1    **Relative roles of genetic variation and phenotypic plasticity in the invasion of**

2    **monkeyflower *Erythranthre gutatta* in New Zealand**

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19    **Abstract**

20    Evolutionary processes which increase the probability of an introduced plant species

21    becoming invasive include high levels of genetic diversity and phenotypic plasticity.

22    Naturalised in New Zealand, monkeyflower, (*Erythranthre gutatta)*, a clonally spreading

23    herb of waterways and seepage areas native to the Western USA, shows marked variation in a

24    range of vegetative, reproductive and inflorescence traits. We used two common gardens

25    differing in elevation to explore the relative contribution of genetic versus plastic variation

26    within nine traits among 34 monkeyflower clones from across the New Zealand South Island.

27    We looked for evidence of clinal variation across elevation gradients and for home site

28    advantage. We found both high genetic diversity and trait plasticity explain the observed

29    variation, although less evidence for adaptive plasticity.  Most genetic variation was observed

30    in the lowland garden (9m a.s.l.), where the overall trend was for above ground dry weight to

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31    be lower, and horizontal shoot length greater, than at the montane garden (560m a.s.l). We

32    found no evidence of local adaptation to any of the measured environmental variables.

33    However, we observed a pattern of higher biomass and higher plasticity at lower versus

34    higher elevations and in clones originating from lower elevation sites.

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37    **Key Words** Phenotypic plasticity, common garden, elevational gradient, *Mimulus gutattus*,

38    rapid evolution

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40    **Acknowledgments**

45    INTRODUCTION

46    Invasive alien plants often show considerable phenotypic variation in their introduced range,

47    explained by local adaptation, phenotypic plasticity (whereby plants are able to adjust their

48    phenotype according to the local environment (Pigliucci et al. 1995; Geng et al. 2007;

49    Pitchancourt and Van Klinken 2012) or a combination of both (Moroney et al. 2013; Si et al.

50    2014).  However, despite a plethora of studies ( Geng et al. 2016; Hiatt and Flory, 2020;

51    Fakhr et al. 2022;), the relative contribution of genes and the environment to such variation

52    remains poorly understood (Vanwallendael et al., 2018; Villellas et al. 2021; Yuan et al.

53    2022). While the success of clonally reproducing invasive species is often attributed to

54    plasticity (Loomis and Fishman 2009; Riis et al. 2010; Keser et al. 2014), quantitative links

55    between plasticity and fitness are rare (Liu et al. 2016; Bufford and Hulme 2021a).  Plastic

56    traits can be neutral or even mal-adaptive, a consequence of genetic correlation or trade-offs

57    (van Kleunen and Fischer 2004) and so evidence of plasticity does not necessarily equate to

58    increased fitness.  Of course, adaptation can play an important role in invasion success, even

59    in clonal plants (Geng et al. 2016).

60    Given that understanding why some species become invasive but others don't is one of the

61    main focal areas of invasion biology (Moloney et al. 2009) this facet of invasion success

62    warrants further investigation (Ghalambor et al. 2007; Geng et al. 2016; Lee-Yaw et al. 2019;

63    Enders et al. 2020). It is especially relevant for clonal ornamental plants given their under-

64    representation in the literature and the predicted global increase in garden escapes with

65    climate change (van Kleunen et al. 2018; Hulme 2020). Many ornamentals reproduce easily,

66    often with a strong clonal component to reproduction and are predicted to be the major pool

67    of future invasive species worldwide (van Kleunen et al. 2018).

68    Local  adaptation allows for invasive success (Lee et al. 2002; Leimu and  Fischer 2008;

69    Colautti and Lau 2015 ; Molina-Montenegro et al. 2018; Lee-Yaw et al. 2019)  by conferring

70    genotypes with a 'home site advantage' (Kawecki and Ebert 2004; Maron et al. 2004; Allan

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71   and Pannell 2011; Bennington et al. 2012), whereby plants grown in their home environment

72   are more fit than plants from elsewhere (but see Lee-Yaw et al. 2019 ).  In contrast

73   phenotypic plasticity allows the same genotype to thrive in a range of environments

74   (Bossdorf et al. 2005; Richards et al. 2006; Hulme 2007; Moloney et al. 2009, ; Bufford and

75   Hulme 2021a; but see Palacio-Lopez and  Gianoli 2011). As with local adaptation, plasticity

76   may evolve post introduction (Lande 2015).  Demonstrating the relative contribution of each

77   evolutionary strategy is difficult for a number of reasons (Noble et al. 2019; Villellas et al.

78   2021) and findings have to date been equivocal (Bossdorf et al. 2005; Richards 2006; Hulme

79   2007; Bock et al. 2015).

80   One approach to untangle the different components (genetic versus plastic) of intra- specific

81   phenotypic variation is to use common garden experiments, where clones from a number of

82   environmentally different populations are grown together under as near -identical conditions

83   as possible (Allan and  Pennell 2009;  Cheplick 2015; Villellas et al. 2021).  If, under the

84   same environmental conditions clones maintain their home site phenotypes, this variation is

85   deemed genetic (Turesson 1922; Nunez-Farfan and Schlichting 2001). In contrast, if under

86   the same conditions the clones from different locations exhibit similar phenotypes the

87   variation is considered plastic. Comparing trait values within and among clones, analysis of

88   variance allocates the proportion of variance within clones into genetic and plastic

89   components. In invasion ecology common garden experiments have been used to compare

90   provenances from native and introduced ranges in the introduced range (Bufford and Hulme

