Functional response predicts invasiveness but not trophic impact

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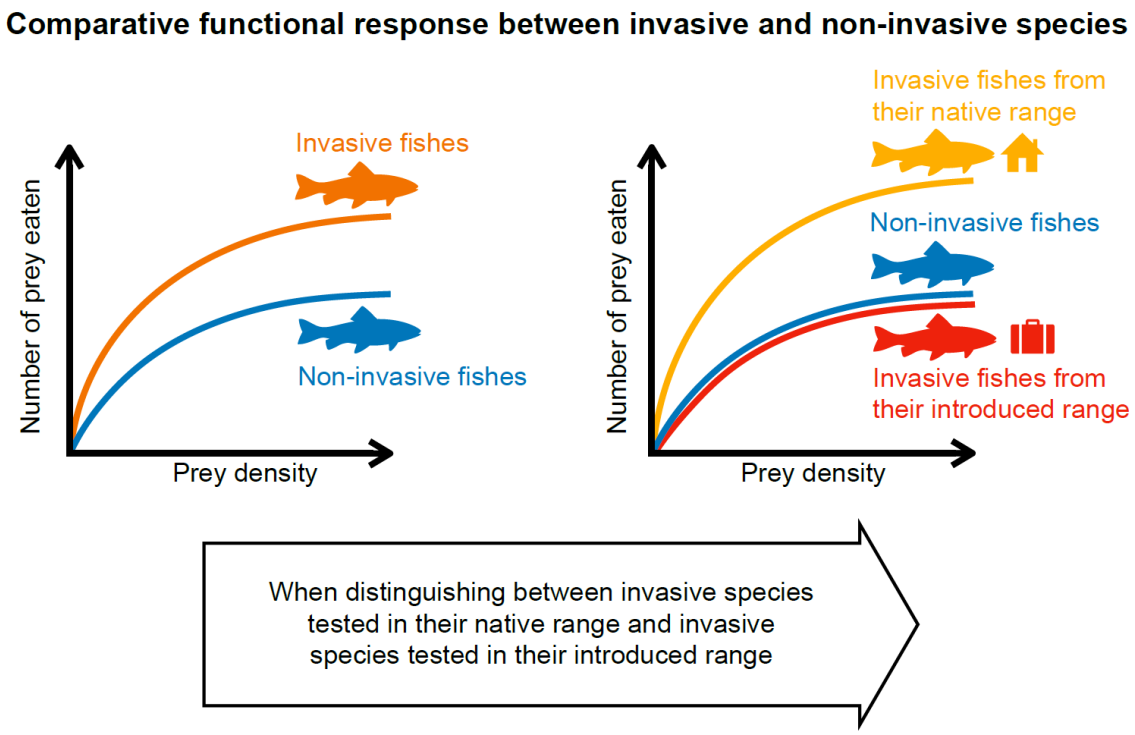
Data accessibility statement: For the purpose of review, the raw dataset files and the complete R script are available in a public repository on Gitlab at the following address: https://gitlab.com/marinecourtois/fr_invasive_status. Submission to a permanent repository, such as Zenodo, will occur upon the eventual final acceptance of the MS.

ABSTRACT. Biological invasions are recognized as one of the primary drivers of biodiversity erosion mainly because invasive species wield greater trophic impact than their non-invasive counterparts. The experimental paradigm for assessing the trophic impact of invasive species is the functional response test. This test is frequently conducted on invasive species sampled within their native ranges, implicitly assuming that such measures can be extrapolated to the invasive range. Using a meta-analysis of 269 functional responses in 45 fish species, we confirm that invasive species exhibited higher functional responses than non-invasive species. However, this pattern holds true only when considering invasive species sampled in their native range. Invasive species studied in their invasive range displayed functional responses comparable to non-invasive species. These results raise questions on the use of functional responses to predict invasiveness and trophic impact and on the mechanisms leading to trait convergence between invasive and non-invasive species in introduced ecosystems.

52 **Graphical abstract:**



53

54 **INTRODUCTION**

55 The interplay between species traits and the biological invasion processes continues to raise
56 fundamental questions about ecological adaptation and species success and has far-reaching
57 implications for biodiversity conservation and ecosystem resilience. Certain traits, such as
58 selfing capacity in plants (Razanajatovo et al. 2016), physiology (Christensen et al. 2021) or
59 personality in animals (Behrens et al. 2020; Chapple et al. 2012; Jolles et al. 2020) can be
60 positively selected by the invasion processes, rendering the species that possess these traits
61 potentially successful invaders. Post-establishment, species traits may be altered in response to
62 new selective pressures within the recipient ecosystem, thereby inducing alterations in the
63 environmental niche (niche shift, Broennimann et al. 2007; Guisan et al. 2014). For instance,
64 the absence of natural enemies, including competitors, predators and parasites, has been
65 identified as an important driver of invasion success (the Enemy Release Hypothesis, Colautti
66 et al. 2004; Heger & Jeschke 2014; Keane & Crowley 2002; Meijer et al. 2016). Random
67 variations in species traits may also be attributed to the founder effect, whereby introduced
68 populations experience a genetic bottleneck whose magnitude is determined by population size,
69 introduction frequency, and distance from source population (Dlugosch & Parker 2008;
70 Dlugosch et al., 2015; Simberloff 2009). As a consequence of these non-mutually exclusive
71 adaptive and neutral processes, species traits can diverge not only between native and invasive
72 geographic ranges but also between introduced populations within the invasive range.

73 Among the traits likely to promote invasion success, those associated with resource
74 acquisition have been extensively studied. Consumers exhibiting high feeding rates and/or
75 broad diets are more likely to satisfy their nutritional needs in novel environments, but also a
76 higher probability of disrupting the balance of local communities. Predation by invasive species
77 is recognized as a major threat to biodiversity and has been estimated to cause a 21% decline
78 in species richness in aquatic habitats (Mollot et al. 2017; Reid et al. 2019). In the invasion

ecology terminology, the Resource Consumption Hypothesis posits that invasive species are more efficient consumers than non-invasive species (Faria et al. 2025; Ricciardi et al. 2013). However, whether this represents a general pattern and functions as a cause or consequence of the invasion process remains to be elucidated.

A validated methodology for quantifying trophic interaction strength consists in modeling the functional response, which is defined as the relationship between *per* capita consumption rate and resource density (Holling 1959). The shape of this response provides insights into potential consequences for resource populations, with certain shapes indicating more destabilizing effect than others (type-II versus type-III functional responses, Daugaard et al. 2019; Murdoch & Oaten 1975; Uszko et al. 2015). Additionally, it provides an overview on consumers' behavior and how they attempt to maximize energy intake while minimizing costs under conditions of resource limitation (Galarowicz & Wahl 2005; Oyugi et al. 2012; Murray et al. 2013). The most prevalent functional response shape is characterized by a saturation curve (Holling 1959) wherein the maximal consumption rate is constrained by handling time, which is defined as the time required for a consumer to subdue, ingest, and digest a resource item (DeLong 2021). The consumption rate at low resource densities provides an indicative of consumer efficiency and is referred to as the space clearance rate or attack rate (DeLong 2021; Jeschke et al 2002; Hassell & May 1973; Holling 1959).

Under the Resource Consumption Hypothesis invasive species are predicted to have higher functional responses than non-invasive species (Bollache et al. 2008; Dick et al. 2013, 2014). If invasive species are predisposed toward strong trophic impacts, populations of the invasive species in the donor area should exhibit higher functional responses than trophic counterparts exhibiting no invasive tendency (Dick et al. 2014). Under these circumstances, functional responses could be used as a screening mechanism for species invasiveness. Conversely, if trophic impact is amplified post invasion in response to new environmental

conditions, such as prey naïveté (Cox & Lima, 2006; Sih et al. 2010), introduced populations (IS-IR) should exhibit higher functional responses than the non-invasive (NIS) counterparts with which they will compete (Xu et al. 2016). From this alternative perspective, comparative functional response is a valuable tool for quantifying the trophic impacts on local resources.

