

1 **Rapid growth and defence evolution following multiple introductions**

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9

10 Abstract

- 11 1. Rapid adaptation can aid invasive populations in their competitive success. Resource-allocation
12 trade-off hypotheses predict higher resource availability or the lack of natural enemies in
13 introduced ranges allow for increased growth and reproduction, thus contributing to invasive
14 success. Evidence for such hypotheses are however equivocal and tests among multiple ranges
15 over productivity gradients are required to provide a better understanding of the general
16 applicability of these theories.
- 17 2. Using common gardens, we investigated the adaptive divergence of various constitutive and
18 inducible defence-related traits between the native North American and introduced European
19 and Australian ranges, whilst controlling for divergence due to latitudinal trait clines, individual
20 resource budgets and population differentiation, using >11,000 SNPs.
- 21 3. Rapid, repeated clinal adaptation in defence-related traits was apparent despite distinct
22 demographic histories. We also identified divergence among ranges in some defence-related
23 traits, although differences in energy budgets among ranges may explain some, but not all,
24 defence-related trait divergence. We do not identify a general reduction in defence in concert
25 with an increase in growth among the multiple introduced ranges as predicted trade-off
26 hypotheses.
- 27 4. *Synthesis*: The rapid spread of invasive species is affected by a multitude of factors, likely
28 including adaptation to climate and escape from natural enemies. Unravelling the mechanisms
29 underlying invasives' success enhances understanding of eco-evolutionary theory and is
30 essential to inform management strategies in the face of ongoing climate change.

32 Keywords

33 Latitudinal adaptation, resource allocation, growth-defence trade-offs, EICA, constitutive defence,
34 inducible defence, invasive species, phenolic compounds

36 Introduction

37 Biological invasions are occurring at an accelerating pace due to the globalisation of anthropogenic
38 activity (Ricciardi, 2007). Individuals colonizing new ranges likely face environments different from
39 those previously experienced (Sax & Brown, 2000; Allendorf & Lundquist, 2003; Chown *et al.*, 2014).
40 Nonetheless, alien populations often display enhanced performance compared to their native
41 counterparts (Blossey & Notzold, 1995; Thébaud & Simberloff, 2001; Parker *et al.*, 2013), and this
42 can be facilitated by rapid adaptation (Chown *et al.*, 2014; Colautti & Lau, 2015; Dlugosch *et al.*,

43 2015a). Therefore, in the face of ongoing environmental change, studies on introduced species are
44 imperative to provide insight into invasive success as well as contemporary evolutionary processes.

45 Resource allocation trade-offs between life-history traits, such as growth rate and reproductive
46 output, feature prominently in evolutionary theories developed to explain the success of invasive
47 species (e.g., Hodgins & Rieseberg, 2011; Kumschick *et al.*, 2013; Turner *et al.*, 2014; Colautti & Lau,
48 2015). For instance, if abiotic stressors are mitigated upon introduction because of increased resource
49 availability, increased investment in colonization or competitive ability could facilitate invasion
50 success (Grime, 1977; Davis *et al.*, 2000; Bossdorf *et al.*, 2005; He *et al.*, 2010; Dlugosch *et al.*,
51 2015b). Similarly, the evolution of increased competitive ability hypothesis (EICA) postulates that
52 release from specialist herbivores within the introduced range favours genotypes allocating resources
53 to growth and reproduction in lieu of defence (Blossey & Notzold, 1995). Evidence for such adaptive
54 divergence of invasive populations is however equivocal (Felker-Quinn *et al.*, 2013) perhaps due to
55 allocation trade-offs among multiple competing functions (Mole, 1994; Züst & Agrawal, 2017),
56 variation in resource availability or acquisition (Uesugi *et al.*, 2017; Züst & Agrawal, 2017), interplay
57 with non-adaptive processes (Lee, 2002; Facon *et al.*, 2006; Prentis *et al.*, 2008; Rius & Darling, 2014;
58 Estoup *et al.*, 2016), or other selective factors, such as climate, playing an important role in governing
59 patterns of trait variation within and between ranges (Lachmuth *et al.*, 2011; Turner *et al.*, 2015).

60 Biotic and abiotic clines impacting plant resistance within ranges (Endara & Coley, 2011;
61 Moles *et al.*, 2011a) can obscure the adaptive underpinnings of trait divergence governed by growth-
62 defence trade-offs in response to changes during invasion in herbivory. For instance, herbivore
63 pressure in the native range is expected to increase towards lower latitudes and potentially drive clines
64 in plant defence in some species (Moles *et al.*, 2011a). This clinal pattern may be absent in the
65 introduced range due to overall lack of herbivory, resulting in non-parallel defence gradients between
66 ranges (e.g. Cronin *et al.*, 2015; Allen *et al.*, 2017). Moreover, high-resource environments support
67 plant species with faster growth that are more vulnerable to herbivores (Coley *et al.*, 1985; Zandt,
68 2007; Endara & Coley, 2011), resulting in latitudinal clines in defence traits. Latitudinal clines in
69 resource availability could subsequently lead to the evolution of high growth and reduced chemical
70 defences at lower latitudes (Woods *et al.*, 2012; Moreira *et al.*, 2014), although this interspecific
71 pattern may have limited application to intraspecific variation (Hahn & Maron, 2016, but see Woods
72 *et al.*, 2012). However, taken together these patterns suggest that the evolutionary consequences of
73 herbivore escape could change along latitudinal gradients (Blumenthal, 2006). Geographical clines
74 therefore need to be considered in tests of adaptive divergence between ranges (Colautti *et al.*, 2009).

75 The complex interplay between the evolutionary mechanisms shaping phenotypic divergence
76 could also confound inferences of adaptation. Distinct demographic processes, including founder

77 effects, genetic drift and admixture, often characterize introduction and alone can lead to divergence
78 between native and introduced populations (Lee, 2002; Facon *et al.*, 2006; Prentis *et al.*, 2008; Rius &
79 Darling, 2014; Estoup *et al.*, 2016). Dissection of the various evolutionary processes that can
80 contribute to trait divergence is required to advance our understanding of rapid spread in invasive
81 species. In addition, the repeatability of evolutionary patterns associated with introductions is unclear,
82 as the majority of studies examining trait evolution following introduction focus on a single invaded
83 range (e.g. Blossey & Notzold, 1995; Joshi & Vrieling, 2005; Hodgins & Rieseberg, 2011; Uesugi &
84 Kessler, 2016, but see Colomer-Ventura *et al.*, 2015). Repeatable trait divergence across multiple
85 invaded ranges would provide support for adaptive divergence of traits during invasion as well as
86 insight into selective mechanisms contributing to invasion success (Hodgins *et al.*, 2018; van
87 Boheemen *et al.*, 2018).