91   2021a; b; Colautti and Barrett 2009 and references within ), alien provenances from just the

92   introduced range (Kollmann and Baneulos 2004; Rapson and Willson 1992; Colautti and

93   Barrett 2013; Monty and Mahy 2009) and provenances in both the native and introduced

94   range (Maron et al. 2004; Flory et al. 2011; Shelby et al. 2016; Berend et al. 2019; Oduor et

95   al. 2016 and references therein). However, often such experiments have been compromised

96   by their design. For example, too few gardens or gardens with very similar environments

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97    (Moloney et al. 2009; Villelas et al. 2021).  Moreover, well designed experiments have

98    shown that contradictory results in different gardens are to be expected and help to untangle

99    genetic versus environmental influences (Maron et al. 2004; Williams et al. 2008; Moloney et

100   al. 2009; Florey 2011; Villelas et al. 2021).

101   We investigate the relative contribution of genotype versus plasticity to the widespread

102   success in New Zealand of the introduced *Erythranre gutatta* (D.C.) G. L. Nelson,

103   (section *Simiolus,* Phrymaceae),  previously known as  *Mimulus gutattus* D.C. Lowry et al.

104   (2019), and commonly referred to as monkeyflower.  Due to its wide range of life histories

105   and environmental tolerance, and its propensity for whole genome duplication, *E. gutatta* has

106   become a model species in evolutionary ecology and invasion biology (Wu et al. 2008;

107   Friedman et al. 2015; Da Re et al. 2020). *E. gutatta* is a widespread, common and rapidly

108   spreading clonally reproducing weed in New Zealand and is of considerable interest because

109   it shows a marked niche-shift, occupying habitats in New Zealand which lie outside of the

110   environmental conditions found in its native range (Da Re et al. 2020).  One explanation for

111   this lack of niche conservatism is that different genotypes (different source populations)

112   respond differently to different environments. Alternatively, the niche-shift may reflect post-

113   introduction evolution, either of plasticity or by local adaptation (Da Re et al. 2020).  While

114   New Zealand *E. gutatta* populations undoubtedly represent bottlenecked populations and,

115   according to (Vallejo-Marin et al. (2021) historical, rather than recent introductions, they do

116   include both native US and bridgehead UK populations, which suggests the potential for

117   novel genetic combinations in New Zealand. How likely this is remains speculative given the

118   primarily clonal nature of *E. gutatta* spread.

119   We undertook a set of common garden experiments to distinguish the extent to which the

120   considerably phenotypic variation observed in *E. gutatta* in New Zealand reflects plasticity

121   versus contemporary evolution leading to local adaptation.  The selection pressure we

122   considered most likely to impact plants from across our sampled sites was elevation,

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123 incorporating a steep cline in temperature and rainfall. We thus chose our two common

124 gardens based on elevation; Ilam (hereafter referred to as the lowland site) and Cass

125 (hereafter referred to as the montane site), at 9 m and 580 m respectively, to expose any GxE

126 effect (different genotypes responding differently to the two environments). Given that our

127 sites spanned the entire length of the South Island, we also looked for evidence of a

128 latitudinal cline in biomass. Our specific hypotheses were that 1) we would detect clinal

129 variation associated with elevation, so that clones from montane populations would be fittest

130 in the montane garden and vice versa. 2) We would detect home site advantage, such that the

131 Cass clone grown in the Cass garden would be the fittest clone in the montane garden and

132 similarly, clones from close to the lowland Ilam garden would be the fittest clones in the

133 lowland garden.

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136 **Methods**

137 **Study species**

138 *Erythranthre gutatta* (D.C.) G. L. Nelson, is the most common species in a large *Mimulus*

139 species complex (Ritland and Ritland 1989). Widespread across the Western US (Friedman et

140 al. 2015; Demarche et al. 2016), *E. gutatta* has become naturalised across Europe and in New

141 Zealand. First recorded in New Zealand in 1878 (Webb et al. 1988), Vallejo-Marin et al.

142 (2021) found that New Zealand populations have been introduced multiple times both

143 directly from native Alaska and by way of a bridgehead from the UK.

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145 **Experimental design**
146 We sampled a single clone from each of 34 distinct locations across the South Island of New

147 Zealand. Locations were never less than 10 km apart and were chosen to be representative of

148  environmental and altitudinal variation across the South Island and included seven

149  geographically isolated regions (Fig 1).

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151  **Fig 1** Sample locations of *E. gutatta* across the New Zealand South Island

152  (https://www.stats.govt.nz). The sites are clustered according to geographical region.

