61 **The green thorns of *Ulex europaeus* play both defensive and photosynthetic roles:**

62 **consequences for predictions of the Enemy Release Hypothesis**

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Abstract The widespread invasive success of *Ulex europaeus*, a thorny shrub native to NW Europe, remains to be understood from a functional perspective. According to the Enemy Release Hypothesis (ERH), lower pressure by vertebrate herbivores in the invaded areas should lead to lower investment in (costly) physical defenses, allowing plants to invest more in growth and/or reproduction. While *U. europaeus* seedlings have spines, adult plants have thorns, which are the main photosynthetic tissue (leaves are reduced to small phyllodes). Therefore, reduced biomass investment in thorns could compromise photosynthesis and growth in the invaded range. We hypothesized that *U. europaeus* plants in invaded ranges should show a reduction in the defensive components of thorns (e.g., softer and less fibrous tissues), but not reduced biomass allocation. We compared *U. europaeus* plants from the invaded (Chile) and native (Spain) distribution ranges regarding: i) spinescence traits (thorn length, width, biomass, slenderness and bending strength) in adult plants, ii) thorn fiber content and digestibility (proxies for palatability) in adult plants, and iii) spine density in seedlings grown in a common garden. As expected, plants in the invaded range showed larger thorns, which contained less cellulose, were slenderer and easier to bend than those from plants in the native range. Likewise, seedlings from the invaded range showed lower spine density and more diameter growth, thus supporting the ERH. We found functional changes in spinescence traits between distribution ranges consistent with the dual role of thorns in *U. europaeus*, and these changes may partly explain its invasiveness.

Keywords: cellulose; gorse; physical defenses; plant-herbivory interactions; spines, thorns

Introduction

129
130   A major goal of invasion ecology is to understand why some exotic species are
131 successful invaders (Catford et al. 2009), and to this end, studies comparing native and invaded
132 distribution ranges are especially relevant (Hierro et al. 2005; Cronin et al. 2015). The enemy
133 release hypothesis (ERH) is one of the main hypotheses with a biogeographical approach to
134 explain the success of exotic invasive plant species (invasive plants, hereafter) (Keane and
135 Crawley 2002; Colautti et al. 2004; Jeschke et al. 2012). The ERH posits that the reduced
136 abundance or absence of natural enemies in the colonized range may allow the invasive plants
137 to invest more in growth and/or reproduction and less in defense (Blossey and Notzold 1995;
138 Keane and Crawley 2002; Colautti et al. 2004). Several studies, particularly evaluating
139 chemical defenses, have verified the predictions of the ERH (e.g., Joshi and Vrieling 2005; Liu
140 and Stilling 2006; Hull-Sanders et al. 2007; Gruntman et al. 2017), but fewer studies have found
141 shifts toward both lower defense and higher growth in introduced populations (Bossdorf et al.
142 2005).

143   Plant physical and structural defenses (e.g., spinescence, pubescence, sclerophylly)
144 respond to vertebrate herbivory pressure (Obeso 1997; Hanley et al. 2007; Gómez and Zamora
145 2002; Musariri et al. 2018). Spinescence, a term including sharp-pointed modifications of leaf
146 parts (spines), stems or branches (thorns) and epidermal outgrowths (prickles), is an effective
147 physical defense against vertebrate herbivores (Cooper and Owen-Smith 1986; Cooper and
148 Ginnett 1998; Milewski et al. 1991; Hanley et al. 2007; Wigley et al. 2019). Sclerophylly
149 (hardened leaves) is a defensive trait effective against both vertebrate and invertebrate
150 herbivores, decreasing the palatability and digestibility of plant tissues through a high content
151 of digestibility-reducing compounds, such as lignin or cellulose fibers, and a low nutrient content

152   (Lundberg and Åström 1990; Turner 1994; Hanley et al. 2007). Some mechanical properties

153   related to sclerophylly, e.g., flexural stiffness and fracture toughness, are predictors of

154   resistance to herbivores (Choong et al. 1992; Lucas et al. 2000; Hanley et al. 2007; Guerra et

155   al. 2010). Plant physical defenses may be affected by extrinsic and intrinsic factors, such as

156   environmental conditions (Gonzáles et al. 2008) and plant ontogeny (Hanley et al. 2007),

157   respectively. For instance, due to limitations in resource acquisition, seedlings often show less

158   investment in physical defenses than mature plants (Boege and Marquis 2005; Hanley et al.

159   2007; Mediavilla et al. 2018; but see Clark and Burns 2015). Nonetheless, physical defenses

160   in seedlings are effective against vertebrate and invertebrate herbivores, yet costly (Cooper

161   and Ginnett 1998; Boege and Marquis 2005; Cash and Fulbright 2005; Barton and Hanley

162   2013).

163   In line with the ERH, a meta-analysis reported that invasive plants in the invaded range

164   generally show lower investment in digestibility-reducing compounds, such as tannins and

165   lignin, compared to the native range (Zhang et al. 2018). Likewise, a perennial daisy showed

166   decreased leaf toughness in the invaded range compared to the native range (Brandenburger

167   et al. 2020). Yet, spinescence traits, such as thorns and spines, have not been compared

168   between invaded and native ranges in any plant invader, to the best of our knowledge. Invasive

169   thorny plants, originally well-armed against vertebrate herbivores, are particularly suitable

170   model species to test predictions of the ERH.