88 The frequency and level of attack can impact the evolution of defence traits (Orrock *et al.*,
89 2015; Bixenmann *et al.*, 2016), which might also be expected to trade off due to their costs and
90 redundancy (Koricheva *et al.*, 2004; Agrawal *et al.*, 2010). Predictable and strong attack should favour
91 constitutive defence, whereas low, infrequent herbivory would favour no, or an inducible response
92 (Agrawal & Karban, 1999; Ito & Sakai, 2009). These responses have been shown to vary over
93 latitudinal clines within ranges (Moreira *et al.*, 2014; Rasmann & Agrawal, 2011). However, the studies
94 exploring evolutionary shifts of constitutive and inducible defences between native and introduced
95 ranges showed mixed results (e.g. Cipollini *et al.*, 2005; Eigenbrode *et al.*, 2008). Various Variable
96 outcomes could result from a decrease in the intensity and frequency of herbivory following
97 introduction (Maron & Vilà, 2001; Agrawal & Kotanen, 2003), including an increase in plasticity
98 (Cipollini *et al.*, 2005; Lande, 2015) or high variability in inducible response among populations
99 (Eigenbrode *et al.*, 2008). Testing such shifts in invasive species would provide insight into factors
100 governing the evolution of induced/constitutive trait defence more generally.

101 *Ambrosia artemisiifolia* is a highly suitable system to study adaptive divergence in defence-
102 related traits during invasion. This native North American weed has successfully established globally
103 (Oswalt & Marshall, 2008), including recent introductions to Europe (~160 years ago Chauvel *et al.*,
104 2006) and Australia (~80 years ago; Palmer & McFadyen, 2012; van Boheemen *et al.*, 2017). Repeated
105 clinal associations were found in *A. artemisiifolia* populations included in the current study, with
106 declines in size and increase in SLA at higher latitudes (van Boheemen *et al.*, 2018), though differences
107 occurred among ranges. At comparable latitudes, European plants were bigger and had lower SLA
108 than natives, while Australian plants had higher SLA leaves (van Boheemen *et al.*, 2018).

109 We test quantitative trait divergence in 1) physical defence (trichome density), 2) chemical
110 defence (phenolic compounds concentration and richness), and 3) inducibility of chemical defence

111 among the native North American and introduced European and Australian ranges in a series of
112 common garden experiments. Trichomes are found on the leaves and the stems of plants and deter
113 herbivores (Kessler & Baldwin, 2002; Dalin *et al.*, 2008; Tian *et al.*, 2012). Phenolics are secondary
114 metabolites that are often thought to confer resistance against herbivores (Bhattacharya *et al.*, 2010;
115 War *et al.*, 2012; War *et al.*, 2018). These compounds are also known to be inducible in response to
116 herbivore damage, as well as simulated herbivory treatments including wounding and methyl
117 jasmonate (MeJA) applications (e.g. Lee *et al.*, 1997; Constabel & Ryan, 1998; Keinänen *et al.*, 2001;
118 Heredia & Cisneros-Zevallos, 2009). We accounted for population structure, which could potentially
119 drive patterns in traits that are non-adaptive, using >11,000 double-digest genotype-by-sequencing
120 SNPs. Moreover, we controlled for defence-related trait variation along latitudinal clines.

121 We predict reduced constitutive defence within the introduced ranges together with elevated
122 inducible response due to lower certainty of attack (Cipollini *et al.*, 2005) and a more plastic
123 (inducible) response in recent colonisations (Lande, 2015). We expect non-parallel defence gradients
124 between native and introduced ranges due to divergence of clines in herbivory (Moles *et al.*, 2011b)
125 and/or variable resource gradients (Blumenthal, 2006; Hahn & Maron, 2016). Finally, we explored the
126 association between defence-related trait divergence and divergence in growth and SLA among ranges
127 as a growth-defence trade-off would result in greater growth in conjunction with reduced defence.
128 However, greater defence could be facilitated by genotypes with enhanced resource acquisition
129 resulting in a positive correlation in traits. By considering the complex interplay of the evolutionary
130 mechanisms impacting defence divergence among multiple ranges, we test evolutionary changes in
131 herbivore defence likely shaped by selection.

132

133 **Methods**

134 *Study species*

135 *Ambrosia artemisiifolia* is a highly invasive, monoecious, self-incompatible annual plant (Brandes &
136 Nitzsche, 2006), most commonly found in disturbed habitats (Bassett & Crompton, 1975; Lommen *et al.*,
137 2017) and is expected to expand its range with ongoing climate change (Chapman *et al.*, 2014). It
138 is the leading cause of hayfever worldwide (Taramarcaz *et al.*, 2005) and has a significant impact on
139 crop yields (Kazinczi *et al.*, 2008). Within Europe, admixture following multiple introductions from
140 distinct native sources has been suggested to have contributed to the success of introduced populations,
141 and genetic variation equals levels observed in North America (Chun *et al.*, 2010; Gladieux *et al.*,
142 2010; Gaudeul *et al.*, 2011; van Boheemen *et al.*, 2017). A subsequent single bottlenecked introduction
143 from Europe has been determined as the origin of the Australian invasion, although the exact European
144 source is unknown (van Boheemen *et al.*, 2017).

145 Within the native range, around 450 herbivores have been associated with *Ambrosia* species,
146 of which about 30% are specific to the *Ambrosia* genus (Gerber *et al.*, 2011). The North American
147 native specialist *Ophraella communa* is shown to exert high levels of damage (Throop, 2005). Up to
148 50 polyphagous insect species have been associated with *A. artemisiifolia* in Europe, yet most cause
149 little damage (Gerber *et al.*, 2011; Essl *et al.*, 2015). *Ophraella communa* has been sighted in Southern
150 Switzerland and Northern Italy since 2013 (Müller-Schärer *et al.*, 2014), where it greatly affects *A.*
151 *artemisiifolia* seedling survival and growth (Cardarelli *et al.*, 2018). In Australia, generalists
152 *Zygogramma bicolorata* (leaf-feeding) and *Epiblema strenuana* (stem-boring) are widespread and
153 seemingly exert some control (Palmer & McFadyen, 2012).

154

155 *Experimental set-up*

156 To explore the divergence of constitutive quantitative defence traits between native and introduced
157 ranges (“constitutive-defence experiment”), while accounting for divergence along latitudinal clines,
158 we collected *Ambrosia artemisiifolia* seeds in 2013-2014 from broad geographical scales within the
159 native North America and introduced Europe and Australia. We raised seedlings in a common garden
160 (for detailed methods, see Supporting Information). Briefly, we stratified seeds for 6 weeks at 4°C
161 (Willemsen, 1975). After a 2-week germination at 30°C with 12h light/dark cycle, we randomly
162 transplanted the seedlings into 100ml kwikpot trays with Debco mix, followed by a second transplant
163 to 0.7L pots containing Debco and 1.5ml slow-release fertilizer (Osmocote Pro, eight to nine months)
164 one month later. We top-watered all plants and artificially manipulated daylight following the light
165 cycle at the median latitude for all populations (47.3°N). To explore constitutive defence, we selected
166 a seedling from four maternal lines, originating from 28 North American, 32 European and 20
167 Australian locations (Supporting Information, Table S1).