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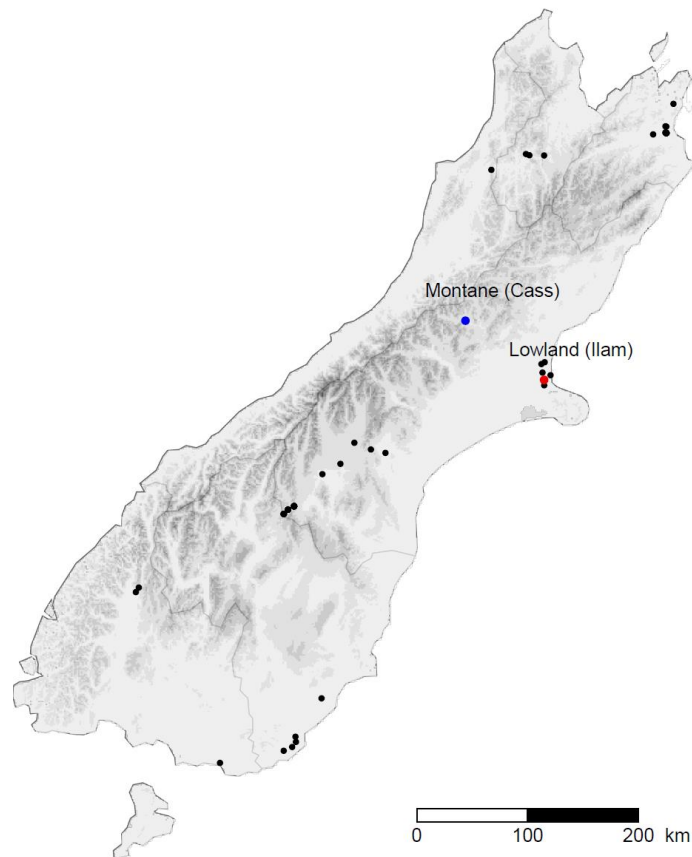


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162  At each sampling site we recorded 16 environmental variables and calculated the annual

163  average temperature, growing season average temperature, average minimum and maximum

164  temperature, extreme minimum and maximum temperature, annual average rainfall, humidity

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165    and precipitation from data collected from local climate stations between 1971 and 2000 (Table

166    S 1). Populations were mostly small patches along stream sides or drainage ditches and we

167    collected stems of *E. gutatta* with basal runners from a single clone from each location. From

168    each clone we propagated twelve replicates from small internode cuttings. To reduce clonal

169    environmental effects as much as possible, cuttings were <2cm long and were in similar

170    developmental and physiological condition (Libby 1962; Weiner et al. 1997). Cuttings were

171    planted in separate 10 X 10 X 10 cm$^3$ pots filled with potting mix. Pots were placed on tables

172    in a glasshouse, with their distribution on the tables randomized weekly. Early in the 2018

173    growing season cuttings were translocated into individual pots (7.5L, 20.5 cm wide x 25.5 cm

174    diameter), lined with plastic bags and filled with a slow release fertiliser potting mix. The pots

175    were moved into the two common gardens.  Half (six replicates per clone) went into the

176    lowland garden on the University of Canterbury Ilam campus (43°31'S 172°35'E and the

177    remainder were set up at a montane garden located at the University of Canterbury Cass field

178    station (43°02'S, 171°45'E).  The montane garden was significantly cooler and wetter than the

179    lowland garden (Table 1).

180    **Table 1** Environmental measures of Ilam, Christchurch and the Cass Field Station. Averages 1971-
181    2000

| Location | Elevation (m) | Annual Average Temperature (°C) | Average Temperature (°C) | Average Min Temperature(°C) | Extreme Min Temperature(°C) | Average Max Temperature(°C) | Extreme Max Temperature(°C) | Annual Average Rainfall (mm) | Humidity (%) | Precipitation (mm) | Max Sunlight Hours | Min Sunlight Hours |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ilam, Christchurch | 9.69 | 12.29 | 14.7 | 9.63 | 0.62 | 19.76 | 32.5 | 131.3 | 75.3 | 10.10 | 15.25 | 8.27 |
| Cass Field Station | 578.81 | 8.22 | 10.72 | 4.17 | -5.3 | 17.27 | 30.06 | 2289.6 | 84 | 192.6 | 15.22 | 9 |

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183  Plants were randomly assigned positions in each common garden and their distributions

184  randomized weekly.  E. *gutatta* occurs primarily in wetlands and riparian areas and thus plants

185  were kept moist with daily automatic watering to limit any effect of drought or precipitation

186  on performance.

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188  **Performance traits**

189  We chose nine quantitative traits which have previously been shown to exhibit marked inter-

190  population variation in *E. gutatta* (eg Hall 2006; van Kleunen and  Fischer 2008). We counted

191  the maximum number of buds on each plant. In mid-April, towards the end of growing season,

192  we measured the vegetative, reproductive and flower traits in both gardens: mean length and

193  width of the largest two leaves, length of the longest horizontal shoot and length between the

194  second and third internodes, the largest flower length, depth and width. All plants were then

195  harvested towards the very end of the growing season in mid-April and dry weight of above

196  ground tissue was measured after drying at 80°C for 72 h. We chose above ground dry weight

197  as our proxy for fitness.

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199  **Statistical analysis**

200  To estimate the total genetic and environmental components of the variation in vegetative,

201  reproductive and flower traits among clones, and their genotype x environment (GxE)

202  interactions, we used  linear mixed-effects models. In the models, each of the quantitative traits

203  were analysed separately, using a logarithmic transformation on each observation after visually

204  inspecting model diagnostics. For the GxE investigation for each response, the expected

205  population effect of the two common garden locations was estimated together with two

206  variance components, quantifying the site-specific variability in the montane garden and the

207  site-specific variability of the garden location effect (ie lowland – montane). This last term in

208  the model allows us to predict the relative garden performance for each clone compared to the

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209   population average. Posterior variance estimates were used to construct 95% confidence

210   intervals for individual random effect predictions. We plotted reaction norms (Schlichting and

211   Pigliucci 1998) of each clone for each of the nine traits to illustrate how the phenotypes of the

212   different genotypes expressed in each of the two gardens.

