

2019

Disentangling the abundance–impact relationship for invasive species

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Recommended Citation

Bradley, Bethany A.; Laginhas, Brittany B.; Whitlock, Raj; Allen, Jenica M.; Bates, Amanda E.; Bernatchez, Genevieve; Diez, Jeffrey M.; Early, Regan; Lenoir, Jonathan; Vilà, Montserrat; and Sorte, Cascade J.B., "Disentangling the abundance–impact relationship for invasive species" (2019). *Proceedings of the National Academy of Sciences*. 408.

<https://doi.org/10.1073/pnas.1818081116>

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1 **Classification:** BIOLOGICAL SCIENCES, Ecology

2

3 **Disentangling the abundance-impact relationship for invasive species**

4

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33 **Running head:** Negative impacts of increasing invader abundance

34

35 **Keywords:** abundance; community ecology; density-dependence; diversity; ecological impacts; invasive
36 species; per capita effect, response curve

37

38 **Abstract**

39 In order to predict the threat of biological invasions to native species, it is critical that we understand how
40 increasing abundance of invasive alien species (IAS) affects native populations and communities. The
41 form of this relationship across taxa and ecosystems is unknown, but is expected to depend strongly on
42 the trophic position of the IAS relative to the native species. Using a global meta-analysis based on 1,258
43 empirical studies presented in 201 scientific publications, we assessed the shape, direction and strength of
44 native responses to increasing invader abundance. We also tested how native responses varied with
45 relative trophic position and for responses at the population vs. community levels. As IAS abundance
46 increased, native populations declined non-linearly by 20%, on average, and community metrics declined
47 linearly by 25%. When at higher trophic levels, invaders tended to cause a strong, non-linear decline in
48 native populations and communities, with the greatest impacts occurring at low invader abundance. In
49 contrast, invaders at the same trophic level tended to cause a linear decline in native populations and
50 communities, while invaders at lower trophic levels had no consistent impacts. At the community level,
51 increasing invader abundance had significantly larger effects on species evenness and diversity than on
52 species richness. Our results show that native responses to invasion depend critically on invasive species'
53 abundance and trophic position. Further, these general abundance-impact relationships reveal how IAS
54 impacts are likely to develop during the invasion process, and when to best manage them.

55

56 **Significance statement**

57 The shape (linear vs. non-linear), direction (negative vs. positive), and strength of the relationship
58 between IAS abundance and native species diversity determines which invaders present the greatest risk
59 to ecosystems. Yet, the form of the relationship between abundance and impact was previously unknown.
60 Our meta-analyses reveal a strongly negative, convex relationship between invader abundance and native
61 populations or communities when invaders are at higher trophic levels. Thus, on average, invasive
62 species' impacts are strongest at low invader abundance, highlighting the need for proactive policies to
63 prevent introduction and eradicate early infestations. When invaders are at the same trophic levels, their
64 impacts tended to be negative and linear, suggesting that treatment could benefit native communities
65 regardless of invasion stage.

66 **Introduction**

67 Invasive alien species (IAS) have negative effects on native species populations (i.e., decreased
68 population sizes) and communities (i.e., reduction in species diversity). These negative impacts have been
69 observed for many invasive alien taxa and across ecosystems (1–5). However, previous syntheses have
70 assessed the effect of invader presence/absence without considering how impact might change with
71 increasing invader abundance. As a result, the general shape of the relationship between invader
72 abundance and native population or community response remains unknown. Understanding how invader
73 impacts change with abundance is critical for predicting the severity of the impacts across recipient
74 habitats (3, 6, 7), assessing the costs and benefits of treatment (8, 9) and prioritizing management actions
75 (10).

76 Frameworks for assessing IAS impacts typically rely on assumed relationships between invader
77 abundance and impact. For example, Parker et al. (11) proposed that an invader's impacts are a function
78 of its total range, abundance, and per capita effect ($I=R*A*E$). This equation specifies that impacts
79 increase linearly with abundance, with no density-dependent relationship between abundance and per
80 capita effect. Later impacts frameworks explicitly hypothesized density-dependent relationships, with
81 impacts increasing or decreasing non-linearly with invader abundance (12, 13). The variety of possible
82 relationships between abundance and impact highlights the strong need for an empirical assessment of
83 this fundamental question across taxa (8). Moreover, it is unknown whether relationships between
84 abundance and impact depend on the trophic positions of invading and native species. One review of
85 invasive impacts studies concluded that there was no clear effect of trophic position on impacts (14),
86 while another meta-analysis focused on marine ecosystems suggested that impacts on native species
87 switched from positive to negative if invaders were in lower vs. higher trophic levels, respectively (4).