Among the growing number of functional response comparisons made on plants, invertebrates, and vertebrates (Alexander et al. 2014; Barrios-O'Neill et al. 2014; Ens et al. 2021; Funk & Vitousek 2007; Howard et al. 2018; 2022; Kattler et al. 2023; Landi et al. 2022), several studies have reported that invasive species exhibit higher space clearance rates and lower handling times than non-invasive species (*i.e.,* trophic analogs from the introduced range without invasive status). A recent large-scale comparative study across a broad range of taxa suggests that this may be a general pattern (Faria et al. 2025), although such studies remain relatively scarce. This scarcity is primarily due to the absence of unifying experimental framework, resulting in a divergence among functional response experiments, particularly in aspects related to the characteristics of the interacting species (size, mass, density), experimental protocol (duration of the test, area, volume and shape of the experimental arena) and the environmental conditions (most notably temperature, which is of primary importance for ectotherm species). This heterogeneity posed considerable challenges to comparative functional responses until the development of a database that systematically collected standardised functional response data from studies conducted worldwide. The FoRAGE database (Uiterwaal et al. 2018) facilitates the investigation of the role of species and environmental characteristics as potential drivers of functional response parameters. Using over 300 fish functional responses from this database, Buba et al. (2022) found that the alien status was not a strong predictor of functional response parameters. However, the majority of the functional responses for invasive species were obtained from populations of their native range. These findings support the hypothesis that increased trophic impact may emerge post-invasion

129 as a consequence of new selective pressures, yet it leaves unresolved the broader question of
130 whether invasive and non-invasive species inherently differ in their functional response.

131 The objectives of this study are twofold. Firstly, we addressed the prevailing hypothesis
132 that invasive species exhibit higher functional responses than non-invasive species. Secondly,
133 the study aimed to establish whether functional responses are consistent when studies are based
134 on invasive species sampled in either their native or their introduced range. Assuming that
135 ecological novelty (*e.g.*, prey naïveté) exerts a more significant influence than preadaptation in
136 increasing the trophic impact of invasive species, we predicted that, invasive species from their
137 introduced range would demonstrate a higher functional response (*i.e.*, higher space clearance
138 rate, lower handling time, or both) than non-invasive species and invasive species from their
139 native range. Should such a discrepancy be observed, it would imply that results obtained from
140 tests carried out on individuals sampled in their native range should be interpreted with caution
141 when employed to predict the trophic impact of a species in its invasive range.

142 We conducted this comparative analysis in 45 freshwater fish species including 23 non-
143 invasive species and 22 invasive species sampled either in their native range or their introduced
144 range. Freshwater fish species are particularly sensitive to biological invasions and alterations
145 to their trophic networks (Albert et al. 2021; Reid et al. 2019; Sayer et al. 2025). They are
146 among the species for which the most data on functional responses are available (Uiterwaal et
147 al. 2018). The analysis of phylogenetic inertia was facilitated by the focus on a single,
148 homogeneous taxonomic group.

149

150 **MATERIAL AND METHOD**

151 **Functional response data.** The functional responses parameters used in this analysis were
152 obtained from the FoRAGE database (version 5 on 20 December 2024, Uiterwaal et al. 2018,

153 Uiterwaal et al. 2022), which is an extensive compilation of functional responses derived from
154 extant literature. These functional response parameters have been standardized to ensure the
155 comparability of the space and time units (see details below). The median values were reported
156 alongside the 95% quantiles of the bootstrapped parameter distributions. The database, when
157 available, also reported information regarding predators (species, body mass, life stage, juvenile
158 or adult), prey (species, body mass, life stage), and the original experimental conditions
159 (temperature, arena dimension). A total of 353 observations of functional responses in
160 freshwater fish species were identified in FoRAGE database (See PRISMA flowchart, Fig. S1).
161 Their functional responses were fitted in the database with a type II model using standardized
162 methods (Uiterwaal et al. 2018). The type II functional response is described by Holling's disk
163 equation (Eq. 1, Holling 1959):

164 $$F = \frac{aD}{1 + aDh}$$

165 This functional response equation relates consumption rate F (number of preys consumed per
166 unit of time) to prey density D (number of preys per unit of space, where space is generally a
167 volume of water in the case of fish species). The functional response is determined by two two
168 key parameters, a and h. The clearance rate or attack rate a (DeLong 2021; Holling 1959)
169 defines the volume of space cleared of prey per predator. It serves as a measure of predatory
170 efficiency at low prey densities (Jeschke et al. 2002). The handling time h corresponds to the
171 time required for a predator to capture, handle, and digest a prey item (DeLong 2021).

172 In the majority of functional response studies, the units of the parameters a and h remain
173 undefined. Authors typically compared responses of several populations within the same
174 species and the same study using identical experimental setup. As the primary focus of these
175 studies was on the significance of the difference between homogeneous experimental groups,
176 direct comparisons were made between the numerical values of the estimates, albeit without a

clear definition of the units. Nevertheless, it is imperative to unambiguously define these units in order to allow meaningful comparisons across studies. In order to express the functional response in homogeneous units, the focus was placed on studies based on 3D arena, i.e. where space units were volumes (See PRISMA flowchart, Fig. S1).

In accordance with the standardized value reported in FoRAGE database, the space clearance rate *a* was expressed in cubic meters per day per predator (units: $m^3.day^{-1}$). The handling time *h* was expressed in time unit times number of predator per number of prey (units: day). Our primary analyses were conducted using these *per capita* units (hereafter referred to as 'standard units'), which focused on the number of prey individuals removed from the environment. However, the number of prey items consumed varied by several orders of magnitude, depending on whether the prey species in question are, for instance, Daphnia or vertebrate species. From the perspectives of functional ecology or predator physiology, the consequences of consuming one prey item are not equivalent when the predator and prey species strongly differ in size. To account for substantial variability in body size, analyses were repeated after converting *a* and *h* into prey and predator biomass (hereafter referred to as 'biomass units'). In these secondary analyses, biomass clearance rate *a* was expressed in cubic meters per kilogram of predator per day (units: $m^3.kg^{-1}.day^{-1}$), and biomass handling time *h* was expressed in time unit times kilogram of predator per kilogram of prey per day (units: day).

The analyses presented herein were based on a total of 269 estimates of *a* and *h*, reported in a total of 45 freshwater fish species from 40 studies (See PRISMA flowchart, Fig. S1). Interspecific differences were analyzed through a comparison of their mean values of the functional response parameters *a*, or *h*, but also the Functional Response Ratio FRR = *a/h*, which has recently emerged as a reliable metric for balancing the two functional response parameters (Faria et al. 2025; Cuthbert et al. 2019b). Due to missing information about prey

body mass in the original articles, the analyses based on biomass units were conducted on 254 estimates for the handling time *h* and FRR a/h.

Invasive status and geographic range of sampling. The functional response database was completed with the invasive status of each freshwater fish species specified as ‘invasive' or ‘non-invasive’. For this purpose, we relied on the Global Register of Introduced and Invasive Species (GRIIS, Pagad et al. 2018), conceived within the framework of the Global Invasive Alien Species Information (GIASI) partnership of the Convention on Biological Diversity (CBD). It provides the first country-by-country checklists of invasive species. This classification has been established on the basis of the number of countries in which the species have been introduced and their ecological impact in the countries into which they were introduced. The classification of a species as ‘invasive’ was determined by its introduction into at least one country outside the limits of its native geographic range, and by the potential threat to native biodiversity that its spread poses, which is referred to as “evidence of impact” in GRIIS database. Following this classification, our study was based on a total of 22 invasive species from 31 studies (168 observations functional response estimates for *a* and *h*), and 23 non-invasive species from 19 studies (101 observation of *a* and *h*). Furthermore, we distinguished between the geographical regions ('native range' vs 'invasive range') from which fish were sampled. All non-invasive species (NIS) were sampled in their native range. However, for invasive species, it was necessary to differentiate between studies conducted on invasive species sampled in their native range (IS-NR, donor population, 13 species from 20 studies, 107 estimates) and those conducted on invasive species sampled in their invasive range (IS-IR, introduced population, 11 species from 13 studies, 61 estimates). The classification of each functional response data in either NIS, IS-NR or IS-IR was determined by comparing the sampling geographic range reported in each original study with the corresponding invasive status and native range referenced in the GRIIS database. All observations identified in the

226 FoRAGE database that did not report information regarding the sampling area of the fish
227 species have been excluded from the analyses (see PRISMA flowchart, Fig. S1).