171   *Ulex europaeus* L. (Fabaceae), a thorny shrub native to NW Europe, is considered

172   among the world's worst invasive species (Lowe et al. 2000; Clements et al. 2001). Once

173   established in the invaded ecosystems, through mechanisms not completely understood, *U.*

174   *europaeus* dramatically increases in size and abundance, creating thick monocultures (Muñóz

2009). Some characteristics that may favor its invasiveness are high growth rate, strong ability to resprout, high seed output, persistent seed bank, and substantial genetic and phenotypic diversity (Reyes et al. 2009; Atlan et al. 2010; Hornoy et al. 2011, 2013; Atlan et al. 2015). In a common garden experiment, *U. europaeus* seedlings from the invaded range were taller than plants from the native range but had similar insect infestation rates and similar concentrations of defensive alkaloids (Hornoy et al. 2011, 2012). Because these studies did not consider physical defenses, it remains an open question whether changes in physical defenses could be associated with the increased growth of *U. europaeus* in the invaded range. In this study, we aimed to answer this question.

In the native range, *U. europaeus* is consumed by wild vertebrate herbivores, such as red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and rabbit (*Oryctolagus cuniculus*) (González-Hernandez and Silva-Pando 1996, 1999; Alves et al. 2006), and by domestic ungulates, such as goats, sheep, cows, and horses (Putman et al. 1987; Howe et al. 1988; Clements et al. 2001; Atlan et al. 2015). In contrast, in the invaded range, specifically in Chile, there is no overlap between the distribution of *U. europaeus*, always close to human-impacted ecosystems, and the distribution of native big vertebrate herbivores, such as guanaco (*Lama guanicoe*), vicuña (*Vicugna vicugna*) or huemul (*Hippocamelus bisulcus*), which are generally restricted to remote, relatively pristine areas (Jaksic 2001; GBIF.org 2021). As to exotic vertebrate herbivores in Chile, those herbivores possibly coexisting with *U. europaeus* in the native range were introduced at least 50 years after *U. europaeus* (Jaksic 1998), a time period long enough for several invasive species to evolve traits related to invasive potential (e.g., growth rate) (Whitney and Gabler 2008; Buswell et al. 2011; Gianoli and Molina-Montenegro 2021). Some of those introduced herbivores hardly subsist in the wild (e.g., European fallow

198   deer, *Dama dama*), while others (e.g., red deer, *Cervus elaphus*) are not present in most of the

199   areas invaded by *U. europaeus* (Iriarte et al. 2005; GBIF.org 2021). In addition, introduced

200   vertebrate herbivores, such as wild rabbits and domestic ungulates, often prefer native plant

201   species over exotics, thus favoring invasion by exotic plants (Jaksic 1998; Holmgren et al.

202   2000; Holmgren 2002; Jaksic et al. 2002; Vázquez 2002; Figueroa et al. 2004; Mitchell et al.

203   2006; Parker et al. 2006; Vavra et al. 2007; Oduor et al. 2010). Moreover, in the invaded range,

204   *U. europaeus* is not commonly used as fodder species for domestic ungulates, as is the case

205   in the native range (Atlan et al. 2015; Dietl et al. 2009). For all the above reasons, *U. europaeus*

206   likely faces lower pressure by vertebrate herbivores in the invaded range, compared to the

207   native range. According to the ERH, the lower herbivory pressure in the invaded range should

208   lead to lower investment in physical defenses and/or increased growth in invasive populations

209   of *U. europaeus*, but this specific hypothesis has not been experimentally tested*.*

210   Concerning the evaluation of the ERH predictions, *U. europaeus* has a particularly

211   interesting biological feature: since leaves in mature plants are reduced to spine-like phyllodes,

212   the green thorns –together with the green branches– are at the same time physical defenses

213   and the main photosynthetic tissue, in terms of mass and surface (Clements et al. 2001; Cubas

214   2008). Therefore, the ERH prediction of a reduction in physical defenses in the invaded range

215   should not result from reduced biomass allocation to thorns, which could hinder plant growth.

216   Instead, structural changes associated with a reduction in the (costly) defensive components

217   of thorns, together with increased growth, should be expected.

218   In the present study, we compared physical defenses between *U. europaeus*

219   populations in the native (Spain) and invaded (Chile) distribution ranges. In adult plants

220   collected from natural field populations, we measured spinescence traits, thorn allocation

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221   parameters and thorn bending strength, as well as fiber content and digestibility of thorns (as

222   proxies for palatability). In addition, we measured spine density and growth in seedlings from

223   both origins (Spain and Chile) grown in a common garden. In the invaded range, we expected

224   to find, compared to the native range: i) higher seedling growth, and ii) spinescence traits

225   associated with a reduction in the defensive components of thorns (e.g., softer, less fibrous

226   tissues with decreased content of digestibility-reducing compounds), which may reduce

227   effectiveness against herbivores.

228

229   **Material and Methods**

230

231   *Study species*

232   *Ulex europaeus* (gorse) is a shrub that can be 2.5 m tall in the native range of

233   distribution, but it can reach over 5 m in the invaded range (Clements et al. 2001; Cubas 2008,

234   Barrera-Cataño et al. 2019). It has two types of branches, one of limited growth that lignifies

235   fast and another of prolonged growth that develops when conditions are favorable and lignifies

236   the next year. The latter type is softer and more flexible. Young plants develop alternate

237   petiolate leaves with 1-3 leaflets, while leaves in the adult plants are modified and reduced to

238   triangular rigid spiny phyllodes (5-12 mm). Therefore, green branches and stems are the main

239   photosynthetic tissues in adult plants. Branches have a spiny end, and each branch develops

240   sharp-pointed stems (primary thorns), which in turn develop secondary and tertiary thorns.

241   Each thorn has a phyllode in its base. See Cubas (2008) for a detailed description and

242   schematic pictures of the described plant parts and Figures 1 and 2 of the present manuscript.