88 Classical ecological theory suggests that when an invasive alien species is at a higher trophic level
89 than a native species, the invader is likely to cause a strong non-linear decline in the native species
90 population due to density dependence and a number of processes that alter the per capita effects of the

91 invasive species (**Fig. 1A**; 15, 16). For example, the introduction of a novel alien predator or herbivore
92 can lead to rapid decreases in native prey or plant population sizes (14, 17). Following this initial decline,
93 native populations might later stabilize at lower sizes by persisting in refuges, through adaptation
94 (evolution, phenotypic or behavioral plasticity), or by reaching a lower carrying capacity balanced by
95 immigration of new individuals. These responses would result in a non-linear relationship between
96 invader abundance and native population size. For example, Benkwitt (18) observed a non-linear decline
97 in sizes of native fish populations following the introduction of the predatory invasive lionfish (*Pterois*
98 *volitans*) in the Caribbean. Impacts at the community level are also hypothesized to be stronger when the
99 IAS is at a higher trophic level than the invaded native species assemblage (19, 20), but the general shape
100 of the relationship is unknown.

101 When an invasive alien species is at the same trophic level as a native species, the invader could
102 cause either a linear or non-linear decline in the native species population size (**Fig. 1B**). Competition is
103 the main mechanism for IAS impact when invasive and native species occupy the same trophic level (21).
104 The impacts of competition could be linear if per capita competitive effects are not density-dependent.
105 However, field studies have also shown that competition can be density-dependent, leading to non-linear
106 declines in native species population sizes (22). Impacts at the community level for IAS at the same
107 trophic level vary with the spatial scale of analysis (23), but the shape of the response relative to invader
108 abundance is unknown.

109 Finally, when an invasive alien species is at a lower trophic level than a native species, the
110 relationship between invader abundance and native species population size could be positive or negative
111 (**Fig. 1C**). The direction of this relationship depends on whether the IAS acts as a novel resource for the
112 native species or reduces resources upon which the native species depends. Previous meta-analyses of
113 invader presence *vs.* absence suggest that negative impacts may be more likely. For example, the presence
114 of invasive alien plants reduces the abundance of native animals (5), particularly native herbivorous
115 insects (24), which are often specialists of native plants (25). Similarly, invasive primary producers in

116 freshwater systems can have a negative effect on native fish (2), likely by disrupting access to resources.
117 The direction of native community-level responses to IAS at lower trophic levels is even less clear.
118 Previous meta-analyses in marine and freshwater ecosystems have found that invaders at lower trophic
119 levels tended to increase (4) or have no significant overall effect on (2) the diversity of benthic
120 invertebrates at higher trophic levels. Thus, impacts at the community level for IAS at lower trophic
121 levels remain poorly understood.

122 Here, we present the first global meta-analysis of responses of native species and communities to
123 gradients of IAS abundance, quantifying the direction, strength and shape of this relationship for different
124 trophic interactions. We develop generalizations based on comprehensive empirical evidence of how the
125 abundance-impact relationship varies between a) native population and community responses (e.g.,
126 individual species abundance *vs.* species diversity), b) invader taxon (plant, animal), and c) recipient
127 habitat (freshwater, terrestrial, marine). This analysis of abundance-impact relationships across
128 ecosystems provides a key test of ecological theory related to species and community-level responses to
129 novel species interactions.

130

131 **Results**

132 We analyzed data from 1,258 unique case studies reported in 201 papers. Of the papers included in
133 the dataset, 94 evaluated invasive plants and 107 evaluated invasive animals (**SI Appendix, Table S3.1**).
134 Almost all of the plant studies were terrestrial, whereas studies of invasive alien animals were well
135 distributed across habitat types. Spatially, most of the data were collected in North America, Europe,
136 Australia or New Zealand (**SI Appendix, Fig. S3.1**). This pattern is consistent with known biases in the
137 invasion ecology literature (26), but the studies nonetheless encompass a broad range of alien taxa across
138 habitat types.

139 Native responses to IAS abundance at the population level had a significantly negative linear
140 component but a significantly positive polynomial component, resulting in a non-linear relationship with
141 the most rapid rate of decline in native populations occurring at low invader abundance (**Fig. 2A,B**;
142 summary statistics for model contrasts are given in **SI Appendix, Table S3.2**). Native species populations
143 declined by an average of 20% as IAS abundance increased (**Fig. 2B**). Native responses to IAS at the
144 community level also had a significantly negative linear component, but no significant polynomial
145 component, resulting in a negative linear shape (**Fig. 2C,D**). Native community metrics (richness,
146 diversity, evenness, or multi-species abundance) declined by an average of 25% as IAS abundance
147 increased (**Fig. 2D**).

