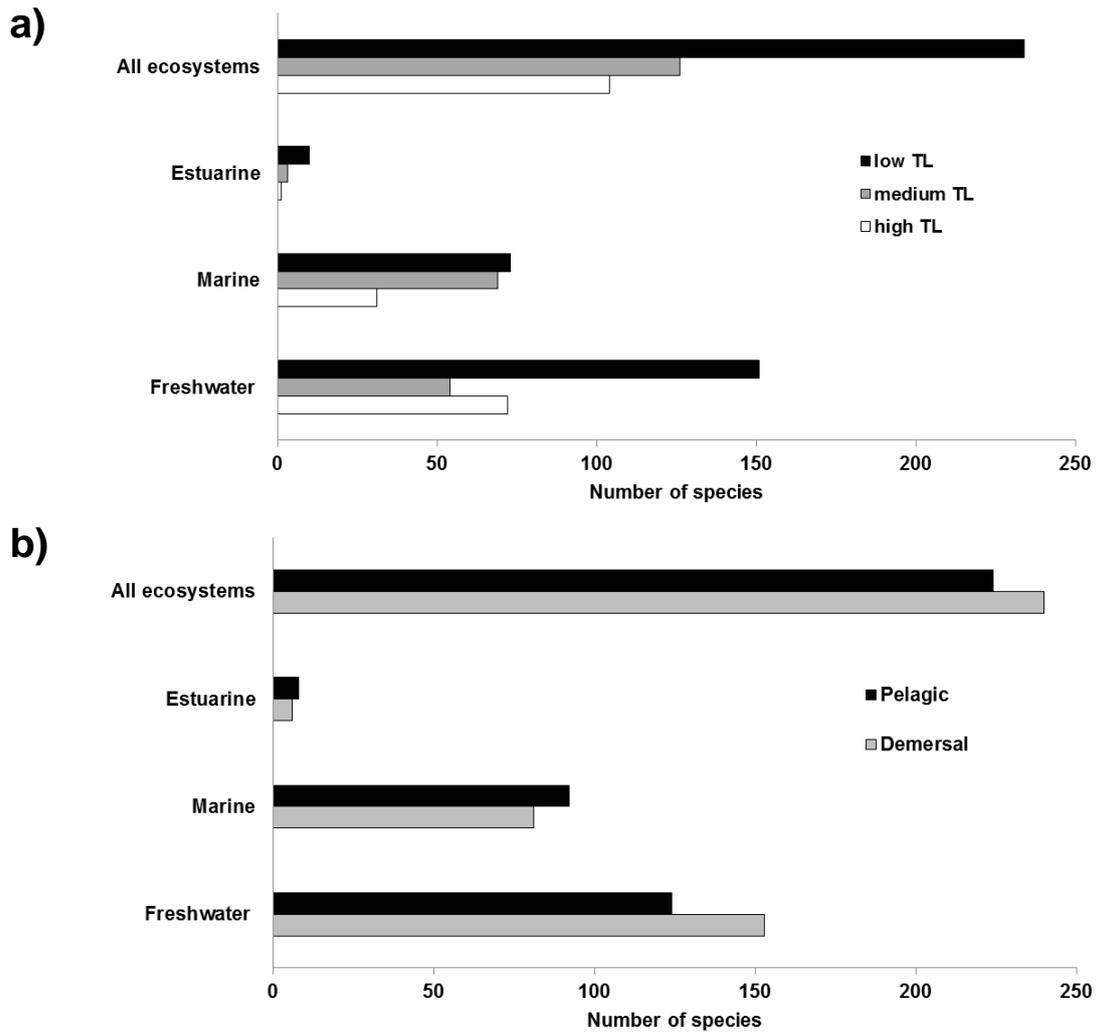


Figure 3. Number of species included in the models found in the systematic review per (a) trophic level (TL) and (b) habitat in each ecosystem type.