228 **Effect of the temperature**. Previous study (Buba et al. 2022) reported an effect of the
229 temperature at which the functional response assays were carried out. The temperature was thus
230 taken into account in the analyses. All observations identified in the FoRAGE database that did
231 not report information regarding the experimental temperature have been excluded from the
232 analyses (see PRISMA flowchart, Fig. S1).

233 **Phylogenetic tree.** Species that share a common ancestor often possess inherited traits due to
234 descent rather than independent adaptation. Some traits exhibit a strong phylogenetic signal,
235 meaning they are conserved along lineages. Consequently, closely related species cannot be
236 considered as independent data points. In addition, certain taxa may be overrepresented in the
237 literature, potentially biasing analyses. Therefore, comparative analyses must incorporate
238 phylogeny to enhance their robustness and reduce potential biases (Cinar 2022; Lajeunesse et
239 al. 2013). Our analyses took into account the phylogenetic relationships between the fish
240 species. The phylogenetic correlation matrix was integrated at species-level in all our models.
241 This matrix was derived from the phylogenetic tree (Fig. 1) constructed for the 45 freshwater
242 fish species present in our dataset, with the R package 'FishPhyloMaker' (Nakamura et al.
243 2021). Within this tree, invasive species were distributed across all families or orders, with no
244 single taxon accounting for a disproportionately large number of species (Fig. 1). Lynch's
245 formula was applied to estimate the phylogenetic signal (or phylogenetic heritability) for each
246 functional response parameter expressed in both standard and biomass units (Garamszegi
247 2014).

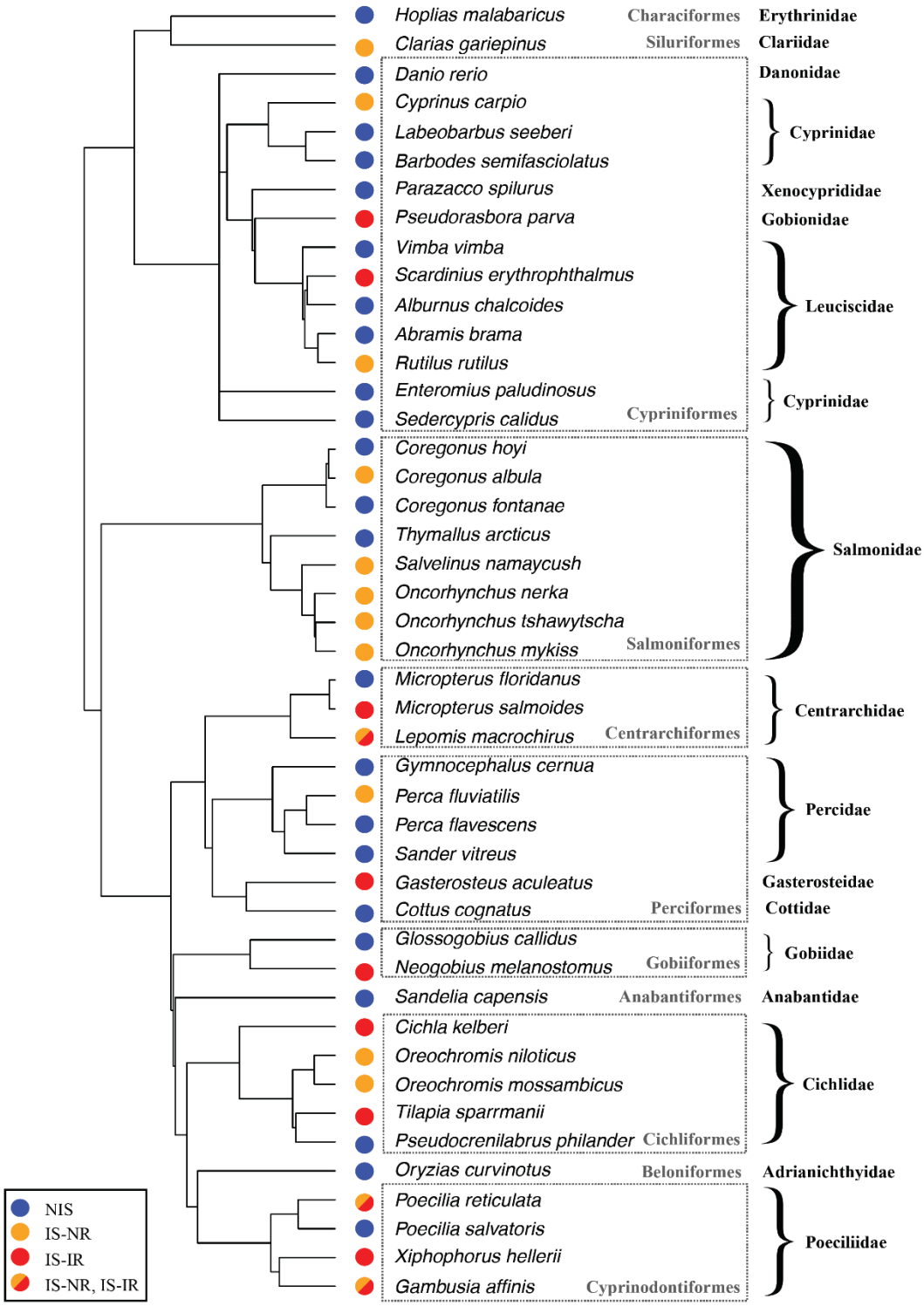


Figure 1: *Phylogenetic tree of the 45 freshwater fish species used in the analyses. Each colored circle in front of the species names illustrates the status of the species: non-invasive species (NIS, blue circle, all were sampled in their native range), invasive species sampled either in their native range (IS-NR, donor populations, orange circle) or in their invasive area (IS-IR, introduced populations, red circle). Some invasive species have been sampled both in their native range and in their invasive range depending on the specific study undertaken (IS-NR and IS-IR, bicolor circle). Taxonomic rank is reported at the order (in grey in dotted boxes) or family level (in bold black, on the right side).*

256 **Statistical analysis.** All analyses were carried out separately for each functional response
257 parameters (*a*, *h*, FRR, both in the standard units and in biomass units). Due to the wide
258 variation between species, the distributions of these parameters were highly skewed. We used
259 log transformation to normalize data and make it symmetric, thus meeting the assumptions of
260 normality and homoscedasticity. There was no missing data in our datasets, thereby enabling
261 model selection based on information theory (Nakagawa & Freckleton 2011) to test whether
262 invasive status (non-invasive vs. invasive species) or sampling range (NIS, IS-NR, IS-IR)
263 explained the differences in functional response parameters.

264 The phylogenetic correlation matrix derived from our phylogenetic tree was used as random
265 variable in all models using a phylogenetic mixed model approach (Hadfield & Nakagawa
266 2010) with the R package MCMCglmm for Bayesian mixed models (Hadfield 2010), assuming
267 a Brownian model of trait evolution (Hadfield & Nakagawa 2010). The Markov-chain Monte
268 Carlo (MCMC) was used with $3x10^5$ iterations, 300 burn-in period and a thinning interval of
269 100 and an inverse-Wishar prior. Prior type had no impact on the conclusions that were drawn
270 from the analyses.