148 Abundance-impact relationships varied substantially and significantly depending on the relative
149 trophic positions of the invasive and native species (**Fig. 3**). When IAS were at a higher trophic level,
150 their impacts on native species populations and communities were strongly negative and non-linear (**Fig.**
151 **3A,D**). As IAS at higher trophic levels increased in abundance, native populations declined by an average
152 of 44% and native community metrics by an average of 52% (**Fig. 3 A,D**). However, IAS impacts
153 weakened as their trophic position shifted from higher to lower (**Fig. 3**). For IAS at the same trophic
154 level, native populations declined by an average of 20% and native community metrics by an average of
155 28%. When IAS were at the same trophic level, their impacts on native species were significantly

156 negative and non-linear (**Fig. 3B**), while their impacts on communities were significantly negative and
157 linear (**Fig. 3E**). When IAS were at a lower trophic level, they had no consistent impact on native species
158 or communities (**Fig. 3C,F**).

159 At the community level, increasing invader abundance had a significant negative effect on native
160 species' richness, Shannon diversity, and Pielou evenness (**Fig. 4; SI Appendix, Fig. S3.2**). Although
161 species richness was by far the most commonly reported diversity metric (85 papers, 218 studies), linear
162 impacts were significantly more negative for native species evenness ($p=0.004$) and diversity ($p=0.04$;
163 **Fig. 4**). On average (across all trophic categories) there were no significant non-linearities between IAS
164 abundance and community-level diversity. However, species richness showed a marginally non-
165 significant negative polynomial term ($p=0.052$; impacts on richness were more likely to be weakest at low
166 invader abundance) and the polynomial term for richness was significantly lower than that for evenness
167 ($p=0.01$; **Fig. 4**).

168 Compared with trophic position, recipient habitat (terrestrial, freshwater or marine) explained little
169 variation in the impacts of IAS on native species and communities (**SI Appendix, Fig. S3.3**). IAS at
170 higher trophic levels generally had strongly negative, non-linear effects on native species and
171 communities regardless of habitat type, with freshwater habitat showing the strongest curvature. IAS at
172 the same trophic level generally had negative linear effects across habitat types, although there was some
173 curvature in freshwater habitat. IAS at lower trophic levels generally had no effect, although species and
174 communities in terrestrial habitats were likely to show a weak negative linear response (**SI Appendix,**
175 **Fig. S3.3**).

176 Responses of native species and communities to IAS abundance varied depending on invader taxon
177 (animals *vs.* plants; **SI Appendix, Fig. S3.4**). At a higher trophic level, invasive animals had significant
178 negative non-linear effects on native species and communities (there were no plants at higher trophic
179 levels). Invasive animals and plants at the same trophic level both drove negative impacts in native

180 species, but responses to invasive animals were significantly non-linear, while those to invasive plants
181 were significantly linear. At lower trophic levels, invasive animals had no consistent impacts, while
182 invasive plants had a small but significant negative linear effect (partial-r $p=0.002$; **SI Appendix, Fig.**
183 **S3.4**). Linear effect sizes did not vary significantly among study types (spatial, temporal, experimental
184 studies; **SI Appendix, Fig. S3.5**).

185 **Discussion**

186 Our global meta-analysis is the first to quantify general trends in the direction, shape and strength of
187 the relationship between IAS abundance and native response across trophic levels, invader taxon and
188 recipient habitat. Negative impacts of IAS clearly predominate across terrestrial, freshwater, and marine
189 habitats, and are caused by both animal and plant invaders. Negative impacts are common when IAS are
190 at higher or the same trophic level as native species, and native population or community declines of 20-
191 25% were typical. Across trophic interactions, invader taxon, and recipient habitat, there were no general
192 trends of invader abundance having a positive effect on native populations or communities. Our results
193 also show that native responses to IAS can be strongly non-linear (convex), suggesting that impacts are
194 strongest at low levels of IAS abundance during the earliest stages of invasion.

195 When IAS were at higher trophic levels, impacts were consistently non-linear for both native
196 populations and communities (**Fig. 3A,D**). A non-linear effect on native species populations is supported
197 by ecological theory of predator-prey interactions (**Fig. 1A**). IAS at higher trophic levels are also thought
198 to have stronger effects on native communities than those at other trophic levels (19). However, a general
199 non-linear effect on native communities has not been previously described. Low invader abundance is
200 most likely to occur early in the invasion process. Thus, early detection and rapid response to new
201 invasions (27, 28) will be most effective for reducing impacts of invasive animals, because they are most
202 likely to impose non-linear effects on recipient habitats (**Fig. S3.4A,B**). Similarly, eradicating animal
203 invaders, such as alien mammals on islands (29), is a much more effective means of supporting native
204 species than reducing the populations of abundant animal invaders. If eradication is not possible, our
205 results suggest that once IAS at higher trophic levels reach high abundance, management will be less
206 effective for mitigating impacts.