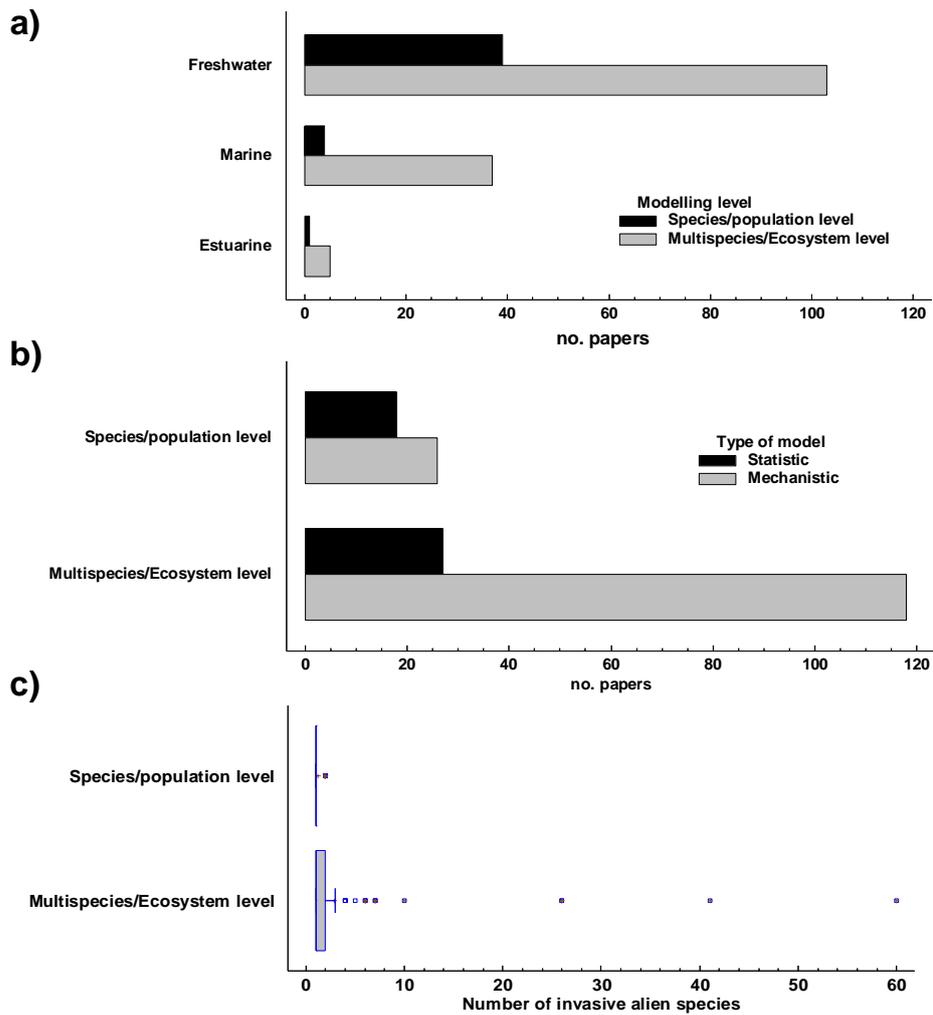


Figure 4. (a) Number of studies of each modelling level found in the systematic review per ecosystem type; (b) number of studies of each type of model per modelling level; and (c) number of IAS included per modelling level.