271 For each functional response parameter (*a*, *h*, or FRR) and for each unit (standard or
272 biomass unit), several competitive models were considered. The simplest model, 'Model 0',
273 solely took into account phylogenetic correlation matrix as random variable. No discrimination
274 was made between invasive status (non-invasive vs. invasive species) or sampling status (NIS,
275 IS-NR, IS-IR). 'Model 1' considered the invasive status, invasive (IS) versus non-invasive
276 (NIS) species, as fixed effect, irrespective of the geographic area in which the species had been
277 sampled. 'Model 2' considered the sampling status as fixed effect. This composite variable was
278 a three-level factor: non-invasive species (NIS, which were always sampled in their native
279 range), invasive species sampled in their native range (IS-NR, donor population), and invasive
280 species sampled in their invasive range (IS-IR, introduced population). Because Model 1 and

Model 2 were not nested, it was not possible to directly compare them using likelihood ratio test. They were compared using information criterion (Burnham & Anderson, 2004). Model selection was performed using the deviance information criterion (DIC, Spiegelhalter et al. 2002). The models with the lowest DIC value were considered the best models. Models with $\Delta DIC > 2$ were considered to have significantly worse fit, and models with $\Delta DIC < 2$ were considered to have equivalent support to the best model (Barnett et al. 2010). All these analyses were repeated separately for each functional response parameter (*a*, *h*, FRR) both in standard units and in biomass units.

The temperature was taken into account as fixed variable. 'Model 3' considered the temperature, the sampling status, and their interaction as fixed effects. The effects of the explanatory variables and their interaction term were analyzed by comparing the DIC of the nested models, using the same model selection procedure as described above.

Data processing and analysis were carried out with the R programming language (version 4.4.3, R Development Core Team 2025).

RESULTS

Effect of the invasive status. The functional response parameters expressed in standard units varied significantly according to the invasive status (non-invasive vs. invasive species). Space clearance rate *a* (posterior mean = -1.07, 95% credible interval 95%CrI = [-1.63; -0.55], pMCMC = 6.7×10^{-04}, Fig. 2A), as well as FRR = *a/h* (posterior mean = -1.8, 95%CrI = [-2.83; -0.94], pMCMC = 3.0×10^{-04}) were significantly higher for invasive species than for non-invasive species, and handling time *h* (posterior mean = 0.82, 95%CrI = [0.18; 1.54], pMCMC = 0.022) were significantly lower for invasive species than non-invasive. Similar effects, though less pronounced, were found for functional response parameters expressed in biomass

305 units: space clearance rate *a* (posterior mean = -0.49, 95%CrI = [-0.94; -0.028], pMCMC =
306 0.043), FRR *a/h* (posterior mean = -1.12, 95%CrI = [-2.01; -0.26], pMCMC = 0.019), and
307 handling time *h* (posterior mean = 0.60, lower and upper 95%CrI= [-0.010; 1.23], pMCMC =
308 0.056).

309 **Effect of the sampling status**. The ΔDIC > 6 in the model selection procedure (Table 1)
310 indicated strong evidence that the 'Model 2' based on sampling status (NIS, IS-NR, IS-IR) was
311 a substantially better fit of the data compared to 'Model 1' based solely on the invasive status
312 (non-invasive vs. invasive species) for all functional response parameters expressed in standard
313 units. When invasive species were separated into two distinct groups, donor populations (IS-
314 NR) and introduced populations (IS-IR), donor populations showed higher space clearance rate
315 *a* (posterior mean = 0.88, 95%CrI = [0.49; 1.27], pMCMC < 3×10^{-04} ; Fig. 2B), lower handling
316 time *h* (posterior mean = -1.18, 95%CrI = [-1.89; -0.44], pMCMC = 1.3×10^{-03} ; Fig. S2A) and
317 higher FRR a/*h* (posterior mean = 2.11, 95%CrI = [1.22; 2.97], pMCMC < 3×10^{-04}, Fig. S2C)
318 than introduced populations. Furthermore, introduced populations and native species did not
319 differ in space clearance rate *a* (posterior mean = -0.56, 95%CrI = [-1.15; -0.02], pMCMC =
320 0.062, Fig. 2B), handling time *h* (posterior mean = 0.038, 95%CrI = [-0.83; 0.82], pMCMC =
321 0.92, Fig. S2A) and FRR a/*h* (posterior mean = -0.51, lower and upper 95%CrI = [-1.55; 0.50],
322 pMCMC = 0.33, Fig. S2C). Fully consistent results were observed for the three parameters *a,*
323 *h,* and FRR expressed in biomass units (Table S1, Fig. S3A,C,E).

324

325 ***Table 1***. *Model selection table for the influence of sampling status on each functional response*
326 *parameter (space clearance rate a, handling time h, and functional response ratio FRR = a/h) expressed*
327 *in standard units. The competitive models were ranked according to their DIC. For a detailed*
328 *description of the three models, refer to the main text.*

Model	**Clearance rate a**		**Handling time h**		**FRR = a/h**	
	DIC	ΔDIC	DIC	ΔDIC	DIC	ΔDIC
Model 2 (sampling status)	579.48	0	1052.58	0	1105.65	0
Model 1 (invasive status)	597.94	18.46	1058.67	6.09	1121.22	15.57
Model 0 (intercept only)	598.97	19.49	1059.72	7.14	1124.03	18.38

329

330 **Effect of the temperature**. For the study of space clearance rate *a*, there was substantial
331 support for an effect of the interaction between the sampling status (NIS, IS-NR, IS-IR) and
332 temperature (ΔDIC > 12 in Table 2). In non-invasive species (NIS), *a* decreased as a function
333 of the temperature (posterior mean slope = -0.095, 95%CrI = [-0.136; -0.0526], pMCMC <
334 3×10^{-04}, Fig. 2C), whereas introduced populations appeared to react positively, but non
335 significantly, to temperature (Table S3). The same pattern was observed for the functional
336 response ratio *a/h* (ΔDIC > 2 in Table 2, Fig. S2D, Table S3). By contrast, the handling time *h*
337 (Table 2, Fig. S2B, Table S3) was unaffected by the temperature (ΔDIC > 3 in Table 2). The
338 analyses based on the dataset in biomass units led to consistent results (Table S2, Fig. S3B,D,F,
339 Table S4).

340

341 ***Table 2***. *Model selection table for the effect of sampling status and experimental temperature on each*
342 *functional response parameter (space clearance rate a, handling time h, and functional response ratio*
343 *FRR = a/h) expressed in standard units. The full model ('Model 3', see main text) and all the nested*
344 *models were ranked according to their DIC. The fixed variables considered were the experimental*
345 *temperature (T°), the sampling status (NIS, IS-NR, IS-IR), and their interaction term T°:status between*
346 *Temperature and sampling status. Degree of freedom (df) for each model is also reported.*

Parameter	**Nested model**			**df**	**DIC**	**ΔDIC**
a	T°	Status	T°: Status	8	565.9	0
	T°	Status		6	578.8	12.89
		Status		5	579.3	13.39
				3	599.0	33.05
	T°			4	601.0	35.01
h		Status		5	1052.6	0
	T°	Status		6	1054.2	1.62
	T°	Status	T°: Status	8	1055.7	3.11
				3	1059.8	7.18
	T°			4	1061.7	9.04
FRR = *a/h*	T°	Status	T°:Status	8	1103.4	0
		Status		5	1105.6	2.18
	T°	Status		6	1107.8	4.38
				3	1124.0	20.64
	T°			4	1126.6	23.17