207 When IAS were at the same trophic level as natives, our results highlight a consistent, negative
208 impact on both populations and communities (**Fig. 3B,E**). This negative impact tended to be linear for

209 community-level metrics. However, our results also suggest that non-linear responses to invaders at the
210 same trophic level are likely when the native response is at the population level (**Fig. 3B**) and particularly
211 when the IAS is an animal (**SI Appendix, Fig. S3.4B**). Density-dependent competition is common in
212 animal species (30). Although density-dependent competition has also been observed for plant species
213 (13, 22), it was not evident in our analysis (**SI Appendix, Fig. S3.4D**). Thus, non-linear relationships
214 between an invasive and native species at the same trophic level appear most likely to occur when the
215 invader is an animal. Our results are also the first to suggest that IAS can precipitate negative, linear
216 effects on native communities at the same trophic level (**Fig. 3E**). For IAS mainly interacting with native
217 communities on the same trophic level (e.g., as competitors), management aimed at reducing IAS
218 abundance could be effective for promoting community diversity at any stage of invasion.

219 We did not find consistent, significant relationships between IAS abundance and native population or
220 community response when IAS were at a lower trophic level (**Fig. 3C, F**). However, negative, linear
221 effects were more likely to be observed when the recipient habitat was terrestrial (**SI Appendix, Fig.**
222 **S3.3C**) and when the invader was a plant (**SI Appendix, Fig. S3.4E**). Previous meta-analyses have
223 suggested that IAS impacts can cascade up to higher trophic levels (2, 5, 24), which could be due to a loss
224 of native resources. For example, native insects tend to be specialists (25); thus, competitive suppression
225 of native plants by invasive alien plants is likely to negatively affect native insects and potentially animals
226 at higher trophic levels that feed on insects (24). In contrast to Thomsen et al. (4), on average we found no
227 consistent impacts of IAS at lower trophic levels in marine habitats (**SI Appendix, Fig. S3.3I**). Some
228 marine IAS are foundation species that create new habitat structure, which can increase space and
229 physical resources for native species (31). Our results for marine habitat suggest that, in these systems,
230 natives may be experiencing both positive and negative effects from IAS (**SI Appendix, Fig. S3.3I**).
231 Overall, the lack of significant positive effects and presence of several weak but significant negative
232 effects suggests that IAS at lower trophic levels tend to remove resources for native consumers rather than

233 add them. Thus, management of invasive abundance at any stage of invasion may provide some benefit
234 for native species at higher trophic levels, particularly for terrestrial plant invasions.

235 Our analysis highlights a consistent, negative effect of IAS abundance across all three community-
236 level metrics (**Fig. 4**). These results contrast with previous findings of increased community richness due
237 to the addition of alien species (32). However, Sax & Gaines (32) focused on the establishment phase of
238 invasion, prior to spread and impact (e.g., 33). Our results show that as invaders become more abundant,
239 community-level impacts are clearly negative. This negative effect was significantly stronger for
240 evenness and diversity than for richness. Species richness is a conservative measure of community-level
241 changes, requiring species extinctions or additions to register change. Metapopulation models of invasive
242 alien plants suggest that they could take hundreds of years to cause extinctions (i.e., a decline in species
243 richness; (7). Our results also suggest that community evenness is likely to decline predominantly linearly
244 whereas richness is more likely to decline more slowly early in the invasion process and more rapidly,
245 later, at high invader abundance (negative polynomial; **Fig. 4; SI Appendix, Fig. S3.2**). This pattern may
246 be due to a tendency of invasive species to affect common native species early in the invasion process,
247 and rare native species only later (34). While extinctions leading to lower richness may not be apparent
248 until later stages of invasion, changes in species abundance and therefore evenness may occur more
249 quickly and appear to be more sensitive metrics of community change (**Fig. 4**).

250 In conclusion, regardless of trophic level, taxon, or recipient habitat, we found that increasing the
251 abundance of IAS has pronounced negative impacts on native species populations and communities. In
252 many cases, negative, strongly non-linear relationships suggest that rapid declines in native species'
253 population sizes can occur at initial stages of the invasion process. The presence of non-linear
254 relationships highlights the increasing need for early detection and rapid response (EDRR) to new IAS
255 (27). EDRR is cost-effective (35) and the only point at which eradication is feasible (36). Increasing trade
256 (37), disturbance (38), and climate change (39) make it likely that IAS will continue to be introduced.
257 Avoiding the ecological impacts of invasive species will require a much stronger commitment to

258 proactive policies designed to prevent novel introductions (38) as well as increased management targeting
259 the early stages of invasion.