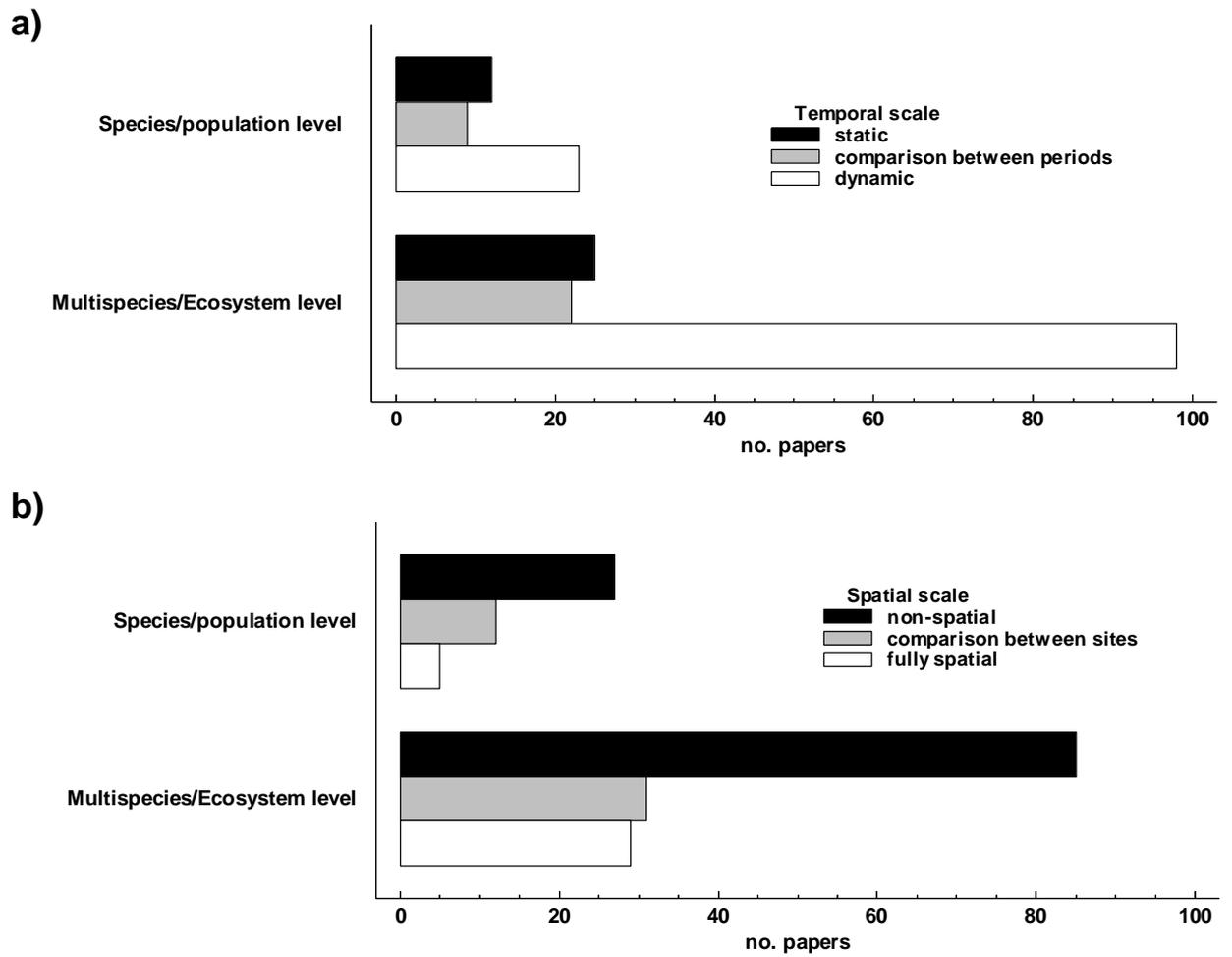


Figure 5. (a) Number of studies found in the systematic review by temporal and (b) spatial scale per modelling level.