168 A separate greenhouse experiment was conducted to test whether the inducibility of defence
169 response varied among plant origins (hereafter, “induction experiment”). We used a subset of
170 populations used in the constitutive experiment (10 North American, 17 European and 12 Australian
171 locations, Table S1). For each population, we selected four maternal lines, and grew two seedlings per
172 line as above. One seedling per maternal line was allocated to either the control or simulated herbivory
173 treatment. We simulated herbivory by vertically cutting off half of the newest fully formed leaf
174 (wounding) and subsequently spraying the whole plant with 1mM methyl jasmonate (MeJA) (Campos-
175 Vargas & Saltveit, 2002; Heredia & Cisneros-Zevallos, 2009; Hodgins & Rieseberg, 2011; Jordan *et*
176 *al.*, 2015). Control plants were not wounded and were sprayed with distilled water.

177

178 *Trait measurements*

179 For the constitutive experiment, we recorded trichome density at the mid-point of each plant under a
180 dissecting microscope (Olympus, SZ-PT) using a 1 cm x 0.3 cm stem area at the mid-point of each
181 plant, nine weeks after the second transplant. Three weeks later, we scanned one young, fully expanded
182 leaf from each plant and calculated leaf area using ImageJ and the R package LeafArea (Katabuchi,
183 2015). We dried leaves at 45 °C for seven days and an addition 12 hours prior to weighing and weighed
184 to the closest milligram. We calculated specific leaf area (SLA) by dividing leaf area by dry leaf weight
185 (mm^2/mg). We deconstructed plants for biomass measurements once the majority of seeds had ripened.
186 We placed aboveground components in paper bags and dried these in ovens at 45 °C for at least 36
187 hours. Before dry weight biomass measures, we dried materials for an additional minimum of 24 hours
188 to ensure the dry weight was constant at the time of measuring and it was not variable due to humidity
189 in the air or incomplete drying. We weighed this shoot biomass to the closest 0.1 gram.

190 Leaf samples for phenolic analyses were collected four weeks after the second transplant by
191 clipping approximately 200 mg of the newest fully expanded leaf, which was flash frozen in liquid
192 nitrogen and stored in a -80 °C. In the induction experiment, we collected leaf samples 24 hours after
193 the final treatment. Samples were extracted in 1 ml of 80% methanol (% by volume in water) using a
194 Qiagen TissueLyser II for 30 seconds at 30 rps twice and centrifuged for 30 minutes at 2700 rpm.
195 Phenolic samples from the constitutive-defence experiment were analysed using HPLC Agilent 1200
196 series (Agilent Technologies Australia, Mulgrave, VIC, Australia) equipped with C18 reverse-phase
197 column (Waters, 5.0 μm , 250 mm x 4.6 mm; Alltech Australia, Baulkham Hills NSW, Australia). The
198 elution system consisting of solvents (A) 0.25% H_3PO_4 in water (pH 2.2) and (B) acetonitrile was: 0–
199 6 min, 0–12% of B; 6–10 min, 12–18% of B, and 10–30 min, 18–58% of B, with a flow rate of 1 mL/min
200 and injection volume of 15 μL (Keinänen *et al.*, 2001). Samples from the induction experiment were
201 analysed with Agilent Infinity 1260 equipped with C18 reverse-phase column (Poroshell 120 EC-C18,
202 2.7 μm , 150 mm x 3.0 mm; Agilent Technologies Australia, Mulgrave, VIC, Australia). The elution
203 method was modified from above and was: 0–2 min, 0–12% of B; 2–3.3 min, 12–18% of B, and 3.3–
204 10 min, 18–58% of B, with a flow rate of 0.5 mL/min and injection volume of 5 μL . In both
205 experiments, phenolic compound peaks were identified to their compound classes using UV spectra
206 and relative abundance was quantified at 320 nm. To estimate phenolic compound richness, we
207 counted the number of detectable peaks. The relative concentration of eight major phenolic peaks was
208 estimated as area under each peak divided by sample fresh weight. Results could not be directly
209 compared as the two experiments were performed in different greenhouses and samples from each
210 experiment were run using different HPLC machines.

211

212 *Statistical analyses*

213 To test if constitutive defence differed among ranges (the constitutive experiment), we examined
214 individual phenolic compound composition in a multivariate analysis of covariance (MANCOVA) and
215 the concentration of individual phenolic compounds, phenolic compound richness, total phenolic
216 concentration, and trichome density in univariate mixed models. To account for latitudinal variation
217 within and among ranges, each multi- and univariate model included range, latitude, their interaction
218 and a latitude² effect as fixed factors. To control for neutral population structure, possibly shaping trait
219 variation between populations, univariate models included q-values as a random effect, as obtained
220 from STRUCTURE analysis performed on genetic data. For the multi- and univariate analyses, we
221 improved normality of the data by square-root- or log-transforming traits where appropriate. For the
222 MANCOVA, we included the concentration of eight major phenolic compounds (Spearman's ρ among
223 peaks < 0.75) and calculated Wilks' λ (multivariate F-value) to measure the strength of the
224 associations. To measure the variance explained by the fixed effects or the full model within the
225 univariate models, we calculated the marginal and conditional coefficients of determination using the
226 MuMIn package (Bartón, 2018). We computed type III Wald F-values with Kenward-Roger degrees
227 of freedom and step-wise removed non-significant effects, starting with the highest order interaction.
228 For univariate models, we plotted the partial residuals of each response variable by ranges, thus
229 accounting for latitudinal clines and neutral population genetic structure and reported these adjusted
230 means and standard errors for each range, calculated using the *phia* package (De Rosario-Martinez,
231 2015).

232 To explore the variation in inducibility among ranges (the induction experiment), we repeated
233 the steps for the constitutive experiment, now including treatment and its interactions with range and
234 latitude as fixed effects. For the MANCOVA, we included five peaks (excluding three with
235 Spearman's $\rho > 0.75$) to increase power of this test (Scheiner, 2001). We retained treatment in these
236 models, as this was the variable of interest. Here, a significant treatment effect would signify an
237 inducible response, whereas a treatment x range interaction would imply this response differs between
238 ranges. A treatment x latitude interaction would indicate different inducibility at different latitudes. To
239 test if variation in induction differed between ranges (Eigenbrode *et al.*, 2008), we compared the
240 coefficient of variation (c_v) using the modified signed-likelihood ratio test for equality with 10^4
241 simulations in the *cvequality* package (Krishnamoorthy & Lee, 2014; Marwick & Krishnamoorth,
242 2018).

243 To examine associations between defence-related traits and plant growth and to assess if
244 divergence in individual resource budgets could have resulted in range differences in defence-related
245 trait investment, we tested responses of phenolic richness, phenolic concentrations or trichome density

246 to shoot biomass or SLA. Each model included a defence-related trait as response, with shoot biomass
247 or SLA, range and their interaction as predictors. We used individual trait values and included
248 individual STRUCTURE q-values and sampling location as random factors. We explored significant
249 range x defence interactions using a Holm p-value correction in the *phia* package (De Rosario-
250 Martinez, 2015). In these models, a negative association between defence-related traits and shoot
251 biomass would suggest a trade-off, while a positive one might indicate differences in resource
252 acquisition. Range differences at similar values of shoot biomass or SLA would indicate defence-
253 related trait divergence independent of genotypic differences in individual resource budgets.