260

261 **Materials and Methods**

262 Literature search

263 We searched the Web of Science core collection for all records through 12/31/2016. Our search terms
264 (**SI Appendix, part 1**) were chosen to identify papers that focused on the impacts of IAS on native
265 populations or communities and that contained information on the abundance or density of the IAS. We
266 assessed the titles of the 7,557 returned papers for those reporting native impacts of an IAS across an
267 abundance gradient. We reviewed the 490 resulting papers to identify those that fit the following criteria:
268 1) it was either explicit or likely that the native response was caused by the IAS, 2) the paper presented at
269 least four IAS abundance values and corresponding native response values such that shape could be
270 measured, and 3) the paper included empirical data.

271 The vast majority of relevant papers focused on single IAS, but we also included papers that involved
272 multiple IAS. We only considered papers where the response variable(s) measured native species
273 abundance (biomass, cover, density, or proportion) and/or measured native community response (multi-
274 species abundance, Shannon diversity, species richness or Pielou evenness). We included observational
275 studies across space (spatial; measurements along an IAS abundance gradient) or over an invasion time
276 series (temporal; IAS abundance changing over time) as well as experimental manipulations of IAS
277 abundance.

278 Data extraction

279 Where empirical data were presented graphically, we used the Web Plot Digitizer application
280 (<http://arohatgi.info/WebPlotDigitizer/app/>) to extract values. If the data were transformed, we back-
281 transformed them. When the raw empirical data were not presented in full, we emailed corresponding
282 authors to request them. When possible, we calculated Shannon diversity and Pielou evenness from
283 abundance and species richness data. Where papers presented multiple datasets, or multiple combinations

284 of IAS abundance and native responses, we extracted these as distinct datasets (hereafter, studies), such
285 that single papers could contribute multiple studies to our analysis.

286 Data categorization

287 We extracted trophic relationships between the IAS and native species or community from the paper
288 or sources cited within the paper. Trophic categories included ‘Same’ when the native and IAS occupied
289 the same trophic level; ‘Lower’ when the IAS was at a lower trophic level than the native; and ‘Higher’,
290 when the IAS was at a higher trophic level than the native. When trophic information was not reported,
291 we categorized some interactions based on kingdom (e.g., invasive plant vs. native plant was always
292 ‘Same’; invasive plant vs. native animal was always ‘Lower’). For studies of invasive alien animal vs.
293 native animal with no trophic information presented in the paper, we used a Google Scholar search for the
294 IAS as well as ‘diet’ or ‘feed’ to identify the relative trophic position of the IAS. In cases where the
295 invasive and native animals were fish, we also searched for trophic status in FishBase
296 (www.fishbase.org). Species whose trophic position changed during their life cycle (e.g., fish can switch
297 from competitors at juvenile stages to predators as adults) and species with unknown trophic positions
298 were excluded from the trophic analyses.

299 In addition to trophic level, we analyzed the results by invader taxon (plant, animal), habitat
300 (terrestrial, freshwater, marine) and study type (spatial, temporal, experimental). Marine algae were
301 categorized as plants. Wetland plants were considered terrestrial, with only floating plants considered
302 freshwater or marine. Experimental studies that took place over space or time were categorized as
303 experimental. Observational studies over both space and time were categorized as multiple.

304 Meta-analysis

305 We used two complementary meta-analyses to evaluate the relationship between IAS abundance and
306 native species’ responses at the population and community level. Results from both meta-analyses were
307 used to determine the direction and strength of linear and polynomial components to the invasive

308 abundance–native response relationship. Results from the second meta-analysis were additionally used to
309 reconstruct the average shape of this relationship. Both meta-analyses used a regression model to extract
310 information on response direction, strength and shape (curvature) from the raw IAS abundance–native
311 response data:

$$312 \quad y = \beta_0 + \beta_{\text{linear}}x + \beta_{\text{poly}}x^2 \quad (\text{Eqn 1})$$

313 where y was the native response, x was the IAS abundance, β_0 was the intercept, β_{linear} was the linear
314 regression term, and β_{poly} was the second-order polynomial regression term. The regression model was fit
315 separately to raw data for each study.

316 The first meta-analysis derived effect sizes from Fisher-transformed partial correlation
317 coefficients associated with each regression term from Equation 1, following (40; hereafter, partial-r
318 meta-analysis):

$$319 \quad r = \frac{t}{\sqrt{t^2 + df}} \quad (\text{Eqn 2})$$

$$320 \quad \text{Effect size} = 0.5 * \ln\left(\frac{1+r}{1-r}\right) \quad (\text{Eqn 3; Fisher transformation})$$

321 where r is the partial correlation coefficient for one of the regression terms in Equation 1 (β_{linear} or β_{poly}), t
322 is the corresponding model t -value, and df are the degrees of freedom associated with the same regression
323 coefficient (40). Partial-r effect sizes were calculated separately for the linear and polynomial terms in
324 Eqn 1, for each study. Effect size measurement error variance (mev) was calculated as $1/(n - 3)$, where n
325 is the sample size for a study (41). We mean-centered the IAS abundance (x) for each study before fitting
326 Equation 1. Repositioning of the x -axis to a mean of zero has no impact on invasive abundance–native
327 response shape, but reduced dependence between linear and polynomial effect sizes within studies (42).
328 Meta-analysis of the partial-r effect sizes allowed us to determine the strength and direction of linear and
329 polynomial components of the regression fit.