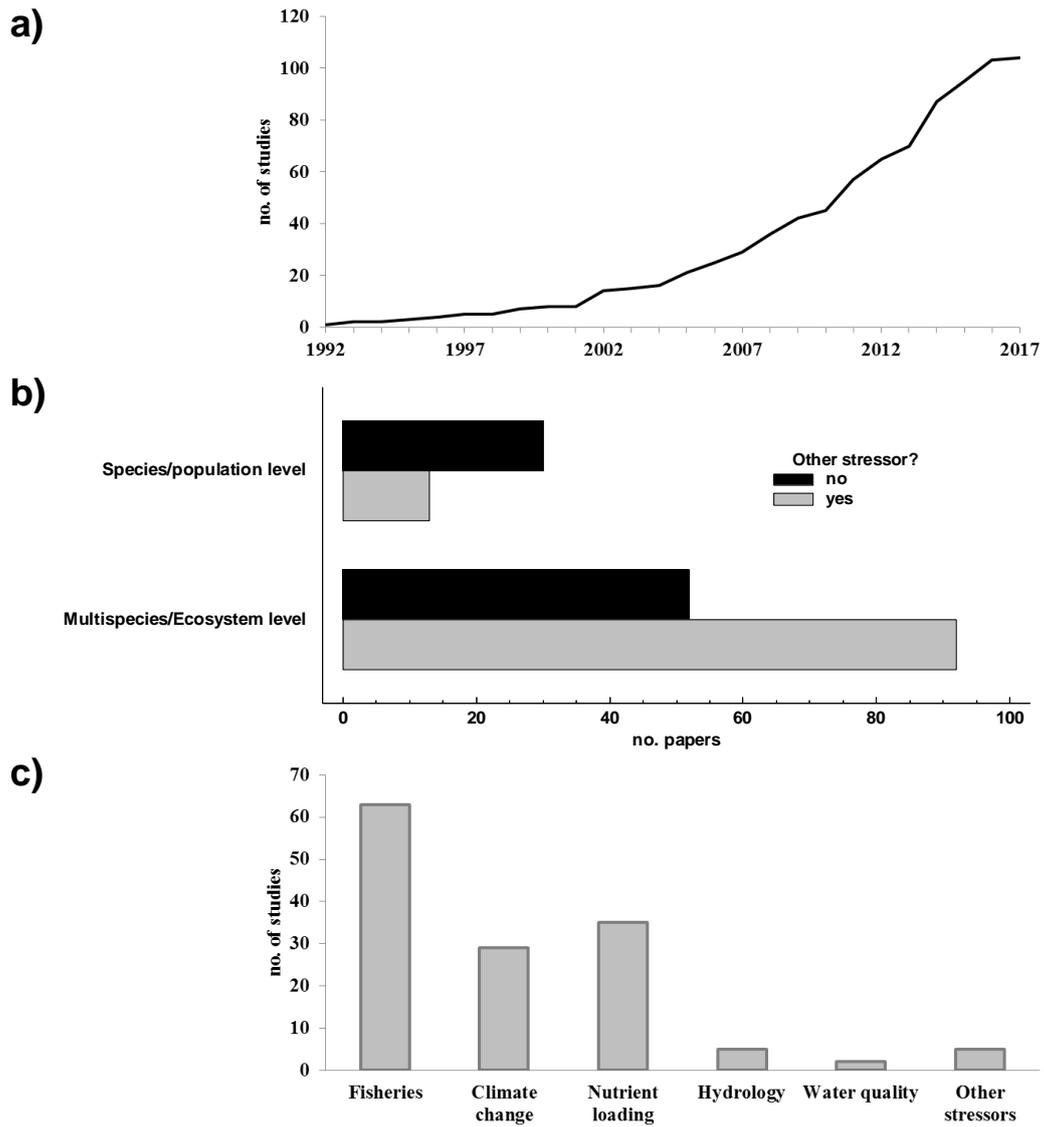


Figure 6. (a) Number of models that were driven by additional stressors found in the systematic review; (b) cumulative number of models that included other stressors over time; and (c) number of models that include each stressor.