213   To visualise the trait differences among the 34 clones and to observe how the same clonal

214   replicates responded in each of the lowland and montane common gardens, we ran a principal

215   component analysis (PCA). Based on the covariance between traits, the scaled and centred

216   clone predictions were summarised in a biplot of the first two principal components. We treated

217   all predictions as new observations, ignoring any further estimation uncertainty. To test for

218   association between all measured traits and elevation we plotted principal component scores

219   vs elevation.  We plotted principal component scores vs all environmental variables to test for

220   association between all measured traits and all environmental site environmental variables

221   (Table S1). All statistical analyses were performed using the open-source program R, version

222   4.0.5 (R Core Team 2018) and package lme4 (Bates et al. 2015).

223

224   **RESULTS**

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226       *Phenotypic variation*

227   All plants survived in both common gardens and we found considerable variation in all

228   measured traits across the two gardens. In the lowland garden the mean dry weight of the largest

229   clone was almost 20 times that of the smallest, with measures of leaf size varying by more than

230   a twofold difference. As result, there were clear morphotypes; while the majority of plants were

231   somewhat intermediate, individual clones ranged from short, horizontally spreading plants to

232   tall, multi-stemmed and multi flowered individuals. In contrast in the montane garden,

233   vegetative traits among clones were markedly less variable and it was more difficult to

234   recognise morphotypes among the clones. However, in the montane garden flower size varied

235   among clones more than in the lowland garden (Fig. 2).  The reaction norms of all clones,

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236    except from Park Terrace, Christchurch, responded in a similar way to the environments in the

237    lowland and montane common gardens (Fig. 2).

238    The first two axes of the PCA together explained 66% of the total variation (Fig 3). Axis 1

239    (38%) correlated most strongly with the following vegetative traits: above ground dry weight,

240    leaf size (length and width), internode length and stolon length. The second axis (28%)

241    correlated most strongly with florescence traits such as flower width and depth. Most variation

242    among clones in the lowland garden was along axis 1, and in the montane garden along axis 2.

243    **Fig 2** Reaction norms of single genotypes - predictions of expected trait variables by clone.

244    Lines connect the predictions for the same genotype at the two different gardens. All

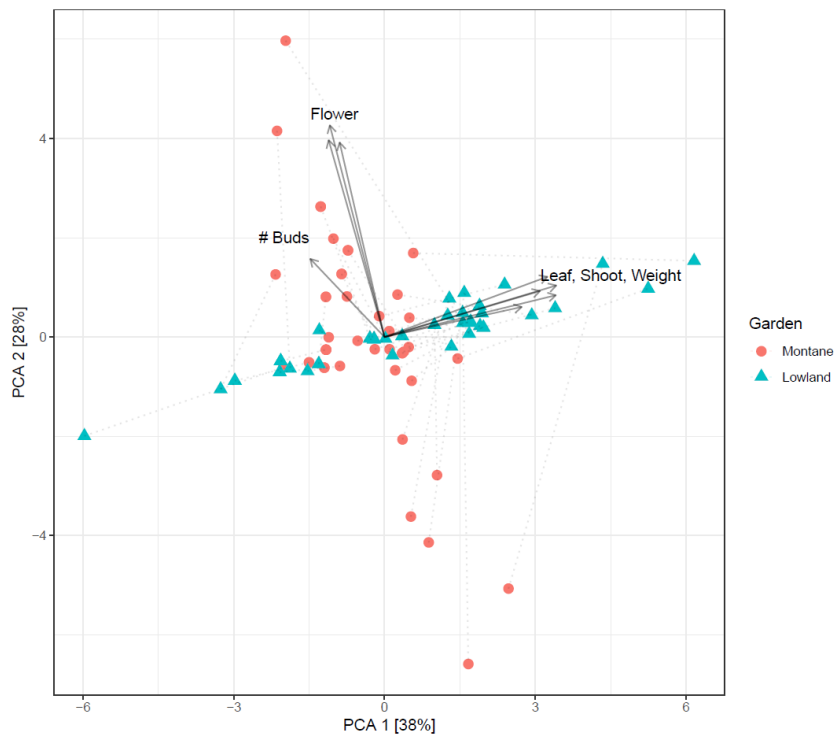245    predictions are presented on the original scale of each measurement.