243   Domestic animals (e.g., sheep and goat) can ingest different parts of *U. europaeus*,

244   including green and lignified thorns, new vegetative buds, bark, and flowers (Atlan et al. 2015;

245   Radcliffe 1986). However, though *U. europaeus* was introduced worldwide as forage,

246   ornamental or hedge plant in the 1800s and 1900s, it is not used as fodder in the invaded

247   range, which, together with the absence of management practices, may have favored its

248   expansion (Atlan et al. 2015). In Chile, it was first reported in 1847, likely introduced from

249   England (Hornoy et al. 2013), being now spread from 33°S to 41°S, reaching high densities

250   and large sizes, and even invading areas of conservation value (Clements et al. 2001; Muñóz

251   2009; Fuentes et al. 2014; Altamirano et al. 2016). The fact that this perennial species has

252   long-lived seeds (more than 30 years) allows it to keep a significant genetic diversity (Atlan et

253   al., 2010; Hornoy et al. 2013).

254

255   *Plant material collection*

256   The collection of branches, thorns and seeds was done during spring 2018 in three *U.*

257   *europaeus* populations each with similar climatic conditions within the native (Pontevedra,

258   Spain) and invaded (Concepción, Chile) ranges (Online resources 1 and 2). Climatic data for

259   the period 1982-2012 were obtained from https://es.climate-data.org. All the sampled

260   populations were located in roadside areas, which reduces the likelihood of the presence of

261   ungulate herbivores, thus resulting in the observed low browsing damages in all populations at

262   both native and invaded ranges (S. Medina-Villar, personal observation). In Spain, *U.*

263   *europaeus* populations located far from roads and urban areas can be heavily browsed by

264   domestic and wild ungulates (S. Medina-Villar, personal observation). We chose *U. europaeus*

265   populations with low herbivory because we did not aim to record the short-term responses to

266 continuous high herbivory (i.e., acclimatization). We rather sought to detect the consequences

267 of long-term contrasting levels of herbivory in the native and invaded ranges, expecting

268 functional changes in *U. europaeus* traits in response to decreased herbivory pressure in Chile.

269 Thus, albeit lightly browsed, the sampled populations in Spain certainly had a longer

270 evolutionary history facing herbivory (around 200 years more) than their Chilean counterparts.

271 In addition, by sampling roadside populations in both ranges (Chile and Spain) we could keep

272 the factor "land use" constant. To measure spinescence traits and fiber content in adult

273 individuals, a total of 60 branches (1 branch x 10 individuals x 3 populations x 2 distribution

274 ranges) were collected. Besides, a pool of seeds from 30 individuals (ca. 25 g of seeds: slightly

275 over 5,000 seeds) were collected in each distribution range. The minimum distance between

276 individuals in each of the six populations sampled was 1 m.

277

278 *Spinescence traits*

279 Branches collected in the field were oven-dried at 60 ºC for at least 48 h before we

280 measured spinescence traits. Measurements were made in green thorns, avoiding senesced

281 parts. Thorn length (L) and thorn-base width perpendicular to the branch (W) were measured

282 in a total of 1200 primary thorns (20 thorns x 1 branch x 10 individuals x 3 populations x 2

283 distribution ranges) using a digital caliper (Figs. 1A, B). Thorn length was measured from the

284 base of the thorn to its tip (Figs. 1A, B). Thorn length has been shown to increase in response

285 to herbivory in other *Fabaceae* species (Young et al. 2003; Wigley et al. 2019). Thorn width

286 can be used to estimate defense effectiveness against herbivores (Pérez-Harguindeguy et al.

287 2013). The L:W ratio was calculated, which is analogous to the slenderness ratio

288   (height:diameter; the inverse of sturdiness) commonly measured in plants (Haase 2008;

289   Valladares et al. 2012).

290   In each branch, four branch segments were randomly subsampled and cut to calculate

291   thorn density (number of thorns per cm of branch segment) and biomass allocation to thorns,

292   i.e., the ratio between the thorn dry weight and the branch segment dry weight (480 branch

293   segments in total = 4 branch segments x 2 branches x 10 individuals x 3 populations x 2

294   distribution ranges). Previous studies in other shrub species have reported a positive

295   correlation between spine density and herbivory pressure (Cavagnaro et al. 2017; Musariri et

296   al. 2018). All the above-mentioned variables were averaged by individual (10 per population).

297   To standardize measurements, all the spinescence traits were divided by branch length.

298

299   *Bending strength of thorns*

300   In freshly collected primary thorns, flexural stiffness (elastic resistance to bending) was

301   estimated by the following formula: $(F/D) \times B^3$, where F is the force, D is the displacement, and

302   B is the span length between supports in the bending test (Hanley et al. 2007). We kept

303   parameters B and D constant and estimated F in a total of 144 thorns (6 thorns x 4 randomly

304   selected individuals x 3 populations x 2 distribution ranges). Using a vise, thorns were fixed at

305   3 cm from the thorn tip by pressing the thorn side (width) that is perpendicular to the branch.

306   At 1 cm from the thorn tip, a plastic container was hanged –using a thread as handle– and an

307   increasing weight was applied to the container (by adding rice) until the thorn bent at a 10°

308   angle. Therefore, B was 2 cm, D was 10° angle, and F was the weight necessary to bend a

309   thorn 10°, which we termed bending strength (Van Gelder et al. 2006; Shah et al. 2017). A

310   scheme of the bending test performed is shown in Figure 1C. The total length of each thorn

311   submitted to the bending test was also recorded because thorn size may influence its bending

312   strength (Van Gelder et al. 2006).