330 The second meta-analysis derived effect sizes from the three regression terms (β_0 , β_{linear} , β_{poly}) in
331 Eqn 1 (hereafter, slopes meta-analysis). However, an analysis of regression terms requires that IAS
332 abundance and native responses (x and y variables) be on a comparable scale (regression terms are scale
333 dependent 43, 44). Thus, we rescaled the raw data (both invasive abundance, x and native responses, y) by
334 dividing by the maximum raw data value to create a scale of 0-1. We then mean-centered the rescaled
335 IAS abundance values, as before, prior to analysis using Eqn 1 to generate three regression-term effect
336 sizes (β_0 , β_{linear} , β_{poly}). We used the regression-model-reported standard error for each regression term as
337 an estimate of effect size mev (44). Results from the slopes meta-analysis were used to determine the
338 shape of the relationship between IAS abundance and native responses, and provided an additional test of
339 the magnitude of linear and polynomial regression terms (**SI Appendix, part 1**).

340 Bayesian mixed-effects models (MCMCglmm in R version 3.5.1 45, 46) were used for all meta-
341 analyses of the IAS–native response relationship, and to test for variation in invasive impacts among
342 different trophic categories, between community- and population-level responses, in different habitats,
343 and between invasive animals and plants. Full analytical details are presented in SI Appendix, part 1.

344 Data availability

345 Citations of papers analyzed in this meta-analysis are presented in SI Appendix, part 2. Data sheets
346 are available at DOI: <https://doi.org/10.7275/tjbv-qn87>. R scripts are available at DOI:
347 [10.5281/zenodo.2605254](https://doi.org/10.5281/zenodo.2605254).

348 **Author contributions**

349 BAB, RW, JMD, AEB, and CJBS designed research with contributions from all authors. All authors
350 reviewed titles and abstracts or compiled data on trophic interactions between invaders and natives. BAB,
351 CJBS, BL, and GB extracted/compiled data. RW designed and implemented the meta-analysis
352 framework. BAB, JMA and RW analyzed the data. BAB led the writing with contributions from all
353 authors.

354

355 **Acknowledgements**

356 We thank E. Beaury, D. Blumenthal, J. Dukes, J. Finn, J. Gill, D. Goldberg, and T. Morelli for
357 valuable discussions. C. Karounos and T. Cross assisted with initial data extraction. This work was
358 initiated at a working group supported by the Albert & Elaine Borchard Foundation and led by CJBS,
359 BAB, AEB and RE. BAB gratefully acknowledges the hospitality of D. Richardson and the Centre for
360 Invasion Biology at Stellenbosch University during an academic sabbatical. MV thanks funding from the
361 projects IMPLANTIN (CGL2015-65346-R) of the Spanish Ministerio de Ciencia, Innovación y
362 Universidades, and i-LINK-1198 from CSIC.