254 To explore if constitutive and inducible defence trade off, we first calculated the induced level
255 of total phenolics for each maternal line as the difference between damage and control treatments of
256 the two half-sibs. This estimate of induction is thought to reduce correlations with control treatment
257 estimates and thus the collinear associations (e.g. due to genotypic biases) will not mask the trade-off
258 associations (Morris *et al.*, 2006). We included population of origin and individual q-values as random
259 factor in these models. A significant negative association between induced and constitutive levels of
260 phenolic concentration and richness would indicate the presence of a trade-off. All statistical analyses
261 were conducted in R v3.4.3 (R Core Team, 2018).

262

263 **Results**

264 *Constitutive defence trait divergence between ranges*

265 We found significant range divergence in constitutive phenolic composition (Table 1a), resulting from
266 differences between the introduced Europe and the native North America ($F_{8,66}=3.280$, $p=0.010$,
267 Wilks' $\lambda=0.716$) (Table 1b). Total phenolic concentration was similar between the native and
268 European populations, but 28% lower in Australia (Table 1b&c, Fig. 1). Phenolic peak richness
269 differed among ranges (Table 1): it was highest in the introduced European range (adjusted mean of
270 43 peaks) followed by the native North American (40 peaks) and introduced Australian ranges (33
271 peaks). Trichome density showed no differences between ranges (Table 1a, Fig. 1). The composition
272 of individual phenolic compounds and peak richness depended on latitude, though no such effect was
273 found for the total phenolic concentration or trichome density (Table 1a, Fig. 2). We did not observe
274 range x latitude interactions for any of the defence-related traits (Table 1a), suggesting latitudinal
275 clines, when present, did not differ between ranges.

276

277 *Inducible defence trait divergence between ranges*

278 We found a significant treatment effect on individual phenolic compound composition in the induction
279 experiment ($F_{5,59}=12.014$, $p<0.001$, Wilks' $\lambda=0.496$) (Table 2). The total phenolic concentration was

280 slightly suppressed in the herbivory-simulating treatment (Table 2, Fig. 3), but the phenolic peak
281 richness did not show a response to experimental treatment (Table 2, Fig. 3). We identified no
282 treatment x range x latitude interactions (Table 2, Fig. 3), suggesting there is no range difference in
283 inducibility clines. Also, the absence of treatment x latitude interactions (Table 2, Fig. 3), suggests an
284 overall lack of latitudinal clines in inducibility. Moreover, no treatment x range interactions (Table 2,
285 Fig. 3) suggests the inducible response did not differ between ranges. We did not find range differences
286 in the variation of inducible phenolic peak richness ($c_v=1.401$, $p=0.496$) or concentration ($c_v=2.297$,
287 $p=0.317$).

288 289 *Associations between defence, biomass and specific leaf area (SLA)*

290 Within each range, phenolic concentration and richness was positively correlated with shoot biomass,
291 whereas we found a negative association between trichome density and shoot biomass (Table 3, Fig.
292 4). We found high-SLA leaves had lower phenolic concentration and peak richness, yet higher
293 trichome density (Table 3, Fig. 4). No interactions were significant between range and predictor
294 variables (shoot biomass or SLA), suggesting these associations among traits were consistent between
295 ranges (Table 3, Fig. 4). These results emphasize the close relationship between plant growth,
296 physiology and defence.

297 When controlling for shoot biomass or SLA, total phenolic concentration in European plants
298 was higher compared to North American individuals of comparable weight (Table 3, Fig. 4), whereas
299 no difference existed in latitude models (Table 1, Fig. 1). Conversely, phenolic peak richness was no
300 longer significantly different between North America and Europe (Table 3, Fig. 4) compared to range
301 comparisons accounting for latitude (Table 1, Fig. 1). Australian plants exhibited lower phenolic
302 concentration and peak richness compared to native or European plants of comparable weight or SLA.
303 Yet, at the same plant weight, Australian plants had higher trichome densities than in the other ranges
304 (Table 3, Fig. 4). These patterns match previous analyses including latitude (Table 1, Fig. 1).

305 306 *Constitutive-inducible trade-offs*

307 Induced levels of phenolic concentration and richness, the response variables, were negatively
308 associated with the predictors, the constitutive levels (concentration: $F_{1,141.88}=76.286$, $p<0.001$;
309 richness: $F_{1,123.81}=78.126$, $p<0.001$; Fig. 5). We found no range differences in either induced response
310 trait (concentration: $F_{2,31.07}=0.265$, $p=0.769$; richness: $F_{2,31.518}=1.719$, $p=0.196$; Fig. 5), nor did we
311 identify interactions between range and the predictor constitutive phenolic concentration
312 ($F_{2,141.11}=0.866$, $p=0.423$). Range x constitutive phenolic peak richness ($F_{2,129.82}=3.045$, $p=0.051$) was

313 marginally significant. These results suggest that constitutive and inducible defence trade off, although
314 there is no difference between ranges.

315

316 **Discussion**

317 In this study, we found evidence for divergence in defence related traits within and between ranges.
318 Repeated latitudinal clines in phenolic richness and individual phenolic composition were identified,
319 suggesting rapid adaptation of phenolics to local environments following invasion. Though we
320 observed reduced phenolic concentration and richness in introduced Australia compared to the native
321 plants while controlling for genetic structure, levels were similar or slightly higher in the introduced
322 Europe compared to native populations at comparable latitudes and energy budgets. In addition,
323 trichome density did not differ among ranges. These patterns are inconsistent with the Evolution of
324 Increased Competitive Ability (EICA) hypothesis. In line with predictions, however, a trade-off
325 between the constitutive and inducible phenolics was observed together with similar phenolic
326 inducibility among ranges. To our knowledge, this is the first study testing the evolution of defence
327 related traits across multiple introductions while exploring the predicted confounding of latitudinal
328 clines, population substructure or genotypic differences in individual resource budgets. Therefore, the
329 apparent absence of the predicted repeated selection against high defence investment following
330 introduction is unlikely to be entirely masked by these factors. We examine these processes in detail
331 and suggest alternative mechanisms driving defence-trait divergence within and among native and
332 introduced ranges.

333

334 *Divergence in constitutive defence-related traits*

335 The rapid and repeated latitudinal divergence in phenolic compound composition and richness
336 populations suggests direct or indirect selection of latitude-associated factors. Corresponding to our
337 findings, typical reported patterns include high growth and low defence at more productive high-
338 resource (Coley *et al.*, 1985; Zandt, 2007; Endara & Coley, 2011), low-latitude environments (Woods
339 *et al.*, 2012; Moreira *et al.*, 2014; Hahn & Maron, 2016, Blumenthal, 2006). Native clines in herbivore
340 load could result in such observations, though the predicted herbivore reduction following introduction
341 should lead to non-parallel defence clines among native and introduced ranges (Cronin *et al.*, 2015;
342 Allen *et al.*, 2017). However, in our data, latitudinal clines in defence-related traits (phenolic
343 compound composition and peak richness) were parallel, which could reflect consistent patterns of
344 selection with latitude in all three ranges. The absence of the predicted patterns could result from
345 parallel clines in herbivore loads in each range or the presence of alternative evolutionary forces
346 driving latitudinal trait divergence in the multiple ranges. Indeed, clinal variation in herbivory is not

347 as common as previously thought (Moles *et al.*, 2011a)), although geographic information on *A.*
348 *artemisiifolia* herbivore pressure is needed.