313

314   *Fiber content of thorns*

315   To analyze fiber content, individual thorn samples from each population were pooled,

316   dried, and then pulverized with a mixer mill (Retsch MM 301). A total of 24 samples (4 pooled

317   samples x 3 populations x 2 distribution ranges) were analyzed for neutral detergent fiber

318   (NDF), acid detergent fiber (ADF), lignin, cellulose, and dry matter digestibility (DMD) using the

319   filter bag technique; this was done in an Ankom Automated Fiber Analyzer A2000 (Ankom,

320   USA), based on the analytical method of Göering and Van Soest (1970).

321

322   *Common garden experiment*

323   In June 2019, air-dried seeds of *U. europaeus* from Concepción (Chile) and Pontevedra (Spain)

324   were sown in square pots (11 x 11 x 12 cm) containing a 90:10 (v/v) mixture of organic substrate

325   (50:50 white peat moss and black peat; Projar Professional Seed Pro 5050;) and vermiculite.

326   Due to seed coat hardiness, seeds were pretreated at 80 ºC for 30 min to ensure germination

327   success. A total of 120 seedlings per distribution range grew for six months in the pots in

328   common environmental conditions (minimum temperature 18 ºC, maximum temperature 25 ºC,

329   watered when needed) in a greenhouse at the Alfonso XIII Botanical Garden (Universidad

330   Complutense de Madrid, Spain). We considered the six-month plants as seedlings because

331   most of them still had their cotyledons. In each seedling the following parameters were

332   measured: the stem diameter below cotyledon insertion, plant height and spine density, which

333   was visually estimated as the percentage of plant height that developed spines. Note that

334 seedlings do not develop thorns, but they show leaves and spines (i.e., sharp-pointed modified

335 leaves). Figure 2 shows seedlings of *U. europaeus* from Spain and Chile.

336

337 *Statistical analyses*

338 Linear Mixed Models (LMM) were performed to assess differences in standardized

339 spinescence variables (L, W, L:W, density and biomass), fiber contents and DMD between

340 distribution ranges (invaded vs native range; fixed factor), using population as random factor

341 to account for population variability. To evaluate the relationship between spinescence

342 variables and branch length in *U. europaeus* from each range, LMM were performed using

343 distribution range as fixed factor, branch length as covariate and population as random factor.

344 Principal Component Analyses were performed to visualize relationships among fiber-related

345 variables (lignin, cellulose, ADF, NDF and DMD) and among spinescence variables in *U.*

346 *europaeus* thorns from native and invaded ranges. Permutational multivariate analysis of

347 variance (PERMANOVA) was used to assess differences between distribution ranges

348 considering all fiber-related variables on the one hand, and all spinescence variables on the

349 other hand. To evaluate the effect of distribution range (fixed factor) on the bending strength of

350 thorns (dependent variable), a LMM was performed using L as covariate and population as

351 random factor.

352   A one-way ANOVA was used to compare the diameter and height of seedlings between

353 distribution ranges (fixed factor). To deal with excess of zeros in spine density of seedlings

354 (dependent variable), we performed a Generalized Linear Model (GLM, family quasibinomial)

355 with distribution range as fixed factor (Zuur et al. 2009). When needed, dependent variables

356 were transformed with log, root-square or power functions to meet homoscedasticity and

357 normality in LMM and ANOVA. Statistical analyses were performed in R software 3.4.3 (R Core

358 Team 2017) using "lmer" function (lme4 package) for LMM, "adonis2" function (vegan package)

359 for PERMANOVA, the built-in R function "prcomp" for PCA, and "glm" function for GLM (Zeileis

360 et al. 2008; Bates et al. 2015; Jari et al. 2020).

361

362 **Results**

363 Spinescence traits in *U. europaeus* plants from the invaded range differed from those of the

364 native range (PERMANOVA, pseudo-F_1 = 30.6, *P* < 0.001; PCA in Online Resource 3). The

365 effect of distribution range was significant for all the branch-length standardized spinescence

366 traits except for thorn density (LMM, Table 1). Specifically, thorn length (L), thorn width (W),

367 L:W, and thorn biomass allocation were greater in the invaded range (Fig. 3). Thorn length and

368 L:W were greater in the invaded range and increased with branch length in both the native and

369 the invaded ranges (Table 2; Fig. 3). Thorn density did not differ between plants from Chile and

370 Spain, decreased with increasing branch length in both distribution ranges, but the slope was

371 greater in plants from the invaded range (Table 2; Fig. 3). Thorn biomass allocation was,

372 overall, greater in the invaded range, decreased with increasing branch length in the invaded

373 range and did not vary with branch length in the native range (Table 2; Fig. 3). Thorns from the

374 native range showed a greater length-corrected bending strength than thorns from the invaded

375 range, being this difference minimized in the longest thorns (Range, F_1 = 9.1, *P* = 0.0035; Thorn

376 length, F_1 = 7.2, *P* = 0.0084; Range x Thorn length, F_1 = 6.0, *P* = 0.0156, Fig. 4).

377 Overall, *U. europaeus* plants from the invaded range differed from those of the native

378 range in fiber-related traits (PERMANOVA, F = 10.9, *P* < 0.001; PCA in Online Resource 4).

379 Fiber contents of thorns tended to be greater in the native range, the differences being

16

380   significant for NDF and cellulose, marginally significant for ADF and non-significant for lignin

381   (Table 3). Our estimate of digestibility (DMD) tended to be lower in thorns from the native range,

382   but differences were not significant (Table 3).

383   Seedlings of *U. europaeus* from the native range showed higher spine density than

384   seedlings from the invaded range (t = 5.5, *P* < 0.001, GLM; Figures 2 and 5). Interestingly,

385   whereas 6-month seedlings did not differ in height (F_1 = 0.11, *P* = 0.7369, ANOVA; Fig. 5),

386   those from the invaded range showed thicker stems (F_1 = 4.5, *P* = 0.0357, ANOVA; Fig. 5),

387   which indicates greater biomass production.