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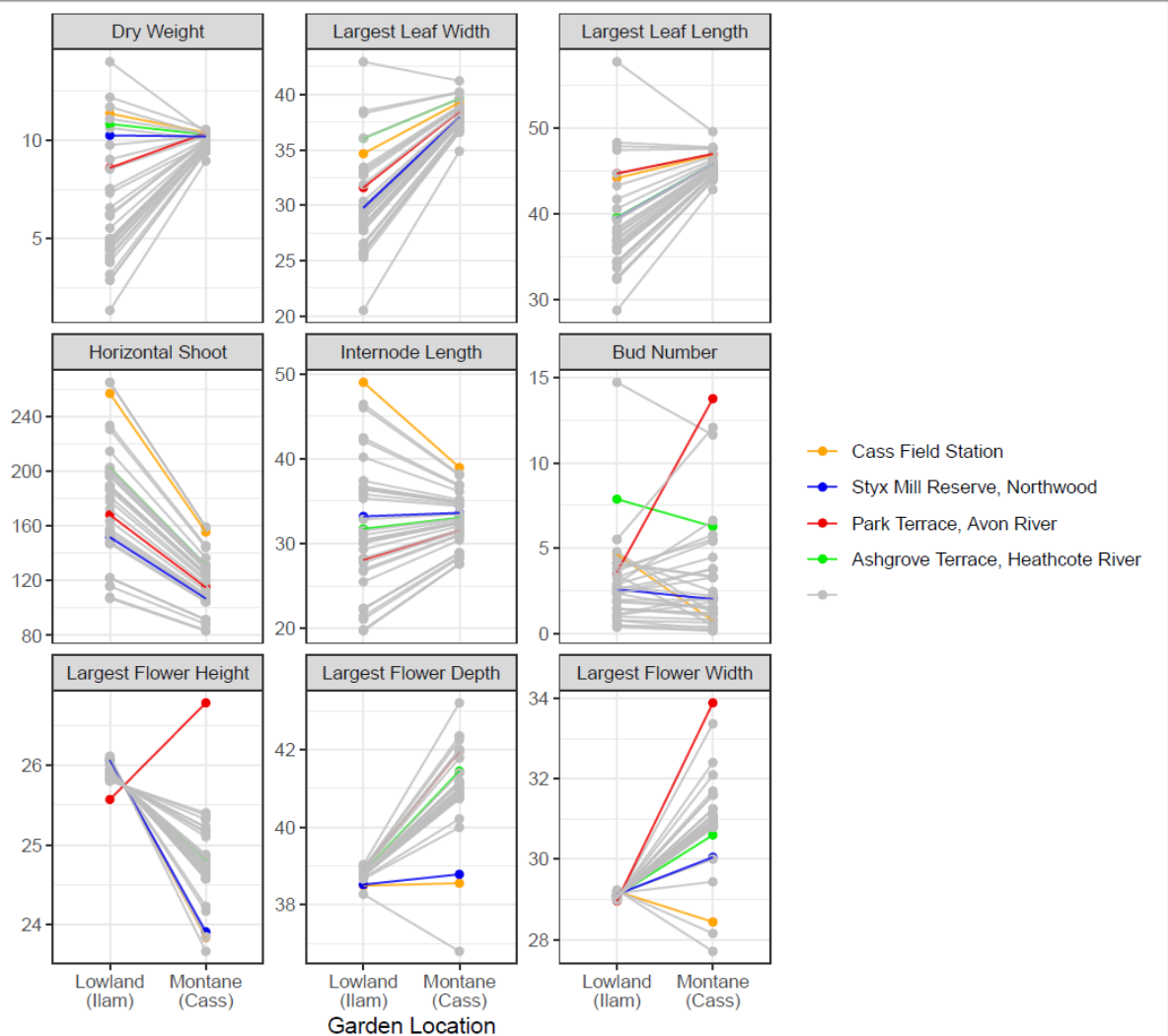
249  **Fig 3** Biplot of the first two principal components, summarising all traits (arrows indicating the rotated
250  coordinate system) for each population-specific prediction. The (0,0) coordinate represents the
251  population average for all traits



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255  All clones show plasticity with variance-changing G x E, and we found marked variation
256  among clones in the degree of plasticity exhibited. For example, two clones from lowland
257  populations in Christchurch showed marked differences in their reaction norms for plant dry
258  weight: the Styx Mill clone showed no shift between elevations while the Park Terrace clone
259  a marked decline in the montane garden (Figure 2). The direction of plasticity also differed
260  among clones, for example despite being collected in the same region and elevation the Styx
261  Mill clone showed a marked decline flower length with elevation while the Park Terrace clone
262  a marked increase in the montane garden. However, while plasticity is common among clones,
263  the rank order of clones remained the same for most traits, except for, the number of buds and
264  flower length where the reaction norm of the Park Terrace was inconsistent with the remaining
265  clones.
266  Evidence for home site advantage would be apparent if the clone from Cass outperformed all
267  other clones in the montane garden and performed less well relative to lowland clones in the
268  lowland garden. This was generally not the case, within the montane garden the Cass clone is
269  within the top few clones in terms of vegetative traits but is outperformed by several lowland
270  clones. It maintains its relatively high ranking in many traits in the lowland garden. Similarly,
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271    there was no evidence at all for the lowland Christchurch sites in the lowland garden

272    outperforming clones from other locales (Fig. 2).

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274           *Genetic versus plastic components to variation*

275    The GLMM analysis to determine total genetic, environmental (residual) and GxE components

276    of the variation in vegetative and reproductive traits among clones revealed that in the lowland

277    garden clone (genotype) explained 33%-45% of the variance in vegetative traits and almost

278    none of the variation in inflorescence traits (Table 2). In contrast in the montane garden it was

279    the inflorescence traits (corolla depth and width and bud number) and stolon length which

280    showed most genetic variability among clones.

281

282    **Table 2** Estimates for site-specific variances by garden location and residual variances together with

283    proportions of explained variance by population [95% confidence intervals]. All estimates are based on

284    logarithmic transformed scales. The total variance among the 34 clones in the Lowland and

285    Montane garden is presented for each measured trait, The residual is the total variance in each

286    measured trait among the 34 clones not explained by garden. The GxE component for each

287    garden is the percentage of variance for each measured trait within each garden

| Trait | $\sigma^2$ Montane | $\sigma^2$ Lowland | $\sigma^2$ Residual | GxE Montane | GxE Lowland |
|---|---|---|---|---|---|
| Dry Weight | 0.01 | 0.80 | 0.99 | 0.01 [0.00; 0.16] | 0.45 [0.30; 0.58] |
| Flower Length | 0.01 | 0.00 | 0.05 | 0.10 [0.00; 0.45] | 0.00 [0.00; 0.29] |
| Flower Depth | 0.01 | 0.00 | 0.02 | 0.21 [0.00; 0.55] | 0.00 [0.00; 0.28] |
| Flower Width | 0.01 | 0.00 | 0.04 | 0.19 [0.00; 0.53] | 0.00 [0.00; 0.28] |
| Leaf Width | 0.00 | 0.06 | 0.08 | 0.04 [0.00; 0.20] | 0.44 [0.28; 0.57] |
| Leaf Length | 0.00 | 0.05 | 0.07 | 0.03 [0.00; 0.15] | 0.41 [0.25; 0.54] |
| Horizontal Shoot | 0.06 | 0.13 | 0.24 | 0.21 [0.06; 0.40] | 0.34 [0.20; 0.48] |
| Internode Length | 0.02 | 0.13 | 0.28 | 0.07 [0.00; 0.23] | 0.33 [0.18; 0.46] |