349 Alternatively, latitudinal clines could arise through direct selection on the alternative functions
350 of phenolic compounds, or indirect selection through genetic covariance with traits under climate
351 mediated selection. Climate was previously shown to be a more important driver of trait divergence
352 compared to enemy release (Colautti *et al.*, 2009; Colautti & Barrett, 2013; Colomer-Ventura *et al.*,
353 2015). Along these lines, climatic differences between the ranges not captured by latitude could
354 contribute to patterns of divergence in Australian defence-related traits. For instance, trichomes protect
355 plants from UV (Bassman, 2004; Hauser, 2014) and selection for this alternate function in high-UV
356 Australia (WHO, 1998) could potentially explain the higher density of trichomes in this range when
357 controlling for plant size. Herbivore exclusion experiments at various latitudes and environments
358 would be important for to disentangling how resource availability, herbivory and other climatic factors
359 might interact during invasion and impact the evolution of growth and defence traits.

360 When correcting for these latitudinal clines, we found conflicting patterns of defence-related
361 trait divergence between the native and two introduced ranges. Genotypic differences in resource
362 acquisition (Van Noordwijk & de Jong, 1986; Agrawal, 2011; Züst & Agrawal, 2017) and historical
363 contingency (Lee, 2002; Facon *et al.*, 2006; Prentis *et al.*, 2008; Rius & Darling, 2014; Estoup *et al.*,
364 2016) can obscure trade-offs predicted under resource-allocation trade-off hypotheses. Accordingly,
365 we show trichome density, phenolic concentration and peak richness were strongly associated with
366 plant biomass and specific leaf area (SLA)(Fig. 4). Contrary to EICA predictions, phenolic peak
367 concentration was significantly higher in Europe compared to native North America at comparable
368 shoot biomass, although this difference disappeared when controlling for latitude or SLA. Similarly,
369 phenolic richness was significantly higher in Europe than North America at equivalent latitudes, but
370 this likely reflects the larger size and lower SLA of European plants at similar latitudes (van Boheemen
371 *et al.*, 2018). However, lower phenolic concentration and peak richness in Australia was still present
372 at similar latitude, biomass or SLA compared to North America. Invasion history is unlikely a major
373 factor in this observed defence-related trait divergence as we accounted for population genetic
374 structure in our analysis.

375 An adaptive reduction of constitutive defence traits following introduction to Europe and
376 Australia was predicted due to a general release from natural enemies. However, levels of chemical
377 defence-related traits (phenolic concentration and richness) were not consistently lower in introduced
378 ranges compared to native populations. Such unexpected findings could have resulted from variation
379 in contemporary herbivory among introduced ranges. Of particular relevance to the EICA hypothesis
380 are specialist herbivores, as herbivory by specialists, but not necessarily generalists, is hypothesized

381 to consistently decline during invasion (Müller-Schärer *et al.*, 2004; Joshi & Vrieling, 2005; Felker-
382 Quinn *et al.*, 2013). Indeed, introduced Japanese *A. artemisiifolia* populations re-exposed to specialist
383 leaf beetle *Ophraella communa* for >10 years were more resistant than herbivore-free populations
384 (Fukano & Yahara, 2012). However, rapid adaptation to *O. communa* is unlikely to have led to the
385 observed elevated European phenolic concentration and richness, as the seeds used in our experiment
386 were collected in 2014 and this beetle is constrained to southern Europe since introduction in 2013
387 (Sun *et al.*, 2017).

388 Alternatively, differences in generalist load between introduced ranges could have resulted in
389 variation in quantitative digestibility-reducing chemicals (e.g., phenolics), which defend against both
390 generalist and specialists (Müller-Schärer *et al.*, 2004). Surveys describe a high diversity of generalist
391 species in Europe (Gerber *et al.*, 2011; Essl *et al.*, 2015) but not in Australia (Palmer & McFadyen,
392 2012) suggesting herbivory in this species is higher in Europe than Australia. However, Genton *et al.*
393 (2005) previously found that compared to native Ontario, the most common forms of damage (chewing
394 and perforation) together with the generalist herbivore load was reduced in introduced France
395 populations consistent with enemy escape in Europe compared to native North America. Contradicting
396 EICA expectations, but consistent with our findings for Europe, the French plants showed no
397 evolutionary loss of defence (Genton *et al.*, 2005). Therefore, although reductions in both specialists
398 and generalist herbivores have been documented in both introduced ranges, we did not find parallel
399 changes in defence-related traits as predicted by EICA, suggesting such predictions are perhaps too
400 simplistic. Nevertheless, a more detailed survey of herbivory, resistance and the mechanisms of
401 resistance across all three ranges is warranted, particularly given the contrasting patterns of divergence
402 in phenolics identified among the two introduced ranges. Moreover, a more detailed analysis of the
403 alternative functions of these phenolics (e.g., allelopathic interactions and plant structure; Bhattacharya
404 *et al.*, 2010; Li *et al.*, 2010) is required.

405 A key assumption of EICA is a resource allocation trade-off between defence and growth.
406 However, even when these traits have evolved in the EICA predicted direction, negative genetic
407 correlations have yet to be detected (Franks *et al.*, 2008; Schrieber *et al.*, 2017; Hodgins *et al.*, 2018).
408 Furthermore, a direct trade-off might not be evident as resource reallocation from other traits, drawing
409 from the same resource pool, could allow for the elevated investment in defence related traits and
410 growth simultaneously (Züst & Agrawal, 2017; Hodgins *et al.*, 2018). For instance, an analysis of
411 climate niche shifts in *A. artemisiifolia* has revealed that Eurasian and Australasian ranges on average
412 experience warmer, wetter climates compared to the North American range (van Boheemen *et al.*,
413 2018). Therefore, reduced investment in abiotic stress tolerance could have allowed for resource

414 reallocation to defence and growth simultaneously. These recently acknowledged complex dynamics
415 underlying competitive ability call for more integrative tests of invasive spread.

416

417 *Constitutive versus induced range divergence*

418 We observed a negative association between constitutive and inducible defence-related traits
419 suggesting a trade-off (Koricheva *et al.*, 2004; Agrawal *et al.*, 2010). A decrease in the level and
420 predictability of attack in the introduced range is expected to cause a reduction in constitutive defence
421 and the maintenance or increase in inducible defence (Cipollini *et al.*, 2005; Orians & Ward, 2010;
422 Lande, 2015). In agreement with this prediction constitutive phenolic levels were reduced in Australia,
423 while inducible response did not differ among ranges. Such maintenance of mean inducibility could
424 result from insufficient herbivore pressure, where a selection-drift imbalance could increase inducible
425 variability (Eigenbrode *et al.*, 2008). Although analysis of neutral markers suggests genetic drift has
426 been particularly strong in Australia (van Boheemen *et al.*, 2017), we did not reveal any increase in
427 inducible variation. The growing body of literature testing constitutive versus inducible defence in
428 native and introduced ranges frequently report inconsistent results varying from reductions, to
429 maintenance, to increases in either defence (Cipollini *et al.*, 2005; Eigenbrode *et al.*, 2008; Beaton *et al.*,
430 2011; Carrillo *et al.*, 2012; Cipollini & Lieurance, 2012; Wang *et al.*, 2012; Wang *et al.*, 2013;
431 Fortuna *et al.*, 2014; Gu *et al.*, 2014; Agrawal *et al.*, 2015; Macel *et al.*, 2017) and calls for more
432 detailed research on the costs-benefit trade-offs of the various responses.