388

389   **Discussion**

390   Our results show that, in the invaded range, adult plants of *U. europaeus* shift towards

391   i) decreased investment in the (costly) defensive components of thorns, i.e., less fibrous,

392   slenderer and easier to bend thorns, which can result in reduced effectiveness against

393   herbivores (Lambert et al.1989; Lucas et al. 2000; Hanley et al. 2007), and ii) increased

394   investment in photosynthetic tissues: increased thorn size and biomass. Plant stems may have

395   both structural and functional roles, which may be in conflict with one another (Speck and

396   Burgert 2011). In the case of adult plants of *U. europaeus*, stems are at the same time physical

397   anti-herbivore defenses, thorns, and the main photosynthetic tissue, as leaves are reduced to

398   small triangular squamous phyllodes (Cubas 2008). This particular feature of *U. europaeus*

399   somewhat challenges the predictions of the Enemy Release Hypothesis (ERH) (Keane and

400   Crawley 2002; Colautti et al. 2004). Thus, a lower herbivory pressure in the invaded range

401   should not lead to a lower investment in thorn size or biomass, because it would reduce

402   interception of photosynthetically active radiation and hence decrease plant growth.

403   Nonetheless, consistent with the fundamental tenets of ERH, the changes in structural design,

404   fiber composition, biomass allocation and strength in *U. europaeus* thorns in the invaded range

405   resulted in these physical defenses likely being less efficient against vertebrate herbivores

406   (Lambert et al. 1989; Read and Stokes 2006; Xu et al. 2013).

407   All the morphological, compositional and mechanical changes observed in thorns in the

408   invaded range may favor the invasive success of *U. europaeus*. For instance, increased size

409   and biomass of the main photosynthetic tissues (green thorns) in the invaded range may favor

410   plant growth because the photosynthetic area (usually leaf area) is the main driver of light

411   interception and ultimately plant productivity (Gifford et al. 1984; Koester et al. 2014;

412   Weraduwage et al. 2015). Moreover, a lower investment in costly fibers, such as cellulose

413   (Poorter and De Jong 1999), in the invaded range leaves more resources available to invest in

414   other plant functions that contribute to vital rates. In line with our results, an experimental study

415   with an evergreen tree species and a meta-analysis showed that the content of digestibility-

416   reducing compounds was lower in plants from the invaded range compared to those from the

417   native range (Montti et al. 2016, Zhang et al. 2018).

418   The reduced bending strength of thorns in the invaded range, a key result concerning

419   physical defense effectiveness, was likely associated with differences in the content of

420   structural compounds (cellulose) and patterns of biomass allocation, resulting in less fibrous

421   and slenderer thorns. We emphasize that, to our knowledge, the reduction in bending strength

422   of a physical defense in the invaded range has not been documented for any invasive plant

423   species. This is rather surprising, given the relevance of physical defenses, such as

424   spinescence traits, for plant protection against vertebrate herbivores (Obeso 1997; Gómez and

425   Zamora et al. 2002; Hanley et al. 2007). It is much more common to find results linked to leaf

toughness, which is generally lower in the invaded range (Agrawal et al. 2005; Liao et al. 2013; but see: Franks et al. 2008; Ridenour et al. 2008). We hypothesize that the reduction in bending strength in *U. europaeus* may be a consequence of the lower selective pressure exerted by herbivores in the invaded range (Jacksic 1998, 2001; Atlan et al. 2015). However, the specific mechanical properties of physical defenses that deter vertebrate herbivores are not completely understood (Read and Stokes 2006; Sanson 2006).

Unlike adult plants, seedlings of *U. europaeus* do not develop thorns, but they do show leaves and spines. Therefore, seedlings are amenable to "traditional" tests of the ERH. We found a negative relationship between physical defense (spine density) and growth (in diameter) in seedlings, with more investment in growth and less in defense in the invaded range, as predicted by the ERH. This shift in resource allocation between defense and growth was not found in earlier studies addressing the relationship between chemical defenses and growth in *U. europaeus* (Hornoy et al. 2011, 2012). In fact, few studies have reported both ERH-predictions, namely decreased defense and increased growth, in the same invasive species (Bossdorf et al. 2005). Seedlings are generally considered to rely more on chemical than on physical defenses against herbivores (Barton and Hanley 2013). However, our results suggest that physical defenses may be relevant during the early establishment of this invasive shrub. Seedlings are commonly highly susceptible to big vertebrate herbivores, such as ungulates, which can easily kill the whole seedling (Rafferty et al. 2005). Nevertheless, spiny seedlings from different species have been shown to effectively deter other herbivores, such as lagomorphs, rodents and invertebrates (Cooper and Ginnett 1998; Boege and Marquis 2005; Cash and Fulbright 2005; Kariyat et al. 2017). Thus, the lower spine density of *U. europaeus* seedlings in the invaded range could result from the release of a variety of

449   herbivores, not only big vertebrate herbivores, which prefer to feed on adult than young plants

450   (Boege and Marquis 2005).

451   From an applied perspective, the results of this study suggest that land managers can

452   take advantage of the high palatability and (likely) reduced effectiveness of physical defenses

453   in plants of *U. europaeus* in Chile to use domestic animals, especially goats, as a measure to

454   control this invasive shrub. The intensive use of goats to control *U. europaeus* resprouts is an

455   effective management practice widely used in New Zealand (Radcliffe 1985, 1986; Howe et al.