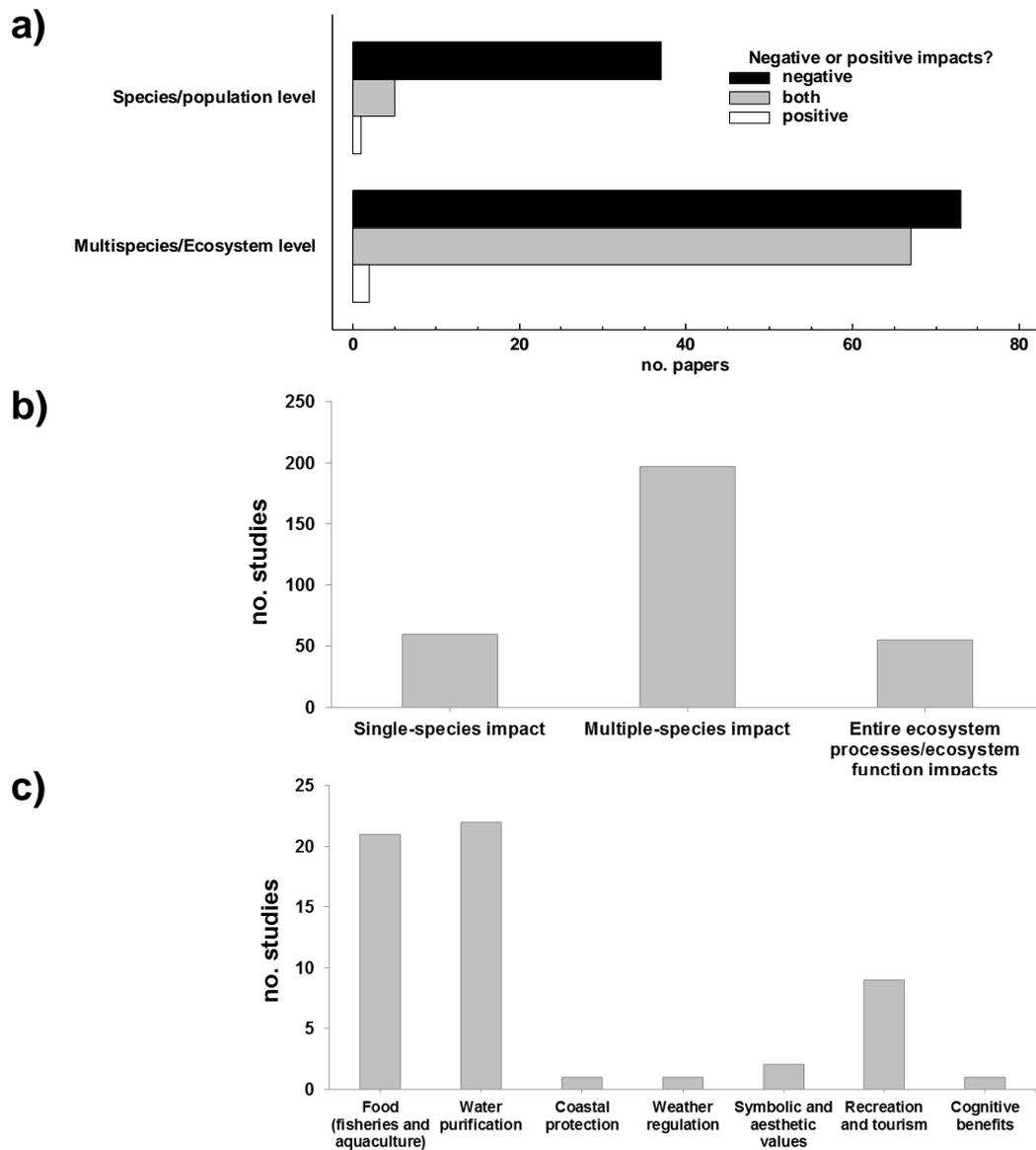


Figure 7. (a) Number of studies that assessed negative, positive or both negative and positive impacts; and overview of the number of studies that reported impacts on (b) biota and (c) ecosystem services.

Tables

Table 1. Number and percentage of IAS found in the selected models per taxonomic group and ecosystem type.

	Freshwater		Marine		Estuarine		Total	
	Number	%	Number	%	Number	%	Number	%
Plants	6	2.2	16	9.3	1	7.1	6	5
Parasites	5	1.8	0	0	0	0	5	1.1
Phytoplankton	3	1.1	3	1.7	0	0	6	1.3
Zooplankton	13	4.7	4	2.3	7	50	24	5.2
Bryozoa	0	0	2	1.2	0	0	2	0.4
Polychaetes	0	0	9	5.2	0	0	9	1.9
Barnacles	0	0	3	1.7	0	0	3	0.7
Mollusks	80	28.9	34	19.7	3	21.4	117	25.2
Ascidians	0	0	2	1.2	0	0	2	0.4
Ctenophores	0	0	16	9.3	0	0	16	3.5
Cnidarians	0	0	7	4.1	0	0	7	1.5
Shrimps	0	0	12	6.9	1	7.1	13	2.8
Crabs	3	1.1	11	6.4	0	0	14	3
Other benthic crustaceans	2	0.7	0	0	0	0	2	0.4
Fishes	161	58.1	54	31.2	2	14.29	217	46.8
Birds	4	1.4	0	0	0	0	4	0.9
Total	277	100	173	100	14	100	464	100

Table 2. Summary table of models found in the systematic review showing the model name, model category, a representative reference and if the modelling approach was coupled with other models (yes or not), temporal scale (ST: static; DY: dynamic; CP: comparative between periods), spatial scale (NS: non-spatial; CS: comparative between study sites; SP: spatial), if the model included other human stressors as drivers and which ones, and if the uncertainty was evaluated (yes or no).