433 Remarkably, we found evidence of a suppression of phenolics in response to herbivore
434 simulation for some populations, especially those with high constitutive levels, in contrast to some
435 previous studies (Lee *et al.*, 1997; Constabel & Ryan, 1998; Keinänen *et al.*, 2001; Heredia &
436 Cisneros-Zevallos, 2009). Conversely, cardenolide suppression was found in various *Asclepias* species
437 at high constitutive levels (Rasmann *et al.*, 2009), though the mechanistic cause was not discussed
438 (Agrawal *et al.*, 2010). We propose that the retraction of phenolics from damaged leaves could indicate
439 a cost-reducing response when the inducible phenolic compounds have alternative functions
440 (Bhattacharya *et al.*, 2010; Li *et al.*, 2010), or function only in particular aspects of defence response,
441 not induced by the treatment. Similarly, perhaps for those individuals already heavily defended with
442 phenolic compounds increased investment in this chemical defence, which failed to deter an attacking
443 herbivore would have diminishing returns, leading to the potential activation of other defence
444 strategies by the plant. Nevertheless, gaining insight into such cost-benefit associations might prove
445 difficult due to, for instance, issues identifying and addressing all factors influencing the investment
446 of defence-related traits (Neilson *et al.*, 2013).

447

448 *Conclusion*

449 We demonstrate divergence of growth and defence traits within multiple introduced ranges that is
450 consistent with rapid adaptation during introduction. Furthermore, we do not find evidence to support
451 the hypothesis that escape from specialist enemies drives the evolution of increased competitive ability
452 in this invasive, as enhanced growth in European populations was not in lieu of defence-related trait
453 reduction. The evolution of growth and defense traits in Australian populations, derived from
454 European founders, occurred rapidly (~80 generations), seemingly unconstrained by strong genetic
455 bottleneck identified in this range (van Boheemen *et al.*, 2017), as measured traits in these two invaded
456 ranges are primarily on opposing ends of the phenotypic spectrum of values. Evidence is growing that
457 adaptation to climate might explain the alarming spread and success of non-natives to a greater extent
458 than release from natural enemies (Colautti *et al.*, 2009; Colautti & Barrett, 2013; Colomer-Ventura *et al.*,
459 *et al.*, 2015). Indeed, we identified repeated latitudinal patterns in phenolics in all three ranges consistent
460 with climate mediated selection, perhaps through corresponding shifts in the biotic community or
461 through direct or indirect selection on phenolics by climate variables. This study emphasizes that
462 intraspecific multi-introduction tests of trait divergence of invasive species provide important insight
463 into contemporary evolutionary process during range expansion.

464

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470

471 **Author contributions**

472 All authors developed the project, with data collection and analyses carried out by LAB and SB,
473 refined by AU and KH. All authors discussed the results, contributed to the MS writing and gave final
474 approval for publication.

475

476 **Data accessibility**

477 Sequence data are available at the National Center for Biotechnology Information (NCBI) Sequence
478 Read Archive under Bioproject PRJNA449949.

479 Scripts are available on https://github.com/lotteanna/defence_adaptation.

480 Data is available on <https://doi.org/10.6084/m9.figshare.8028875.v1>

481

482

483 **Fig. 1.** Partial residual defence trait responses (phenolic concentration, peak richness and trichome density) of *A.*
484 *artemisiifolia* populations to range, accounting for latitudinal clines and neutral population structure. Different letters
485 indicate significance for pairwise range comparisons (Table 1).

486
487 **Fig. 2.** Population mean response of phenolic peak richness to range (native North America, blue triangles; introduced
488 Europe, green squares; introduced Australia, red circles) and latitude in *Ambrosia artemisiifolia*, with predicted latitudinal
489 clines (\pm 95% confidence interval) corrected for neutral population structure.

490
491 **Fig. 3.** Partial residual defence trait responses (phenolic concentration and peak richness) of *A. artemisiifolia* populations
492 to control (solid symbols) and herbivore simulating treatment (wounding + MeJA, dashed transparent symbols), with
493 covariates of range, accounting for latitudinal clines and neutral population structure. Letters indicate significance of effect
494 (Table 2).

495
496 **Fig 4.** Defence trait responses (phenolic concentration, peak richness and trichome density) of *A. artemisiifolia* individuals
497 to range (native North America (blue triangles); Europe (green squares); Australia (red circles)), shoot biomass (left panels)
498 or specific leaf area (right panels) with model predictions (\pm 95% confidence interval, Table 3).

499
500 **Fig. 5.** Inducible (D: wounding + MeJA; C: control) versus constitutive (control) defence trait responses (phenolic
501 concentration and peak richness) of *A. artemisiifolia* populations among ranges (native North America: blue triangles;
502 Europe: green squares; Australia: red circles) with model predictions (\pm 95% confidence interval).

503
504

505 **Table 1.** *Ambrosia artemisiifolia* defence-related trait responses (population means) to range, latitude, their interaction and
 506 latitude² (to account for non-linear relationship) in the constitutive experiment in multivariate (individual phenolic
 507 compounds) and univariate analyses (a), with dissection of significant range effects (p<0.05) in post-hoc tests (b). We
 508 reported Wald type III F (a) or χ^2 test values (b), Kenward-Roger degrees of freedom (subscript), significance (symbols).
 509 In the multivariate analysis, Wilk's λ measure the strength of the association, in univariate analyses, marginal (R²m) and
 510 conditional (R²c) coefficients measure the variance explained by fixed effects or full models. Models were step-wise
 511 reduced starting with the highest order non-significant interaction and univariate analyses included neutral population
 512 genetic structure as a random effect.