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295    *Plastic variation*

296    For all of the measured traits except for stolon length and number of buds, the environmental

297    effect of garden was greatest in the montane garden, where almost all of the clones have higher

298    above-ground dry weight, greater leaf areas and longer internode lengths than in the lowland

299    garden (Fig. 4). This environmental component is large, ranging from ~ 20 to 50% difference

300    between gardens, depending on trait.

301

302    **Fig 4** Estimated relative effect of garden location Lowland/Montane and 95% confidence intervals. An

303    estimate of 1 indicates the same expected response at both garden locations, Estimates > 1 correspond

304    to a larger average response in the lowland compared to the montane garden and estimates of <1 indicate

305    a greater average response in the montane, compared to the lowland garden.

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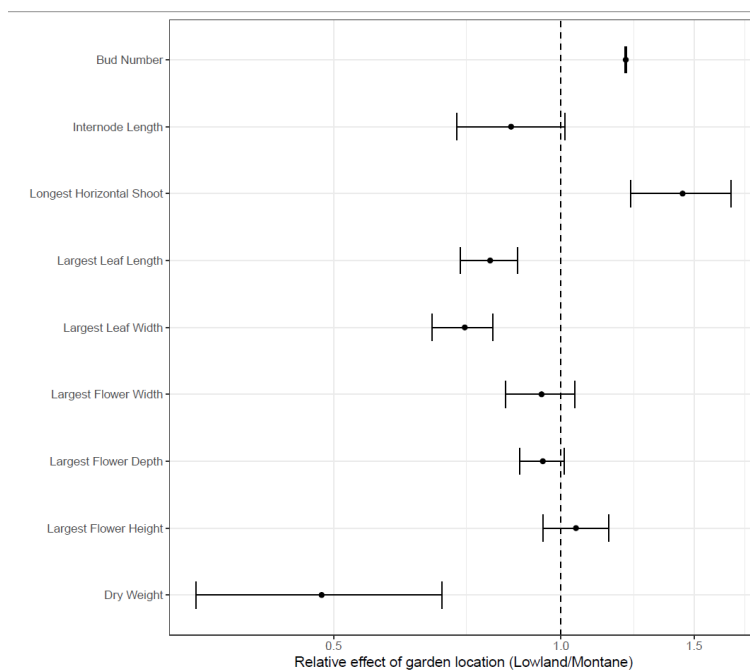


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309    The importance of an environmental component to variance is also illustrated by the patterns

310    for a selection of individual clones (Fig. 5, the individual response of each trait in all clones to

311    the two garden environments is presented in Fig 1 Supplementary Information). For example,

312    the clone originating from the montane (Cass) garden site showed one of the strongest and most

313    consistent plastic responses across all traits when moved to the lowland garden, producing

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314  longer horizontal shoots and internodes, and more flowers than in its home montane

315  environment (Fig. 5). In contrast, the clones from the lowland Travis Wetland and Ashgrove

316  Terrace sites close to the lowland common garden showed a similar, if less pronounced

317  response to the two garden environments  (Fig 5). In the lowland environment stolon length is

318  markedly longer relative to the montane garden in all clones, although the degree of between-

319  garden differences (plasticity) varies among clones. In contrast to the other traits, number of

320  buds are fairly similar in both gardens for most clones, although where there are plastic

321  response these vary in direction among clones. A few clones e.g., Ashgrove Terrace clone, do

322  show a strong environmental response (Fig 5). As expected, we found far more within-clone

323  variation in vegetative and reproductive (length of horizontal shoot and bud number) than floral

324  traits.

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326  **Fig 5** Predicted clone-specific relative effects of garden location Lowland/Montane and 95%

327  confidence intervals. Clones are ordered from highest (990m) to lowest (0m) elevation of the

328  sampling location. A value of 1 indicates the same expected population average at both

329  locations, Estimates > 1 correspond to a larger average response for a clone in the lowland

330  garden compared to montane garden.