456   1988; Popay and Field 1996); however, this control procedure requires clipping of adult plants

457   and numerous goats to eat the resprouts. On the other hand, a high invasive potential could

458   be expected for other *Fabaceae* species with photosynthetic thorns, such as *Ulex galli*, *U. minor*

459   (Stokes et al. 2003) and *Prosopis kuntzei* (Böcher 1977), because they could also be partially

460   released from the growth-defense tradeoff in the invaded ecosystems. Finally, we have

461   captured only a subset of the geographic distribution of the study species in its native and

462   invaded range, which calls for caution in extrapolating our results to other geographic areas.

463   Some traits, such as the contents of lignin and cellulose in the plant cell wall, may respond to

464   abiotic conditions, such as drought, high and low temperatures (Le Gall et al., 2015; Liu et al.

465   2018). Sampling populations of *U. europaeus* from areas with different climatic conditions,

466   within both native and invaded ranges, would broaden our understanding of the contribution of

467   the ERH to explain its invasion patterns and the underlying plant traits.

468

469   **Conclusions**

470   This study evidences the role of spinescence traits in the invasiveness of an aggressive

471   and successful thorny shrub, *U. europaeus*. In particular, it shows that in the invaded range

472   (Chile) adult plants of *U. europaeus* shift resource allocation, increasing the amount of

473   photosynthetic tissue (thorn size and biomass) and decreasing the investment in the defensive

474   components of thorns by producing less fibrous, slenderer and easier to bend thorns. The latter

475   may translate into reduced effectiveness against herbivores. In the early stages of

476   establishment (seedling stage), lower investment in spines and increased growth in the invaded

477   range may partly explain the invasion success of *U. europaeus*, according to the ERH. As far

478   as we know, this is the first report of such modification in thorns or spines of a woody species

479   between invaded and native ranges. Whereas higher investment in growth in the invaded range

480   (larger thorns) may provide competitive advantages over native plants, higher investment in

481   defense in the native range (stronger, more fibrous, and robust thorns) may better protect *U.*

482   *europaeus* against a higher herbivory pressure. The present study illustrates the need of

483   refinement of ERH predictions to consider additional functions of plant antiherbivore defenses,

484   such as photosynthesis in the case of *U. europaeus* thorns.

485

486   **Acknowledgements**

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Table 1. Linear Mixed Models assessing the effects of distribution range (native vs. invaded, fixed factor) on branch length-standardized thorn length (L, cm), thorn width (W, mm), L:W ratio, thorn density (number of thorns per cm of branch segment) and thorn biomass allocation (thorn:branch segment mass ratio) in adult plants of *Ulex europaeus* from the invaded and the native range. Population was entered as random factor.

	F (df = 1)	P
Thorn length (L)	54.04	**<0.0001**
Thorn width (W)	11.72	**0.0011**
L:W	35.40	**<0.0001**
Thorn density	1.21	0.3334
Thorn biomass allocation	19.13	**<0.0001**

Table 2. Linear Mixed Models assessing the effect of distribution range (invaded vs. native, fixed factor), branch length (covariate) and their interaction on thorn length (L, cm), thorn width (W, mm), L:W ratio, thorn density (number of thorns per cm of branch segment) and thorn biomass allocation (thorn:branch segment mass ratio) in *Ulex europaeus*. Population was entered as random factor.

	Distribution Range (R)		Branch length (BL)		R x BL	
	F ($df = 1$)	*P*	F ($df = 1$)	*P*	F ($df = 1$)	*P*
Thorn length (L)	10.46	**0.0023**	22.63	**<0.0001**	1.12	0.2946
Thorn width (W)	3.67	0.0618	3.02	0.0882	1.07	0.3062
L:W	5.63	**0.0213**	14.40	**0.0004**	0.19	0.6647
Thorn density	3.17	0.0818	24.43	**<0.0001**	5.43	**0.0235**
Thorn biomass allocation	12.19	**0.0009**	4.13	**0.0467**	5.79	**0.0193**

Table 3. Content (%) of lignin, acid detergent fiber (ADF), neutral detergent fiber (NDF), cellulose and dry matter digestibility (DMD) in *Ulex europaeus* thorns from the invaded (Chile) and the native range (Spain). Results of the Linear Mixed Models (LMM) assessing the effect of distribution range (invaded vs native) as fixed factor are also shown. Population was entered as random factor.

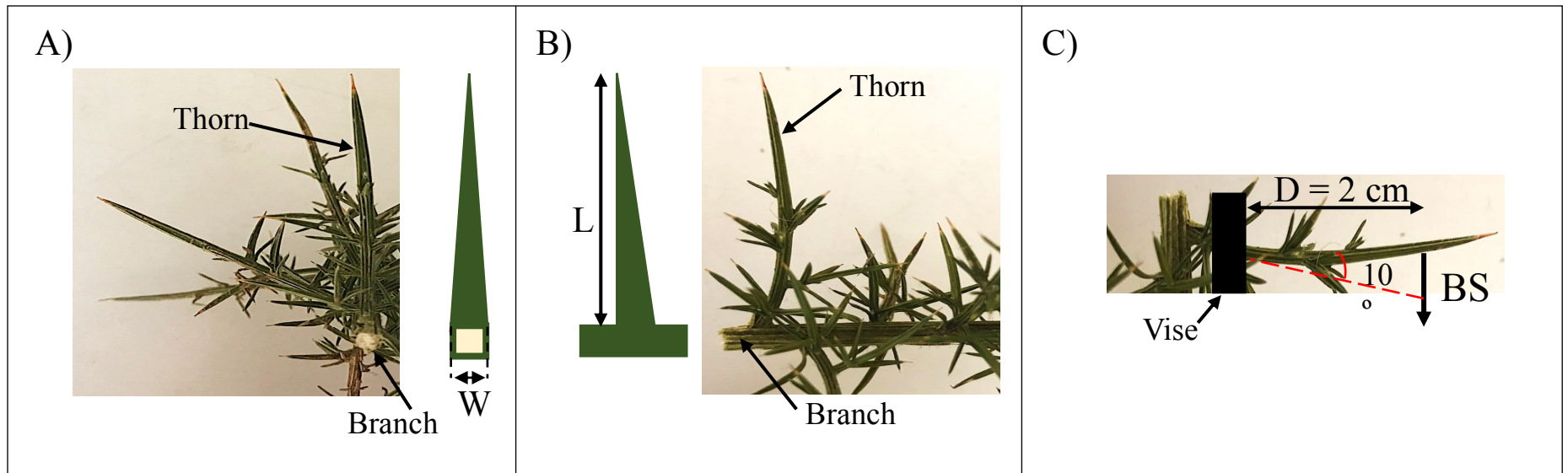| | Mean ± SE | | LMM | |
	Invaded range	Native range	F	P
Lignin	16.2 ± 1.9	21.7 ± 2.1	2.10	0.2236
ADF	34.6 ± 3.4	45.1 ± 1.4	7.35	0.0543
NDF	45.5 ± 2.2	58.8 ± 1.9	10.70	**0.0291**
Cellulose	28.9 ± 2.6	46.7 ± 2.3	16.99	**0.0131**
DMD	47.0 ± 2.1	38.3 ± 2.0	3.34	0.1384