513 ns: p>0.1; #: p<0.1, *: p<0.05; **: p<0.01; ***: p<0.001

514

a.	Range	Latitude	Latitude ²	Range: Latitude	R ² m	R ² c
Individual phenolic compounds composition	4.520 _{16,132} ***, $\lambda=0.417$	6.928 _{8,66} ***, $\lambda=0.544$	2.814 _{8,66} *, $\lambda=0.746$	0.849 _{16,128} (ns), $\lambda=0.817$		
Phenolic concentration	8.601 _{1,71.918} ***	0.934 _{1,73.244} (ns)	0.036 _{1,72.973} (ns)	0.127 _{1,70.054} (ns)	0.189	0.290
Phenolic richness	7.615 _{2,58.48} **	7.79 _{1,71.66} **	0.046 _{1,53.51} (ns)	2.027 _{2,69.64} (ns)	0.177	0.688
Trichome density	0.663 _{2,71.183} (ns)	1.825 _{1,66.941} (ns)	3.148 _{1,74.991} #	0.121 _{2,69.141} (ns)	0.055	0.055

515

b.	North America - Europe	North America - Australia	Europe - Australia
Individual phenolic compounds composition	3.280 _{8,66} **, $\lambda=0.716$	1.580 _{8,66} (ns), $\lambda=0.840$	1.994 _{8,66} (ns), $\lambda=0.805$
Phenolic concentration	1.397 ₁ (ns)	9.311 ₁ **	17.321 ₁ ***
Phenolic richness	4.783 ₁ *	12.725 ₁ ***	15.843 ₁ ***

516

517 **Table 2.** *Ambrosia artemisiifolia* defence-related trait responses (population means) to range, latitude, treatment, their interactions and latitude² in the inducible experiment in multivariate
518 (individual phenolic compounds) and univariate analyses. Range, latitude, their interaction or latitude² were included as covariates and significant results were not explored further. We
519 reported Wald type III F, Kenward-Roger degrees of freedom (subscript), significance (symbols) (a). In the multivariate analysis, Wilk's λ measure the strength of the association, in
520 univariate analyses, marginal (R^2_m) and conditional (R^2_c) coefficients measure the variance explained by fixed effects or full models (a). Models were step-wise reduced starting with the
521 highest order non-significant interaction and univariate analyses included neutral population genetic structure as a random effect. *ns*: $p > 0.1$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

	Range	Latitude	Latitude ²	Range:Latitude	Treatment	Treatment:Range	Treatment:Latitude	Treatment: Range: Latitude	R ² _m	R ² _c
Individual phenolic compounds concentration	7.591 _{10,118} ***, $\lambda=0.370$	10.637 _{5,59} ***, $\lambda=0.526$	4.818 _{5,59} **, $\lambda=0.710$	2.311 _{10,118} *, $\lambda=0.699$	12.014 _{5,59} ***, $\lambda=0.496$	0.326 _{10,112} (ns), $\lambda=0.944$	0.977 _{5,58} (ns), $\lambda=0.922$	1.357 _{10,108} (ns), $\lambda=0.789$		
Phenolic concentration	4.970 _{2,30.905} *	5.932 _{1,31.505} *	1.577 _{2,28.556} (ns)	1.745 _{1,31.505} (ns)	4.241 _{1,35.628} *	0.005 _{2,32.285} (ns)	1.077 _{1,35.428} (ns)	1.417 _{2,31.192} (ns)	0.201	0.457
Phenolic richness	3.764 _{2,29.93} *	4.700 _{1,31.08} *	1.340 _{2,28.24} (ns)	6.030 _{1,30.95} *	0.850 _{1,35.33} (ns)	0.091 _{2,32.1} (ns)	0.825 _{1,34.89} (ns)	1.923 _{2,30.78} (ns)	0.323	0.723

522

523 **Table 3.** Constitutive defence trait response of *Ambrosia artemisiifolia* individuals to shoot biomass, specific leaf area and
 524 their interaction with range (a), with dissection of significant range effects ($p < 0.05$) in post-hoc tests (b). We reported
 525 corresponding figure, Wald type III F (a) or χ^2 test values (b), Kenward-Roger degrees of freedom (subscript) and
 526 significance (symbols). Marginal (R^2_m) and conditional (R^2_c) coefficients measure the variance explained by fixed effects
 527 or full models (a). Models were step-wise reduced starting with the highest order non-significant interaction and included
 528 population origin and neutral population genetic structure as random effects.

529 ns: $p > 0.1$; #: $p < 0.1$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

a.

Predictor	Response	Figure 4	Range	Predictor	Range:Predictor	R^2_m	R^2_c
Shoot biomass	Phenolic concentration	A	19.321 _{2,79.435} ***	31.098 _{1,181.299} ***	1.441 _{2,184.26} (ns)	0.160	0.189
	Phenolic richness	B	18.96 _{2,79.29} ***	53.389 _{1,180.51} ***	1.565 _{2,187.82} (ns)	0.199	0.224
	Trichome density	C	10.242 _{2,79.4} ***	18.49 _{1,174.06} ***	0.525 _{2,180.84} (ns)	0.093	0.103
Specific leaf area	Phenolic concentration	D	6.162 _{2,71.167} **	38.464 _{1,208.912} ***	0.98 _{2,202.53} (ns)	0.202	0.269
	Phenolic richness	E	5.349 _{2,69.16} **	42.692 _{1,217.97} ***	0.32 _{2,202.6} (ns)	0.215	0.331
	Trichome density	F	1.828 _{2,71.7} (ns)	10.994 _{1,204.66} **	1.196 _{2,206.12} (ns)	0.049	0.121

530

b.

Predictor	Response	Figure 4	North America - Europe	North America - Australia	Europe - Australia
Shoot biomass	Phenolic concentration	A	5.846 ₁ *	22.155 ₁ ***	40.087 ₁ ***
	Phenolic richness	B	2.546 ₁ (ns)	26.667 ₁ ***	37.964 ₁ ***
	Trichome density	C	2.255 ₁ (ns)	13.049 ₁ ***	21.047 ₁ ***
Specific leaf area	Phenolic concentration	D	2.152 ₁ (ns)	5.032 ₁ *	12.485 ₁ **
	Phenolic richness	E	0.459 ₁ (ns)	6.655 ₁ *	10.643 ₁ **
	Trichome density	F	-	-	-