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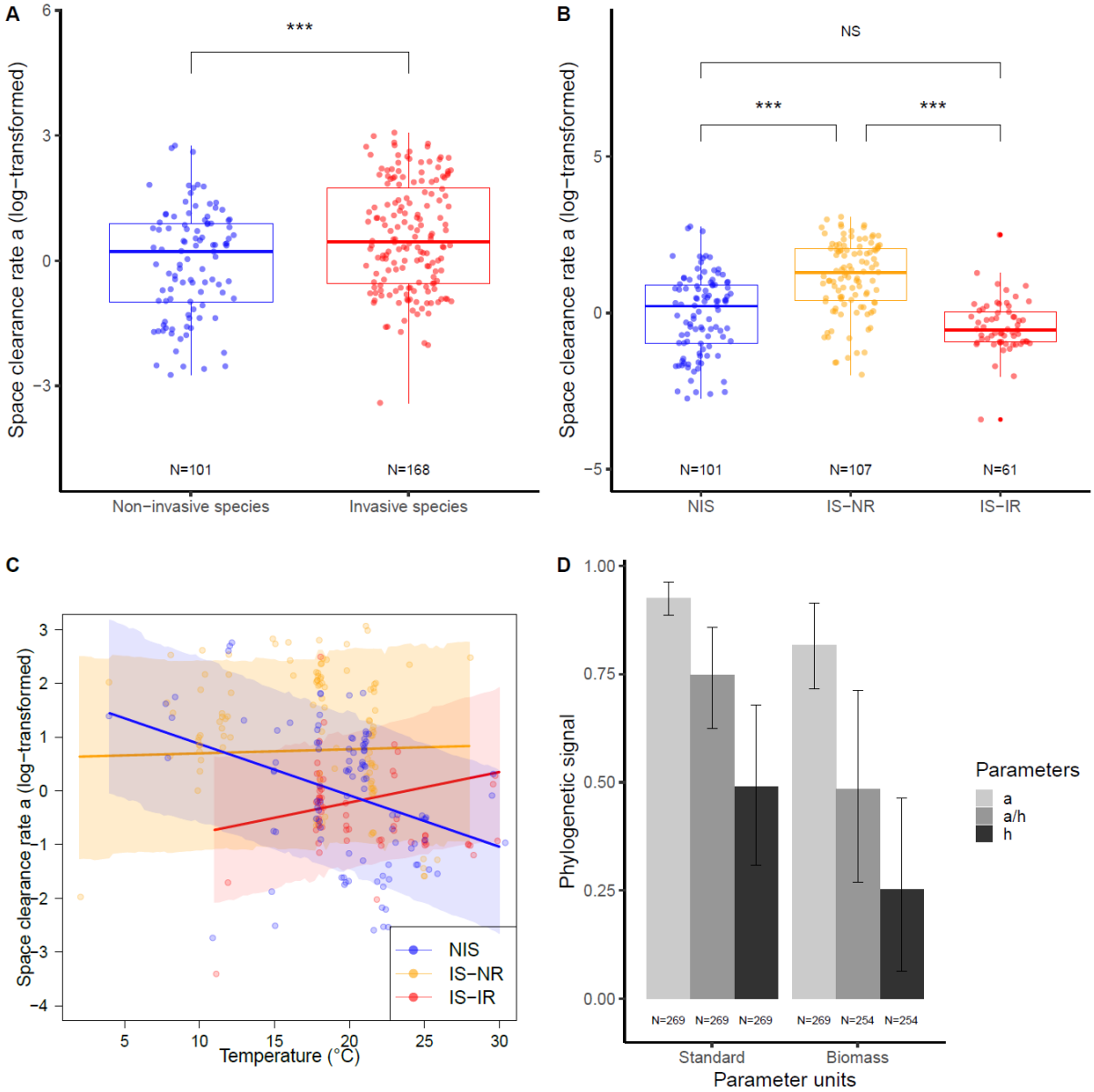

Figure 2: *The functional response parameters are expressed in standard units (log-transformed).* **A)** *Boxplot of space clearance rate as a function of the invasive status, non-invasive vs. invasive species.* **B)** *Boxplot of space clearance rate as a function of the sampling status, which was either non-invasive (NIS, in blue, all were sampled in their native range), invasive species sampled in their native range (IS-NR, donor populations, in orange) or invasive species sampled in their invasive range (IS-IR, introduced populations, in red).* **C)** *Interaction between sampling status and temperature.* **D)** *Barplot of the phylogenetic signal for the various functional response parameters (space clearance rate a, handling time h and functional response ratio FRR = a/h) expressed in standard or biomass units. These signals were calculated using Lynch's phylogenetic heritability formula (Garamszegi, 2014). The sample size (N) is indicated below each group when relevant. The sample size differed for the analyses in biomass unit due to unreported values. Each data point corresponds to the report in a specific article of one estimated value of clearance rate for one species. Multiple data points may correspond to the same species studied across different articles. The mixed-effect model incorporates multiple imputations and accounts for phylogenetic inertia. "***" indicates pMCMC < 0.001, and NS pMCMC > 0.05.*

Phylogenetic signals. The phylogenetic signals were greater than 0.50 for all functional response parameters, with the strongest effect observed for the space clearance rate (a = 0.93, 95%CI = [0.89; 0.96] in standard units, a = 0.82, 95%CI = [0.72; 0.91] in biomass units, Fig. 2D). A phylogenetic signal of 0 indicates phylogenetic independence, whereas a signal of 1 indicates very strong variation in the parameter with phylogeny (Freckleton et al. 2002). These results underscore the importance of including phylogeny in comparative analysis of functional response.

DISCUSSION

The results presented here compiled over 269 functional responses from 45 freshwater fish species to test whether invasive species are stronger consumers than non-invasive species while accounting for the area where invasive species were tested, phylogeny and temperature. Overall, invasive species exhibited higher functional responses compared to non-invasive species, but surprisingly this difference was driven by the invasive species tested in their native range. These results question the paradigm that drives the comparison of functional response between invasive and non-invasive species and suggest new hypotheses regarding how the invasion process can make species traits evolve.

When invasive species were not differentiated based on whether they were sampled in their native (donor population, IS-NR) or invasive range (introduced population, IS-IR), it was found that they had overall higher functional responses than non-invasive species, with significantly higher space clearance rates and a tendency for lower handling times. The results remained valid when the functional responses were expressed in ‘standard units' (per capita) or in ‘biomass units’, which accounted for the wide variability in body mass of prey and predator species across studies. These results are consistent with the prediction and underlying hypothesis of the comparative functional response approach, which states that invasive species

392 are better consumers than non-invasive species. This explains their success in becoming
393 invasive and their impact on the invaded ecosystems. (see the Resource Consumption
394 Hypothesis, Faria et al. 2025 ; Dick et al. 2014 ; Ricciardi et al. 2013). Until the present work,
395 this hypothesis had been supported by empirical functional response studies in various taxa
396 (Alexander et al. 2014; Barrios-O'Neill et al. 2014; Crookes et al. 2019; Cuthbert et al. 2019a;
397 Howard et al. 2018 ; Laverty et al. 2015; Paterson et al. 2015; Mofu et al. 2019; Madzivanzira
398 et al. 2021) but validation from more than one large-scale comparative approach was needed
399 (Faria et al. 2025). However, when the geographic range in which the functional responses of
400 invasive species were sampled was taken into account, it appeared that the general pattern of
401 higher consumption rate in invasive species compared to non-invasive species was largely
402 driven by studies based on donor populations (IS-NR).

403 Invasive species from their native range indeed exhibited significantly higher space
404 clearance rates *a* and lower handling times *h* than non-invasive species, which is in line with
405 the pre-invasion scenario in which some species would be predisposed to be invasive (Cadotte
406 et al. 2018; Hulcr et al. 2017; Schlaepfer et al. 2010; Suarez & Tsutsui 2008). In the previous
407 and unique comparative study also using the FoRAGE database, 309 functional responses
408 involving freshwater and marine predatory fishes were compiled to test the role of size, activity
409 level, temperature and invasive status as potential predictors of functional response parameters
410 (Buba et al. 2022). Invasive species were not classified based on their study area, but it
411 happened that the majority were investigated in their native range, allowing direct comparison
412 with our study. Although their results were qualitatively consistent with ours, they only found
413 a minimal connection between space clearance rates and invasive status. The reason could be
414 that the authors did not account for phylogenetic inertia.