Fig. 1. Proximal (A) and lateral (B) view of a branch segment of *Ulex europaeus* (picture) complemented with a basic scheme of a single thorn showing some spinescence traits measured: thorn length (L) and, thorn base width perpendicular to the branch (W). Scheme showing the bending test applied to the thorns (C). D: the displacement from the vise to the point where the weight is applied in the bending test; BS: bending strength (flexural resistance, see text for additional details).

Fig. 2. Seedlings of *U. europaeus* from the invaded (Chile, left panel) and the native range (Spain, right). Note that the seedling from Spain developed more spines than that from Chile.
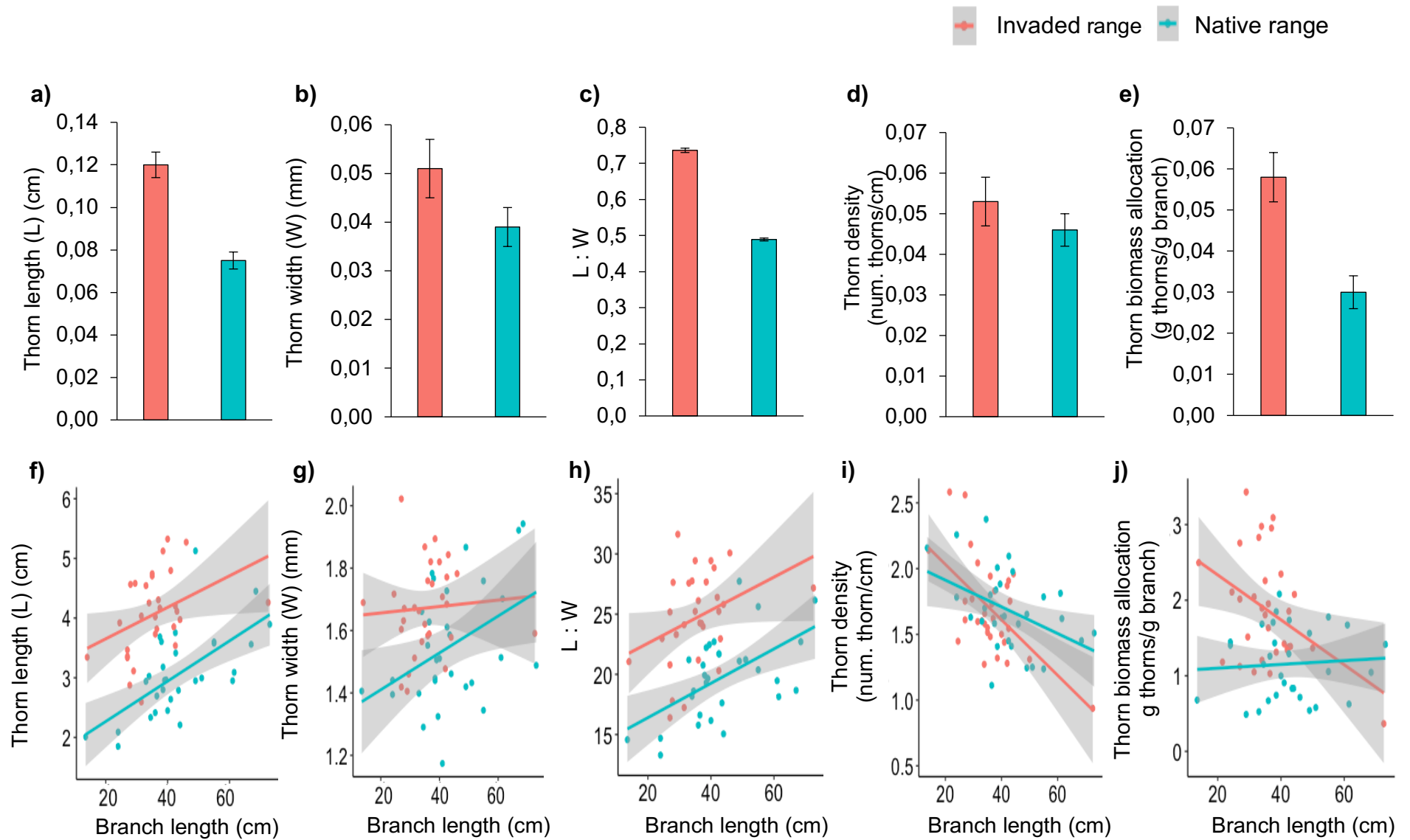
Fig. 3. Mean (± SE) branch length-standardized spinescence variables thorn length (L), thorn width (W), L:W (thorn slenderness), thorn density and thorn biomass allocation (**a, b, c, d** and **e,** respectively) and the linear regressions of the same spinescence variables (no