Model name	Model category	Representative reference	Coupled	Temporal scale	Spatial scale	Other stressor	Which stressor	Uncertainty
Species/population level (17.4% of the total models)								
Statistic (57.6 % of species/population models)								
1	ANCOVA	Gribben and Wright (2006)	no	DY	CS	no		no
2	Linear models and structural equation modelling	Correa and Hendry (2012)	no	ST	CS	no		no
3	Multiple regression model	Van Zuiden et al. (2016)	no	DY	NS	yes	Temperature	no
4	Quantile regression models	Crane et al. (2015)	no	CP	NS	yes	Temperature	no
5	Behavioural choice model	Beville et al. (2012)	no	ST	NS	yes	Fishing	no
6	Bayesian hierarchical model	Cha et al. (2013)	no	CP	CS	no		yes
7	Poisson model and linear regression model	Ricciardi et al. (1995)	no	DY	CS	no		no
8	Generalised linear model (GLM)	Onikura et al. (2013)	no	ST	SP	no		no
9	Two-tiered modelling approach	Stapanian et al. (2009)	no	DY	NS	no		no
10	GIS-based spatial model	Woodford et al. (2011)	no	ST	SP	no		no
11	Species distribution model	Olden et al. (2011)	no	DY	SP	yes	Recreational users of lakes	no
12	Geostatistical model	Rowe et al. (2015b)	no	DY	SP	no		yes
Mechanistic (42.4% of species/population models)								
13	Von Bertalanffy growth model	Crane and Einhouse (2016)	no	CP	NS	no		no
14	Bioeconomic model	Liu et al. (2014)	no	DY	NS	yes	Fishing	yes
15	Hedonic price	Olden and Tamayo (2014b)	no	ST	NS	no		no
16	Schaefer model	Kateregga and Sterner (2009b)	no	DY	NS	yes	Fishing	no
17	Individuals-based models	Caldow et al. (2007)	no	DY	NS	no		no
18	Stage and age-structured models	Ferguson et al. (2012)	no	ST	NS	no		no

Multispecies/ecosystem level (82.6% of the total models)

Statistic (17.3% of multispecies/ecosystem models)

19	Linear model	Community	Bajer et al. (2016)	no	ST	CS	no		no
20	Least-squares regression	Community	Ricciardi (2003)	no	CP	CS	no		no
21	Multiple regression model	Community	Clavero et al. (2013)	no	ST	NS	yes	Footprint	no
22	Hierarchical Bayesian model	Community	Nilsson et al. (2012)	no	ST	CS	no		yes
23	Generalised linear model (GLM)	Community	De Amorim et al. (2015)	no	ST	CS	no		no
24	Generalised additive model (GAM)	Community	Knapp (2005)	no	CP	CS	no		no
25	Species occupancy models, boosted regression trees and linear and logistic regression models	Community	Macdonald et al. (2012)	no	ST	CS	no		no
26	Partial least square path model	Community	Jellyman and Harding (2016)	no	ST	NS	no		no
27	MARSS model	Community	Kratina et al. (2014)	no	CP	CS	yes	Temperature	no
28	Intervention time series model	Community	Pace et al. (1998)	no	DY	CS	no		yes
29	Structural equation modelling	Community	Pagnucco and Ricciardi (2015)	no	ST	CS	no		no
30	Transfer function (TF) models	Community	Aravena et al. (2009)	no	DY	CS	yes	River discharge and temperature	no
31	Species distribution model	Community	Wenger et al. (2011)	no	DY	SP	yes	Temperature	no

Mechanistic (82.7% of multispecies/ecosystem models)

32	Size-structured model	Community	Green et al. (2014)	no	DY	NS	yes	Fishing	yes
33	Bioenergetic model	Bioenergetics model	Walrath et al. (2015)	no	DY	NS	no		no
34	Age-structured model with bioenergetic model	Bioenergetics model	Stewart et al. (2010)	yes	DY	NS	yes	Temperature	no
35	Bioenergetic model coupled with phytoplankton growth model	Bioenergetics model	Reed-Andersen et al. (2000)	yes	DY	NS	no		yes
36	Integrated ecological-economic model for the Black Sea anchovy fishery	Bioeconomic model	Knowler (2005)	yes	DY	NS	yes	Fishing and nutrients	no
37	Integrated economic-biological model	Bioeconomic model	Settle and Shogren (2002)	yes	DY	NS	yes	Fishing	no
38	Ecological and economic model	Bioeconomic model	Grosholz et al. (2011)	yes	DY	CS	yes	Fishing	yes
39	Social-ecological model	Bioeconomic model	Roy et al. (2011)	yes	DY	NS	yes	Temperature and nutrient loading	yes
40	Mathematical model of the food web	Biogeochemical model	Fontaine and Stewart (1992)	yes	DY	NS	yes	Nutrient loading and pollution	no
41	Lake autotrophic model	Biogeochemical model	Higgins et al. (2014)	no	DY	NS	yes	Nutrient loading	no