415 The high functional response of donor populations (IS-NR) suggests that comparative
416 functional responses could be used to screen species for invasiveness with the aim of identifying

417 likely future invaders and preventing invasion (Hulcr et al. 2017; Van Kleunen et al. 2010).
418 Theory can help explain why species predisposed to invasiveness would not cause imbalance
419 to their community and remain unnoticed. When interspecific competition is greater than
420 intraspecific competition, superior competitors are predicted to exclude inferior competitors
421 (competitive exclusion, Bøhn et al. 2008; Gause 1934; Hardin 1960; Paine 1966; Tilman 1994).
422 According to optimal foraging theory, the most successful and therefore most frequently
423 encountered species should be the preferred resources of higher trophic-level natural enemies
424 such as predators and parasites (Ishii & Shimada 2012; Lacher et al. 1982; Pyke 1984). As a
425 result, natural enemies promote coexistence at the lower trophic level by decreasing the strength
426 of competitive exclusion (Chase et al. 2002; Chesson & Kuang 2008; Stump & Chesson 2017).
427 Competitors would exhibit their high potential once released from their natural enemies, as
428 occurs in the invasive range or in the experimental setting of functional response derivation.

429 Contrary to our prediction that prey novelty in the invasive range would benefit
430 introduced populations (IS-IR) through increased predation rates, their functional response ratio
431 was, on average, equivalent to that of non-invasive species (NIS) and lower than that of donor
432 population (IS-NR). This decrease was mainly driven by smaller space clearance rates and
433 could result from environmental constraints operating in the recipient ecosystem and leading to
434 trait convergence between introduced populations (IS-IR) and resident non-invasive species
435 (Craven et al. 2018). Comparative functional response studies involving donor (IS-NR) and
436 introduced (IS-IR) populations of the same invasive species, while also accounting for the time
437 elapsed since introduction, could help identify which mechanisms could explain trait
438 convergence in the recipient ecosystems. Indeed, environmental filtering (Gaston et al. 2009;
439 Keddy 1992), intra- and inter- generational phenotypic plasticity (within or between
440 individuals), or genetic changes (Marzluff 2012) could all be relevant factors. Whether invasive

species actually perform better in their introduced range remains controversial depending on the taxa studied (Parker et al. 2013).

A limitation of our study is that we estimated global differences between IS-NR and IS-IR, without direct comparison of donor (IS-NR) and introduced (IS-IR) populations within the same species. Data are currently lacking to perform such Comparative Functional Response approaches (CFR, Cuthbert et al. 2019b; Faria et al. 2023, 2025). Only three invasive species have been studied in both their native and invasive ranges.

This result also challenges the general assumption of a positive relationship between resource intake and performance (Brown et al. 2004; DeLong et al. 2021 ; Kooijman 2010), in that metabolically efficient species might not be those with high feeding rates, and therefore high functional responses, but those able to maintain viable metabolic rates while reducing the amount of resources required. Such “thrifty” species would have more chances to persist in ecosystems where ecological niches are occupied and become integrated into the local trophic network. Despite the bunch of literature on the crucial role of physiology in shaping the evolutionary trajectories and biogeographic distributions of non-invasive species (Somero 2002, 2005), there are to date few studies aimed at assessing the physiology of invasive species. Compared to non-invasive species, they would be more eurytherms (Kelley 2014, but see Boher et al. 2018), have higher mass-specific metabolic rates (Lagos et al. 2017), and be more efficient in both energy conversion and food intake (Kooijman 2010; Taylor & Dunn 2018) with ecomorphological advantages for feeding efficiency (Luger et al. 2020). Whether these findings are congruent with our results needs further research on the link between metabolism and functional response parameters.

Another important finding of our study concerns the negative consequences that climate change could have on recipient communities. The relationship between space clearance rate and temperature was indeed significantly negative in non-invasive species but tended to be

466 positive in invasive species tested in their introduced range. This means that a warmer
467 temperature could exacerbate the difference in functional response and likely the asymmetry in
468 competition between non-invasive (NIS) and invasive (IS-IR) species in recipient ecosystems.
469 Our result brings support to the literature suggesting that invasive species would often be less
470 vulnerable to warming because of predisposing physiological patterns, including energetic
471 performance and thermal tolerance (Bates et al. 2013; Kelley 2014; Komoroske et al. 2021;
472 Penk et al. 2019), their establishment being favored in certain ecosystemic contexts (Keller &
473 Shea 2021; Sorte et al. 2010; Stachowicz et al. 2002).

474 To conclude, our study calls into question the shortcut that invasive species have higher
475 functional responses than non-invasive species, without considering whether they were studied
476 in the native or introduced range. Ecological filters leading to trait convergence (at least from
477 the functional response perspective) between invasive populations and resident non-invasive
478 species seem to be at work in recipient communities and a promising avenue of research would
479 be to compare species traits, with a focus on metabolism, between donor and introduced
480 populations of the same invasive species but also between a recently introduced invasive
481 population with one that has been established for longer. From a broader perspective, this comes
482 down to asking how the invasion process shapes ecological niches through time (Ackerly 2003;
483 Broennimann et al. 2007; Mukherjee et al. 2012; Stiels et al. 2015; Wiens & Graham 2005).
484 Furthermore, the absence of differential functional response between invasive species in the
485 introduced range and non-invasive species raises concerns about the exclusive use of
486 comparative functional responses to predict the trophic impact of an invasive species.
487 Functional response should be used in combination with other metrics, such as species
488 abundance, to better predict impact (Dickey et al. 2020; Laverty et al. 2017). Our study also
489 reveals that global warming might exacerbate asymmetric competition between invasive and
490 non-invasive species as space clearance rate was found to decrease with temperature in non-

invasive species. We focused on freshwater fishes towards which functional response literature is largely uneven and biased, probably because freshwater research offers ideal model species and experimental conditions for functional response derivation. Extending our approach to other taxa is needed to know to what extent our results reflect general patterns.