branch length-standardized) as a function of branch length (**e**, **f, g**, **h**, **i** and **j**, respectively) in *Ulex europaeus* individuals from the invaded and native ranges (Chile and Spain, respectively). Statistical results are shown in Table 1 and 2.
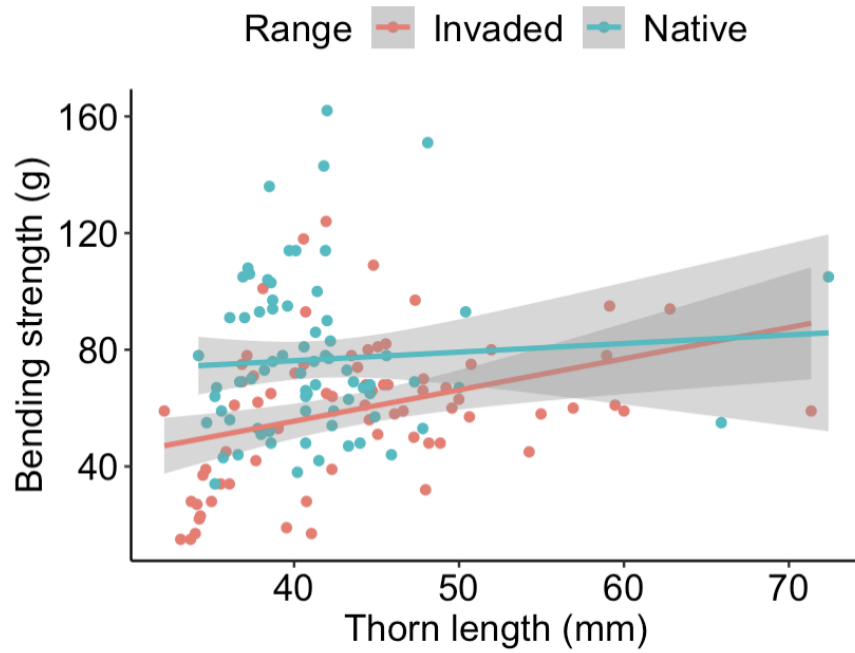
Fig. 4. Linear regression for bending strength as a function of thorn length in *Ulex europaeus* from invaded and native distribution ranges (Chile and Spain, respectively; Range). Bending strength was significantly influenced by Range, Thorn length and their interaction (statistical results in the text).
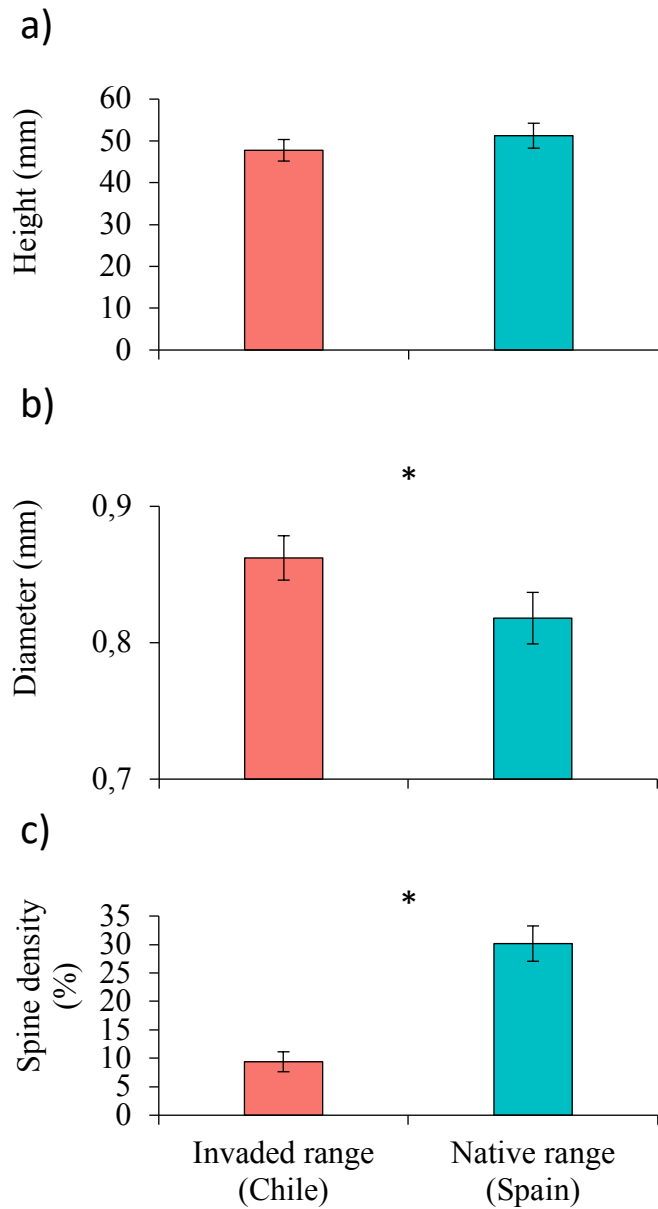
Fig. 5. Mean (± SE, n = 120) of the variables: a) height (mm), b) stem diameter (mm) and c) spine density (%) of *Ulex europaeus* seedlings from the invaded and the native distribution range (Chile and Spain, respectively; Range). Asterisks indicate significant differences between ranges after a linear mixed model (population as random factor) for each variable.