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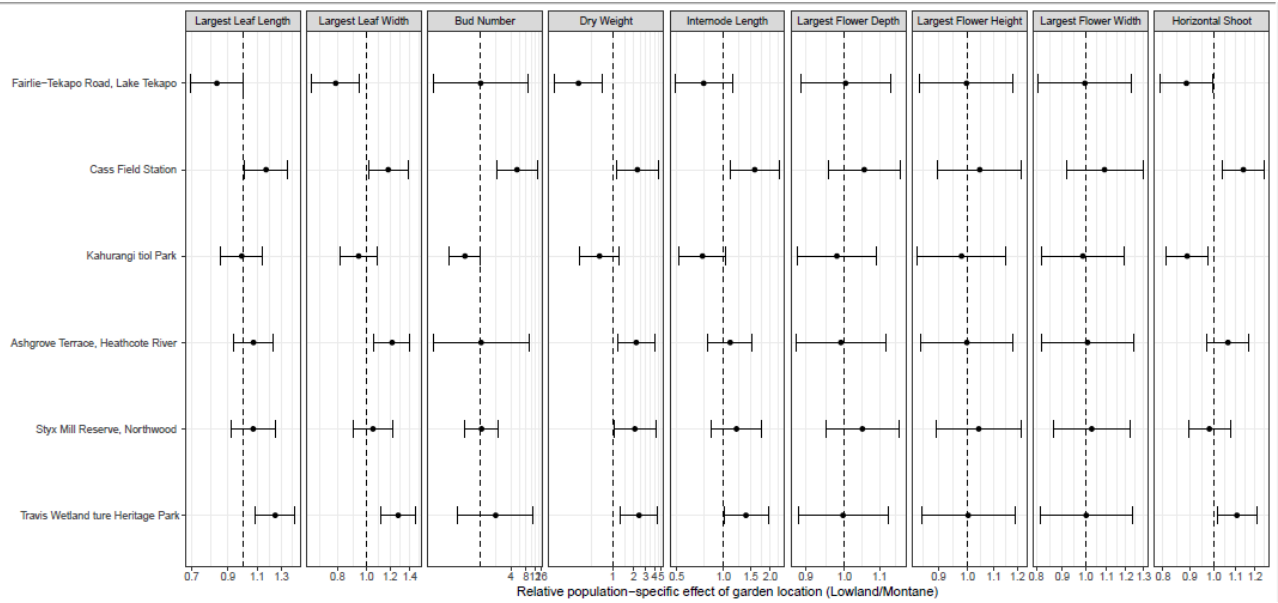
*Evidence for adaptation*

When the PC scores were plotted against each of the source environmental variables independently, for each clone in each of the lowland and montane garden, elevation explained some of the variation in vegetative traits. This was most obvious in the clones growing in the lowland garden, where the clones from lower elevation source sites were overall markedly larger in comparison to clones from higher elevation source sites (Fig 6).

**Fig 6** Dependency between Principal Component scores and elevation of sample locations separate for the two garden locations. The predictions of a linear regression model are added.



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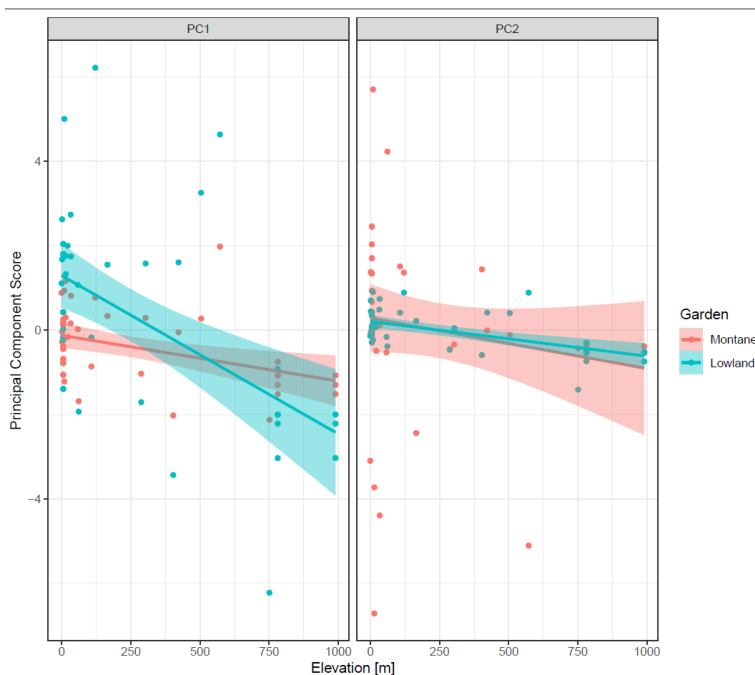
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343 Clones from lower elevation sites were more plastic than those from higher elevations (Fig. 7).

344 This influence of source elevation on individual clone responses to garden locations is most

345 obvious for above ground dry weight, stolon length and internode length. In contrast, elevation