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SUPPLEMENTARY MATERIAL

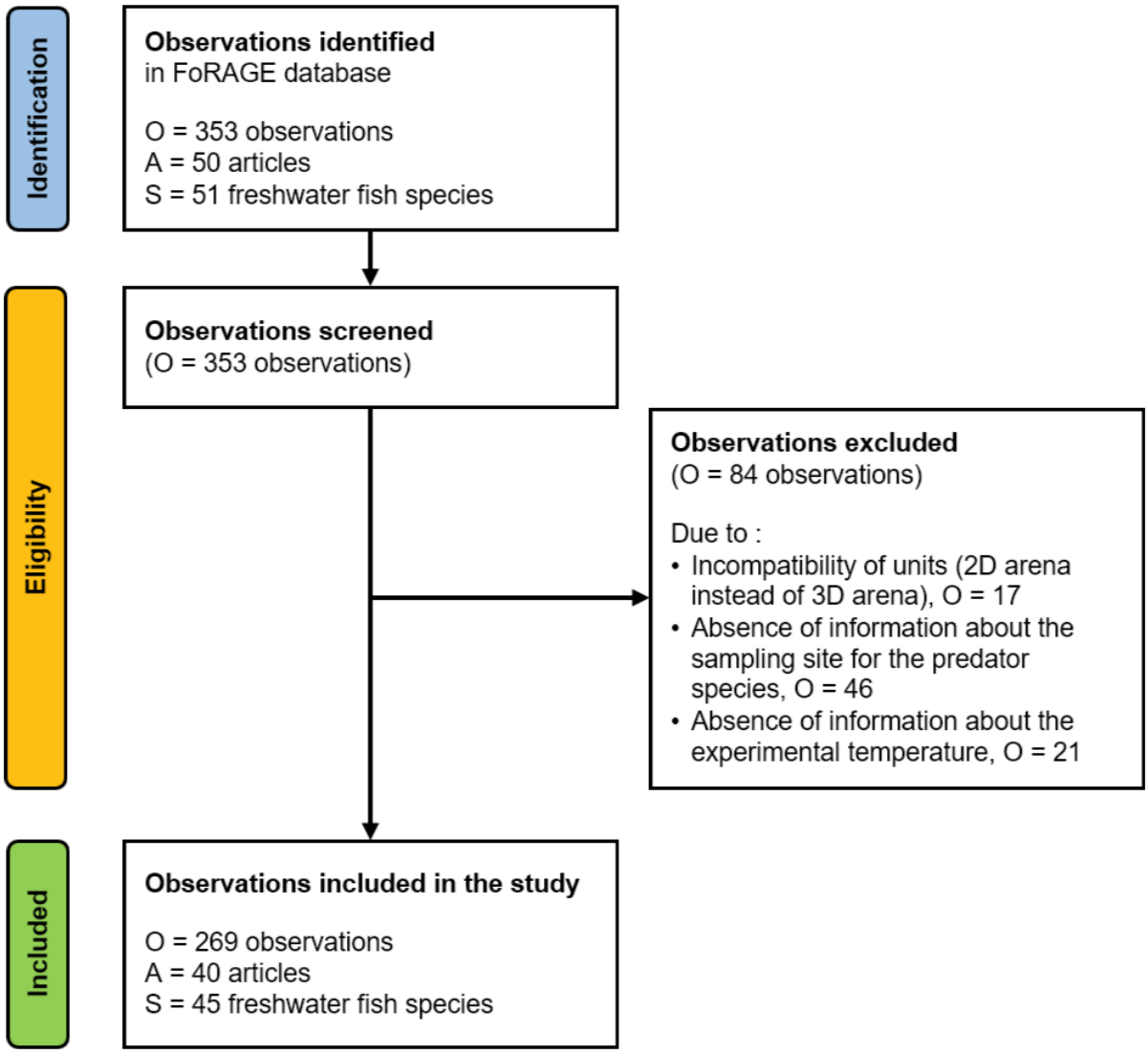

Figure S1. *PRISMA flowchart showing the number of observations (O, i.e. number of estimated functional response curves reporting the space clearance rate* a *and the handling time* h*), the number of articles (A), and the number of freshwater fish species as predator (S).*

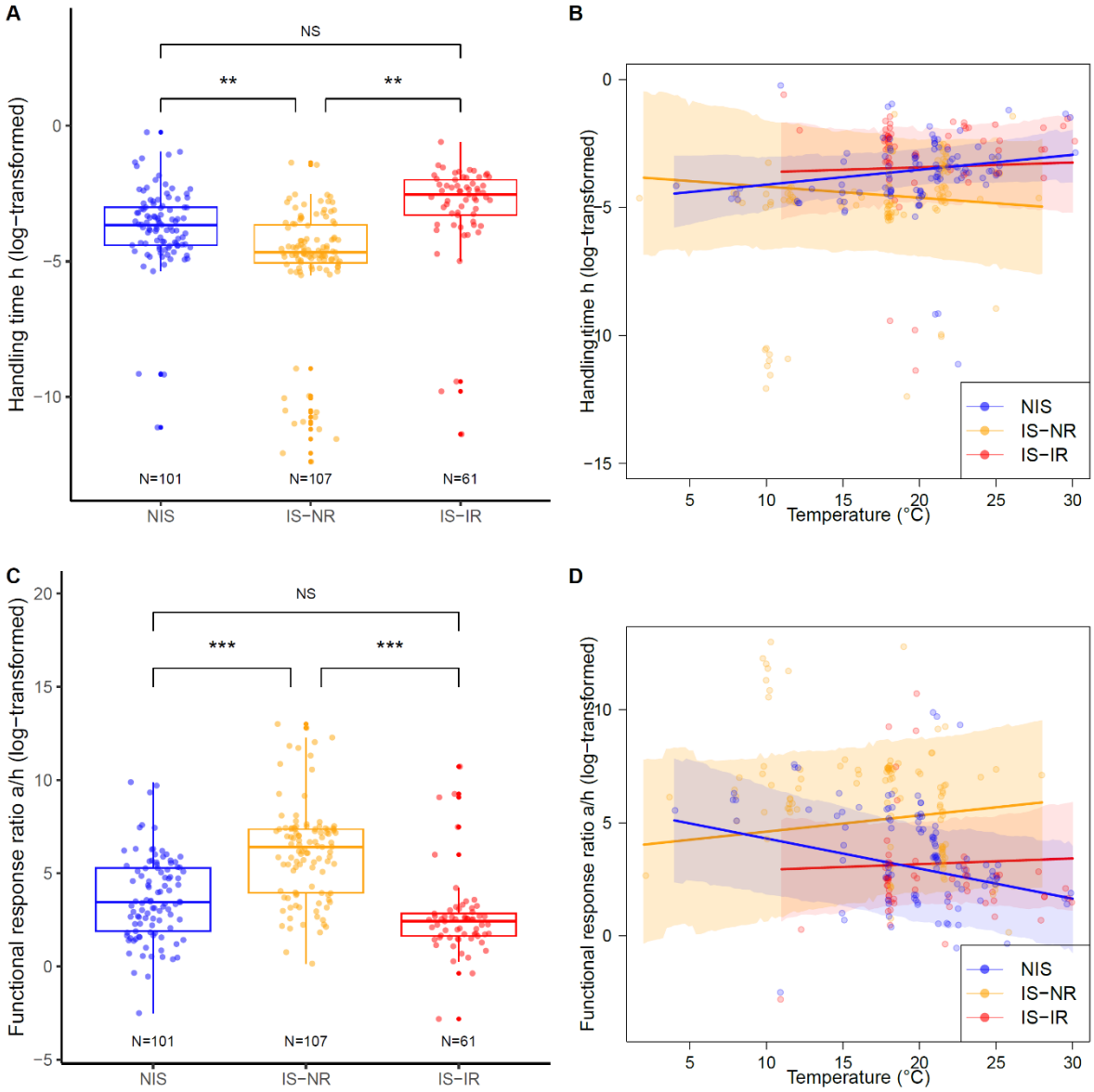

Figure S2. *The functional response parameters are expressed in standard units (log-transformed).* **A)** *Boxplot of handling time (h) as a function of the sampling status, which was either non-invasive (NIS, in blue, all were sampled in their native range), invasive species sampled in their native range (IS-NR, donor populations, in orange) or invasive species sampled in their invasive range (IS-IR, introduced populations, in red).* **B)** *Effect of the interaction between sampling status and temperature on the handling time.* **C)** *Boxplot of functional response ratio (FRR = a/h) as a function of the sampling status.* **D)** *Effect of the interaction between sampling status and temperature on the functional response ratio (FRR = a/h). The sample size (N) is indicated below each group when relevant. Each data point corresponds to the report in a specific article of one estimated value of clearance rate for one species. Multiple data points may correspond to the same species studied across different articles. The mixed-effect model incorporates multiple imputations and accounts for phylogenetic inertia. "***" indicates pMCMC < 0.001, "**" pMCMC < 0.01 and NS pMCMC > 0.05.*