531

532

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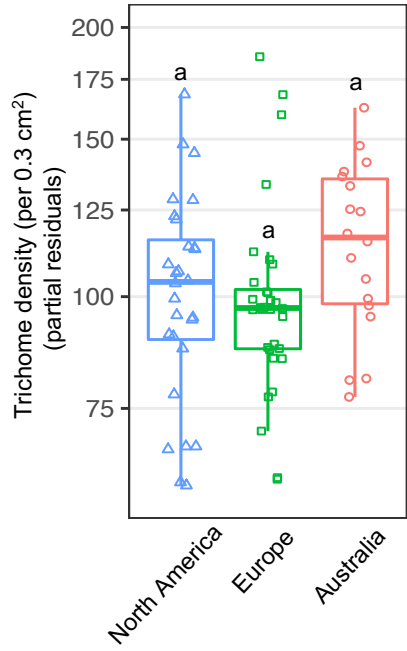
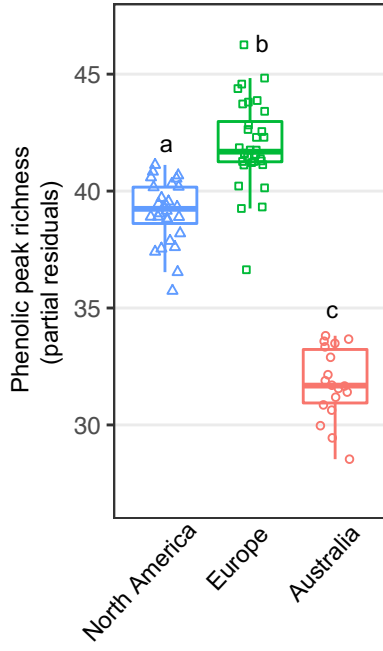
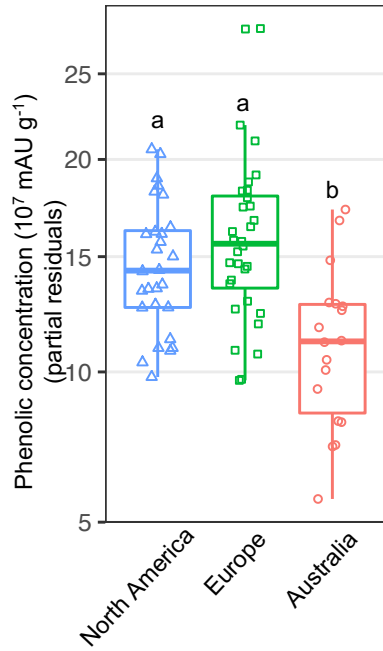
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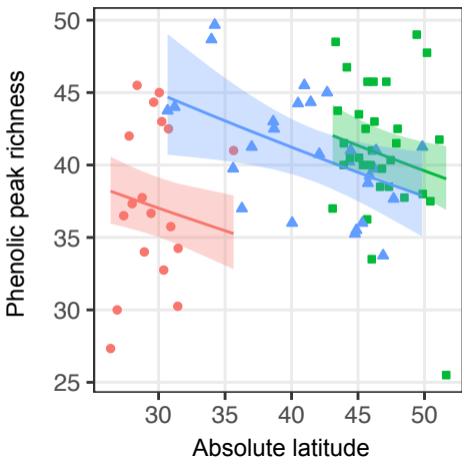
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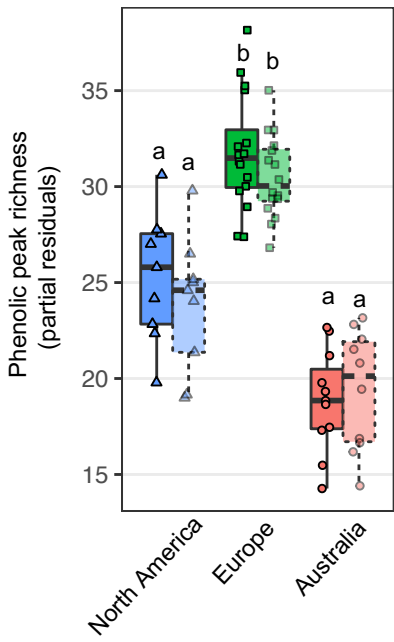
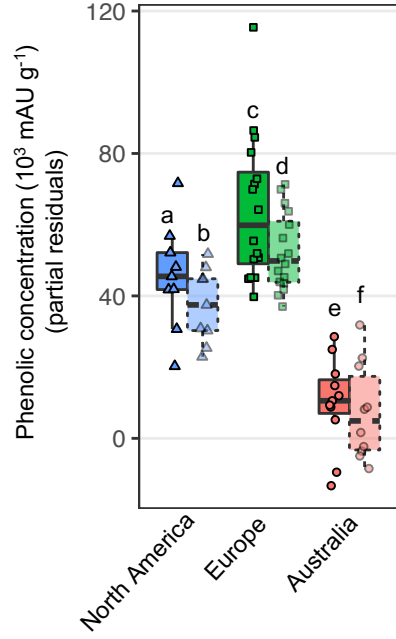
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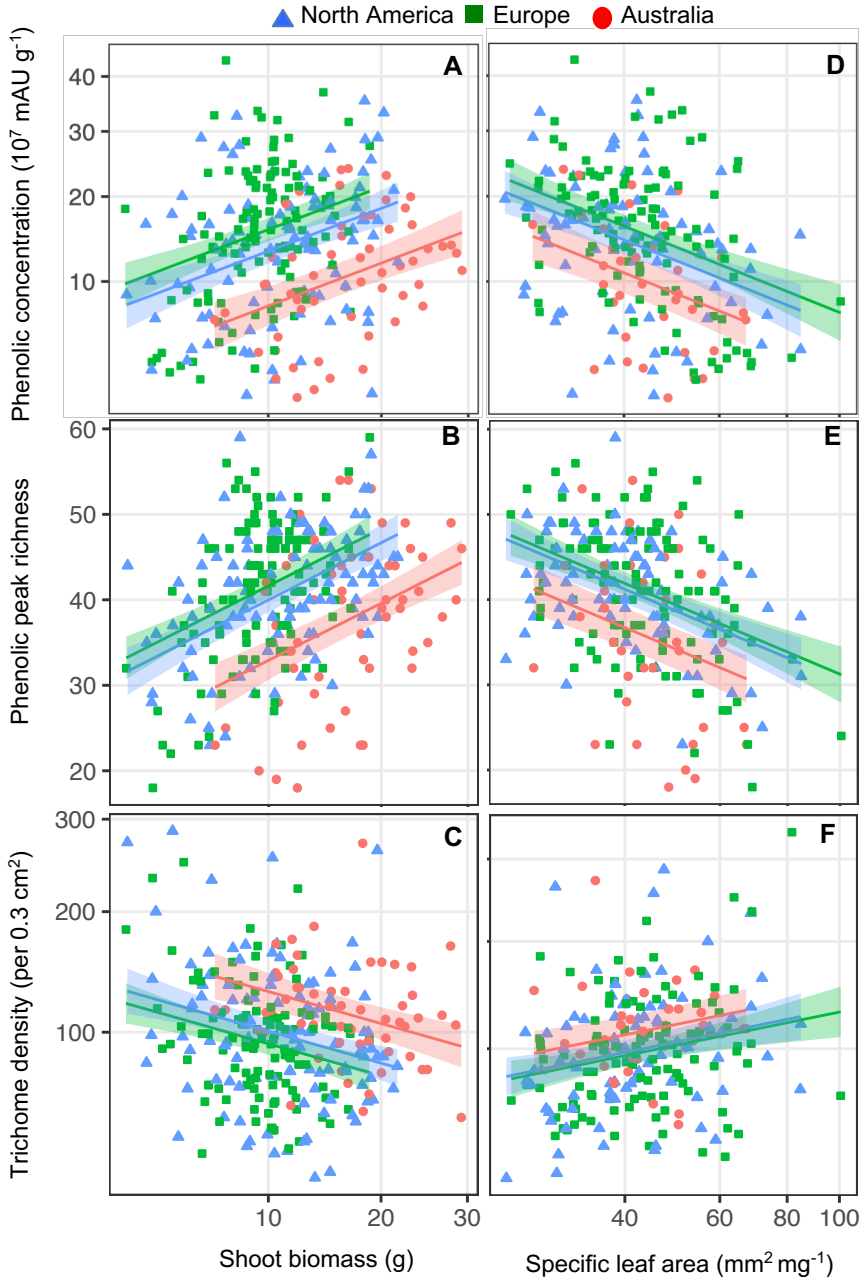
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