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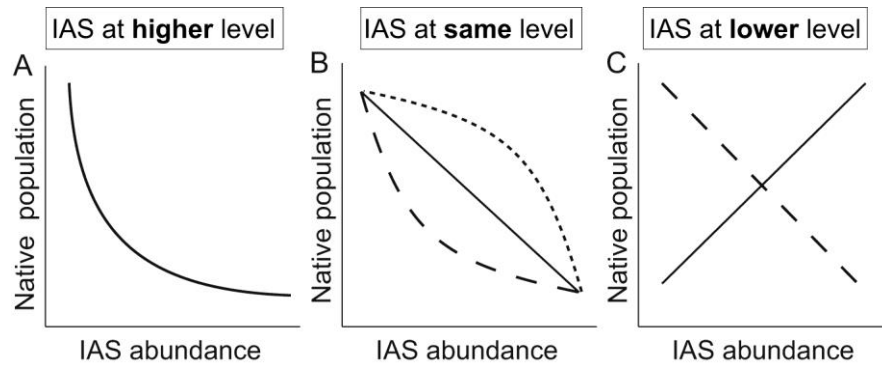
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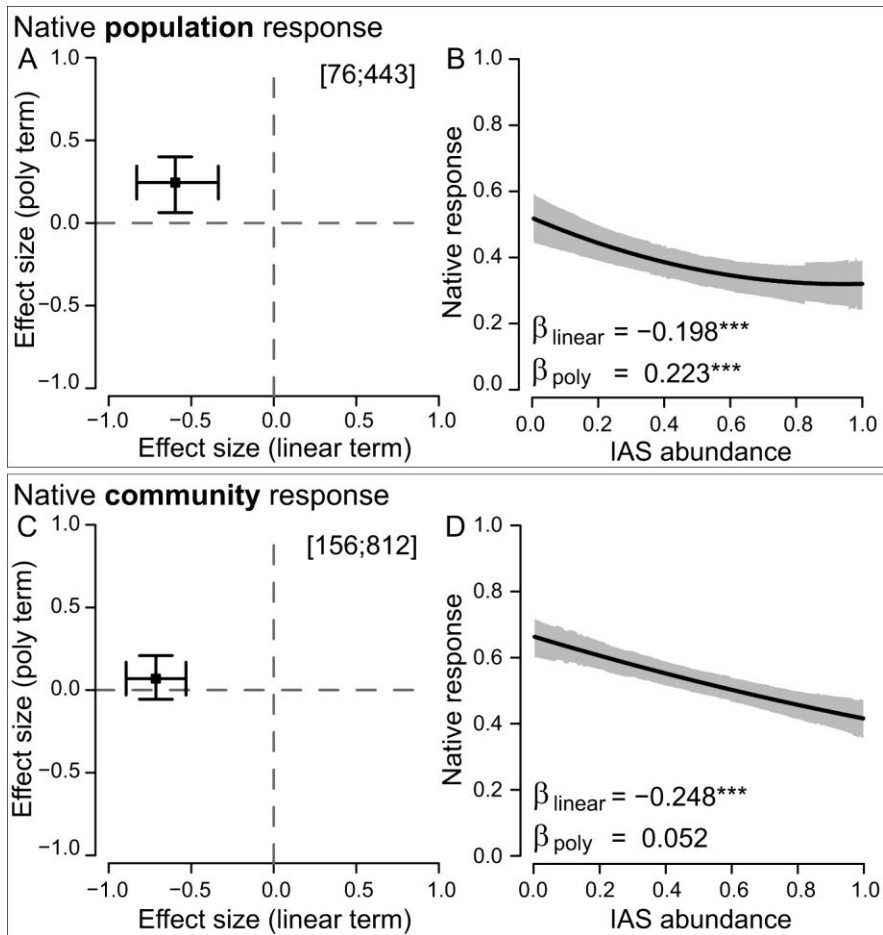
457 **Figures**



458

459 **Figure 1.** Hypothesized relationships between IAS abundance and native species' population response.
460 A) IAS at higher trophic levels could prey upon natives, leading to a non-linear decline of native species
461 population sizes. B) IAS at the same trophic level could compete with natives, leading to a linear decline
462 (solid line) if competition is independent of density, or a non-linear decline (dashed lines) if competition is
463 density-dependent. C) IAS at lower trophic levels could provide food or habitat resources, leading to a
464 linear population increase (solid line), or could reduce resources for native species, leading to a linear
465 decrease (dashed line).