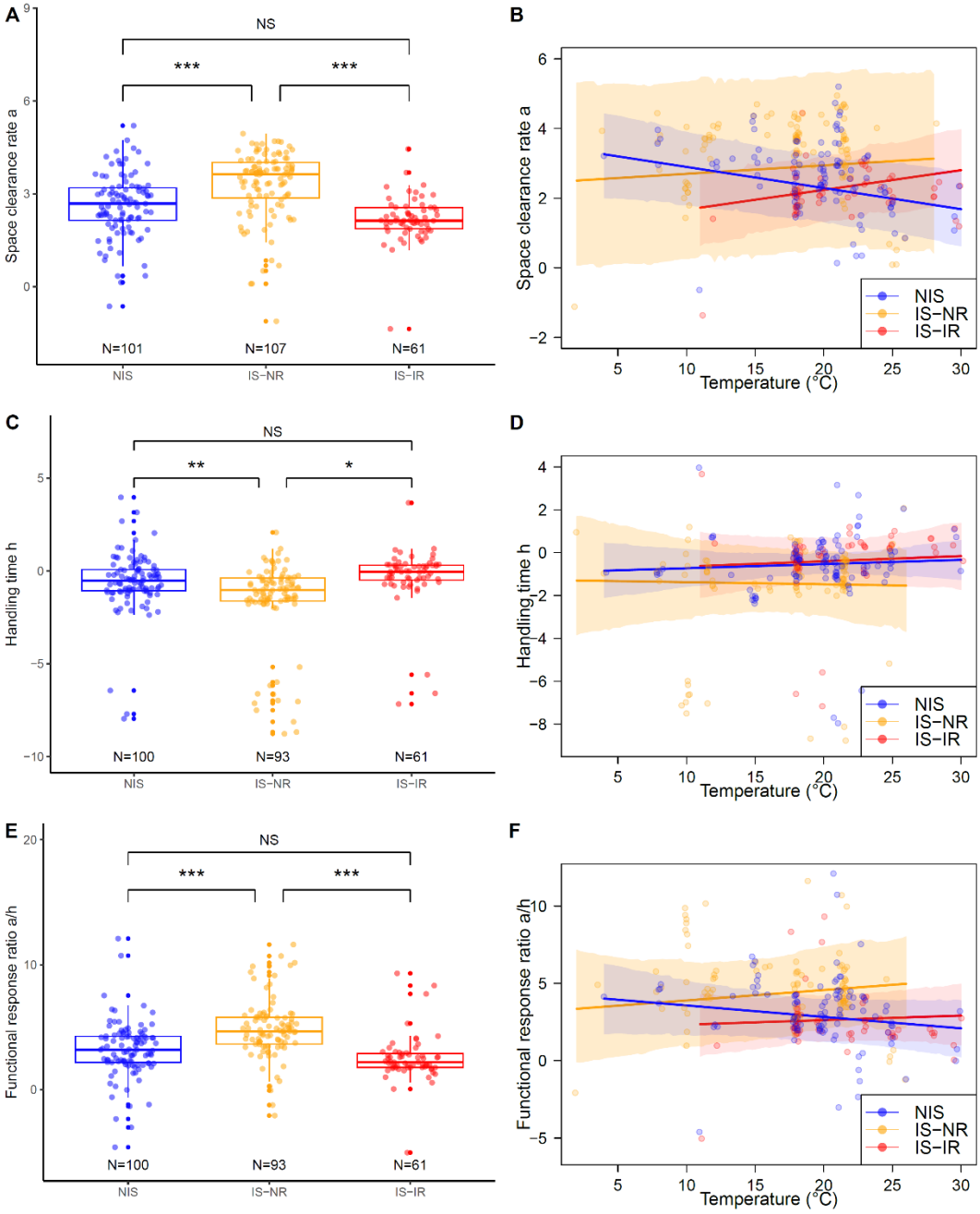

Figure S3. *The functional response parameters are expressed in biomass units (log-transformed).* **A)** *Boxplot of space clearance rate as a function of the sampling status, which was either non-invasive (NIS, in blue, all were sampled in their native range), invasive species sampled in their native range (IS-NR, donor populations, in orange) or invasive species sampled in their invasive range (IS-IR, introduced populations, in red).* **B)** *Effect of the interaction between sampling status and temperature on the space clearance rate (a).* **C)** *Boxplot of handling time (h) as a function of the sampling status.* **D)** *Effect of the interaction between sampling status and temperature on the handling time (h).* **E)** *Boxplot of functional response ratio (FRR = a/h) as a function of the sampling status.* **F)** *Effect of the interaction between sampling status and temperature on the functional response ratio (FRR = a/h). The sample size (N) is indicated below each group when relevant. Each data point corresponds to the report in a specific article of one estimated value of clearance rate for one species. Multiple data points may correspond to the same species studied across different articles. The mixed-effect model incorporates multiple imputations and accounts for phylogenetic inertia. "***" indicates pMCMC < 0.001, "**" pMCMC < 0.01, "*" pMCMC < 0.05, and NS pMCMC > 0.05.*

Table S1. *Model selection table for the influence of sampling status on each functional response parameter (space clearance rate a, handling time h, and functional response ratio FRR = a/h) expressed in biomass units. The competitive models were ranked according to their DIC. For a detailed description of the three models, refer to the main text.*

Model	**Clearance rate a**		**Handling time h**		**FRR = a/h**	
	DIC	ΔDIC	DIC	ΔDIC	DIC	ΔDIC
Model 2: sampling status	627.61	0	1035.15	0	1103.01	0
Model 1: invasive status	656.45	28.84	1035.88	0.73	1113.16	10.15
Model 0: intercept	654.51	26.90	1036.99	1.84	1114.46	11.45

878 ***Table S2.*** *Model selection table for the effect of sampling status and experimental temperature on each*
879 *functional response parameter (space clearance rate a, handling time h, and functional response ratio*
880 *FRR = a/h) expressed in biomass units. The full model ('Model 3', see main text) and all the nested*
881 *models were ranked according to their DIC. The fixed variables considered were the experimental*
882 *temperature (T°), the sampling status (NIS, IS-NR, IS-IR), and their interaction term T°:status. Degree*
883 *of freedom (df) for each model is also reported.*

Parameter	Nested model			df	DIC	ΔDIC
a	T°	Status	T°:Status	8	609.7	0
		Status		5	627.5	17.85
	T°	Status		6	629.3	19.64
				3	654.6	44.94
	T°			4	656.1	46.47
h		Status		5	1035.2	0
				3	1037.0	1.83
	T°	Status		6	1038.0	2.81
	T°			4	1040.2	5.06
	T°	Status	T°:Status	8	1040.9	5.72
FRR *a/h*	T°	Status	T°:Status	8	1100.8	0
		Status		5	1103.0	2.21
	T°	Status		6	1104.9	4.60
				3	1114.4	13.58
	T°			4	1116.7	15.87

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886 ***Table S3.*** *Effect of the experimental temperature for each functional response parameter (space*
887 *clearance rate a, handling time h, and functional response ratio FRR = a/h) expressed in standard units,*
888 *and for each sampling status (NIS, IS-NR, IS-IR). The posterior mean of the slope with 95% credible*
889 *interval, and pMCMC are reported. "***" indicates pMCMC < 0.001, "**" pMCMC < 0.01, "*"*
890 *pMCMC < 0.05.*

Parameter	Sampling status	Posterior mean	95% CrI	pMCMC
a	NIS	-0.095	[-0.14, -0.052]	$< 3\times10^{-04}$ ***
	IS-NR	0.0078	[-0.046, 0.056]	0.767
	IS-IR	0.056	[-0.0073, 0.11]	0.072
h	NIS	0.054	[-0.019, 0.13]	0.15
	IS-NR	-0.044	[-0.19, 0.087]	0.52
	IS-IR	0.020	[-0.11, 0.16]	0.76
FRR *a/h*	NIS	-0.13	[-0.11, -0.011]	0.014 *
	IS-NR	0.069	[-0.062, 0.20]	0.32
	IS-IR	0.025	[-0.12, 0.18]	0.75

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Table S4. *Effect of the experimental temperature for each functional response parameter (space clearance rate a, handling time h, and functional response ratio FRR = a/h) expressed in biomass units, and for each sampling status (NIS, IS-NR, IS-IR). The posterior mean of the slope with 95% credible interval, and pMCMC are reported. "*" pMCMC < 0.05.*

Parameter	Sampling status	Posterior mean	95% CrI	pMCMC
a	NIS	-0.060	[-0.11, -0.011]	0.017 *
	IS-NR	0.025	[-0.029, 0.075]	0.34
	IS-IR	0.056	[-0.0034, 0.12]	0.072
h	NIS	0.018	[-0.061, 0.090]	0.61
	IS-NR	-0.010	[-0.17, 0.14]	0.96
	IS-IR	0.024	[-0.087, 0.14]	0.68
FRR *a/h*	NIS	-0.074	[-0.19, 0.035]	0.20
	IS-NR	0.067	[-0.12, 0.24]	0.51
	IS-IR	0.030	[-0.11, 0.19]	0.69