42	Bioenergetic model coupled with eutrophication model	Biogeochemical model	Bierman et al. (2005)	yes	DY	SP	yes	Temperature and nutrient loading	yes
43	Coupled model of bioenergetic-based anchovy population dynamics and lower trophic food web structure	Biogeochemical model	Oguz et al. (2008)	yes	DY	NS	yes	Fishing and nutrient loading	no
44	Reactive-transport model	Biogeochemical model	Norkko et al. (2012)	no	DY	NS	no		no
45	Total phosphorous mass model	Biogeochemical model	Gudimov et al. (2015)	no	DY	SP	yes	Nutrient loading	yes
46	Simplified lake ecosystem mathematical model	Biogeochemical model	Magnea et al. (2013)	no	DY	NS	yes	Nutrient loading	no
47	Biophysical model	Biophysical model	Rowe et al. (2015a)	yes	DY	SP	no		yes
48	Ecosystem model developed for the Port Phillip Bay Environmental Study	Hydrodynamic-biogeochemical model	Murray and Parslow (1999)	yes	DY	SP	yes	Nutrient loading	no
49	Hydrodynamic model	Hydrodynamic-biogeochemical model	Macisaac et al. (1999)	yes	DY	SP	no		yes
50	ELCOM-CAEDYM	Hydrodynamic-biogeochemical model	Schwalb et al. (2014)	yes	DY	SP	yes	Temperature and nutrient loading	yes
51	3D SPBEM	Hydrodynamic-biogeochemical model	Isaev et al. (2016)	yes	DY	SP	yes	Temperature and nutrient loading	no
52	Lake Michigan ecosystem model (LM-Eco)	Hydrodynamic-biogeochemical model	Miller et al. (2010)	yes	DY	SP	yes	Temperature and nutrient loading	no
53	Two-dimensional hydrodynamic and water quality model (CE-QUAL-W2)	Hydrodynamic-biogeochemical model	Zhang et al. (2011)	yes	DY	SP	yes	Nutrient loading	no
54	2-dimensional physical and biological/reactive-transport model	Hydrodynamic-biogeochemical model	Laruelle et al. (2009)	yes	DY	SP	yes	Nutrient loading	no
55	PEGASE with POTAMON model	Hydrodynamic-biogeochemical model	Pigneur et al. (2014)	yes	DY	SP	yes	Temperature, nutrient loading and hydrodynamic	no
56	Dynamic ecosystem model of the lower trophic levels	Hydrodynamic-biogeochemical model	Fishman et al. (2009)	yes	DY	SP	yes	Temperature and nutrient loading	no
57	Ecological model BIOGEN	Hydrodynamic-biogeochemical model	Lancelot et al. (2002)	yes	DY	SP	yes	Temperature and nutrient loading	yes
58	Dynamic water quality model	Hydrodynamic-biogeochemical model	Glaser et al. (2009)	yes	DY	SP	yes	Nutrient loading	no
59	One-dimensional physical-biological ecosystem model	Hydrodynamic-biogeochemical model	Oguz et al. (2001)	yes	DY	SP	yes	Nutrient loading	no
60	Ecological-mathematical model	Hydrodynamic-biogeochemical model	Volovik et al. (1995)	no	DY	SP	yes	Temperature	no
61	CIMPAL	Conservative additive model	Katsanevakis et al. (2016)	no	ST	SP	no		
62	DPSEIR	Conceptual integrated model	Cook et al. (2014)	no	ST	NS	yes	Fisheries and temperature	
63	Loop models of ecological and socio-economic systems	Qualitative model	Ortiz and Stotz (2007)	no	DY	NS	yes	Fisheries	
64	Mathematical model of trophic interactions	Food-web model	Padilla et al. (1996)	no	DY	CS	no		yes

65	Pelagic food web	Food-web model	Amundsen et al. (2013)	no	CP	NS	no		no
66	Intermediate complexity for ecosystem assessments (MICE)	Food-web model	Blamey et al. (2014)	no	DY	NS	yes	Fishing	yes
67	Ecological Network Analysis	Food-web model	Miehls et al. (2009)	no	CP	CS	no		no
68	Ecopath with Ecosim (static)	Food-web model	Downing et al. (2012)	no	CP	NS	yes	Fishing	no
69	Ecopath with Ecosim (dynamic)	Food-web model	Kao et al. (2014)	no	DY	NS	yes	Fisheries and nutrient loading	no
70	Atlantis	End to end model	Nyamweya et al. (2016)	no	DY	SP	yes	Fisheries, nutrient loading and temperature	no

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