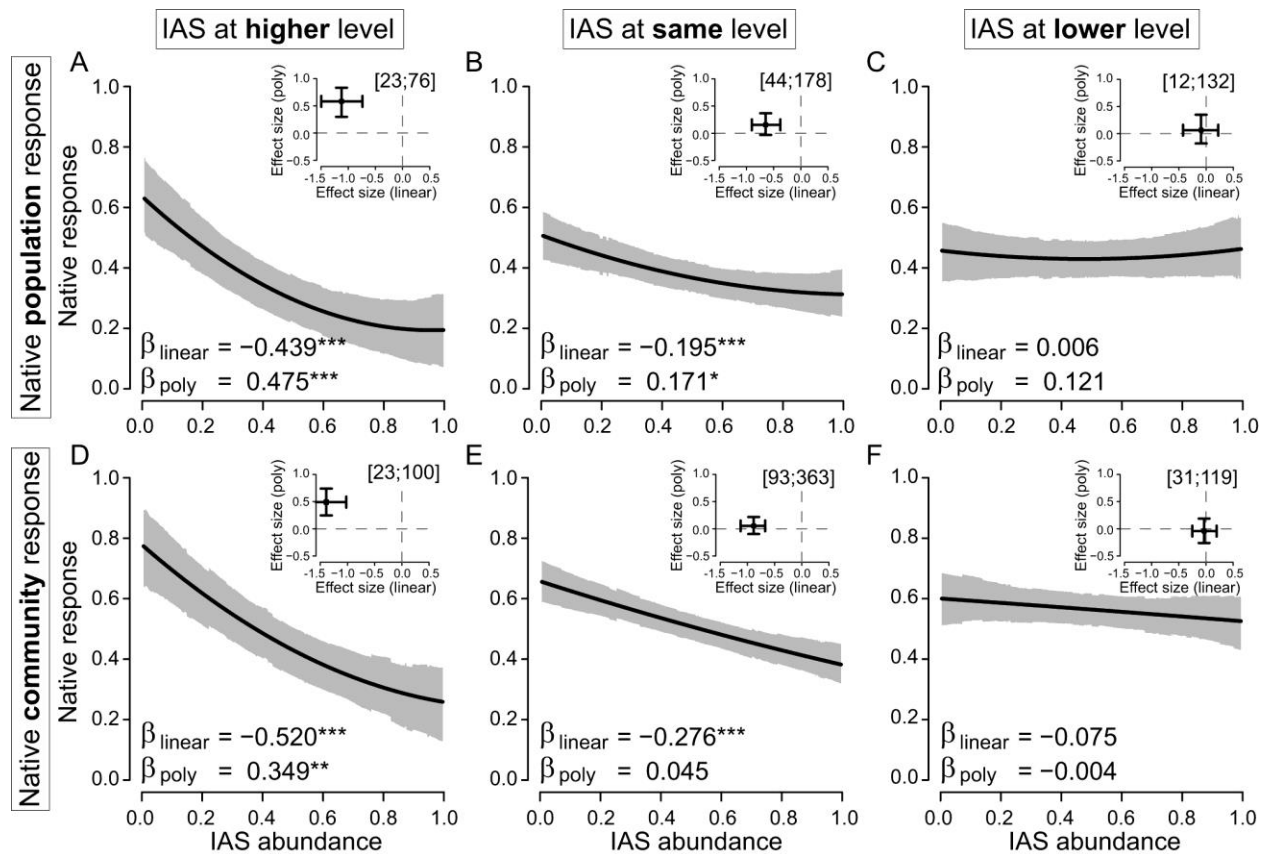
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468 **Figure 2.** The shape of native species' responses is non-linear at the population level but linear at the
 469 community level. A) and C) present analyses based on partial-r; B) and D) present the slopes analyses.
 470 Numbers in brackets are total papers and studies analyzed. Effect size estimates in A) and C) are
 471 statistically supported when 95% credible interval bars do not cross the zero lines. Slopes plots show
 472 model predictions (black line) with gray shading indicating the 95% credible zone. Significant linear (β_{linear})
 473 or polynomial (β_{poly}) regression terms are indicated by asterisks (***) $p < 0.001$.

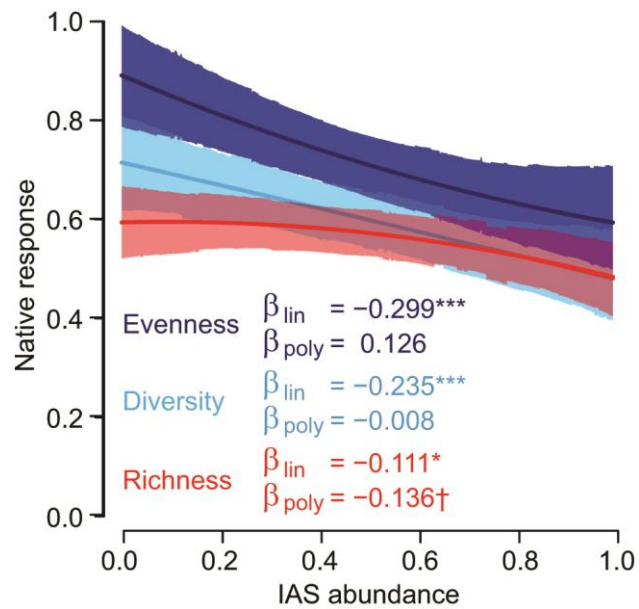
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476 **Figure 3.** The shape and strength of IAS impacts on native species and communities depends strongly
 477 on relative trophic position. Results from the slopes meta-analyses are shown in the main panel and
 478 results from the partial-r meta-analyses are inset. (A-C) Native species' population responses to invaders
 479 at higher, the same, and lower trophic levels, respectively. (D-F) Native community-level responses to
 480 invaders at higher, the same, and lower trophic levels, respectively. Significant linear (β_{linear}) or polynomial
 481 (β_{poly}) regression terms are indicated by asterisks (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

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483

484 **Figure 4.** IAS have significant negative linear effects on native community-level richness (red), diversity
 485 (cyan), and evenness (blue). There were significant differences between community-level responses for
 486 both linear and polynomial terms, which are reported in the results. Lines show model predictions with
 487 shading indicating the 95% credible zone. Significant linear (β_{linear}) or polynomial (β_{poly}) regression terms
 488 are indicated as follows: † $p < 0.10$; * $p < 0.05$; *** $p < 0.001$).