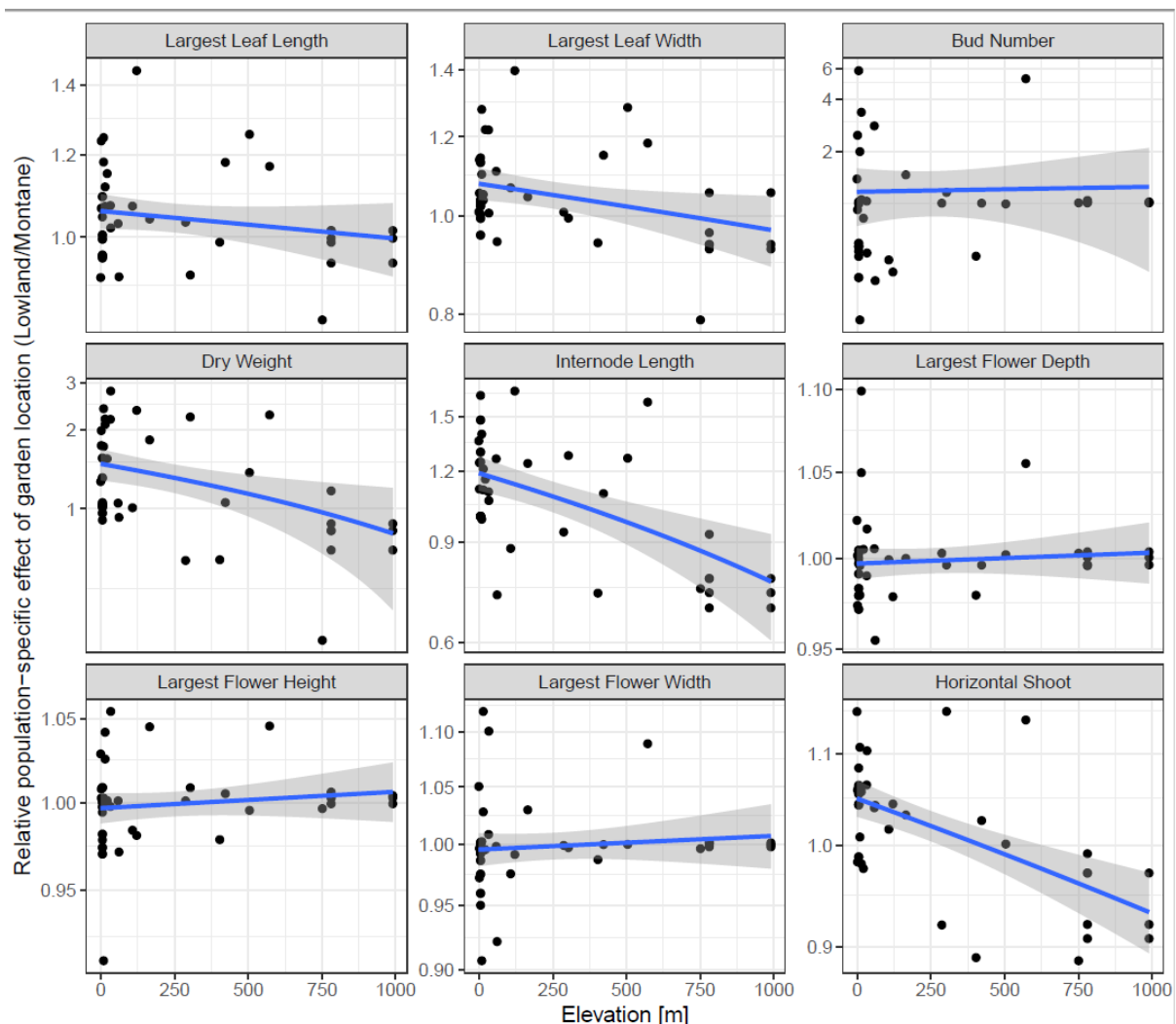346 at source location had no marked effect on relative garden response in bud number or flower

347 characteristics (Figure 7).

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349 **Fig 7** Dependency between the relative clone-specific effect of garden locations and elevation

350 of sample location. The predictions of a (log)-linear model for each of the measured variables

351 is added.



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355    DISCUSSION

356    The aim of our study was to describe some of the phenotypic variation in *E. gutatta* clones

357    from across New Zealand and to partition this variation into genetic and plastic components.

358    We hoped to untangle the relative importance of genetic versus plastic effects in the success

359    of *E. gutatta* as an invasive clonal plant, something which might shed light on its modelled

360    niche shift in New Zealand (Da Re et al. 2021).  Specifically we tested hypotheses of

361    adaptation to elevation and home-site advantage. While we acknowledge that one clone per

362    site excludes any measure of intra-population variation, we are confident that most sites

363    comprised one or a very few clones.

364

365           *Phenotypic variation*

366    Results from our common garden experiment showed that as expected, there were both

367    genetic and environmental components to the variance in all traits measured. However,

368    sorting out the relative contribution of each component and answers about local adaptation

369    became possible only because we used two common gardens and ensured that these gardens

370    were located towards each of the two elevational extremes of source populations (Allan and

371    Pennall 2009; Scheepens et al. 2010; Berend et al. 2019;). We found markedly different

372    results between gardens; in the lowland garden a major proportion of variation in the five

373    measured vegetative traits (above ground dry weight, leaf width, leaf length, horizontal shoot

374    length and internode length) was explained by genetic differences among the clones, while in

375    the montane garden variation in above ground dry weight, leaf width and leaf length was

376    almost entirely masked by plastic responses. In contrast, among-clone genetic differences in

377    flower traits was visible in the montane garden, but hidden in the lowland garden.  However,

378    caution is necessary here as conclusions may depend on which fitness measures are used

379    (Villellas et al. 2021).  Moreover, plastic responses, some passive and non-adaptive (Liu et al.

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380    2016) especially in vegetative traits, may mask genetic traits under favourable conditions

381    (Villellas et al. 2021).

382    Previous studies using common garden experiments to explore variation within introduced

383    species in their new range (Williams et al. 2008; Flory et al. 2011), or to investigate home site

384    advantage (Allan and Pennal 2009) have also found marked differences in trait expression

385    among gardens. The more similar the garden environment to the native range, or home site, the

386    better adapted and therefore fitter the plants should theoretically be. We found limited support

387    for a home-site advantage, with plants collected in the environs of each common garden not

388    beings consistently superior to clones from other locations.

389

390          *Genotypic variation*

391    In the lowland garden, plants ranged from tall, multiple stemmed, large-leaved individuals with

392    abundant flowers through to low growing clones with long horizontal shoots to small

393    individuals with few flowers. Our model predicts that up to 45% of the variance in plant dry

394    weight and 34 % of the variance in length of horizontal shoots was genetically determined.

395    Taken together, the variance in vegetative, and reproductive traits we observed in the lowland

396    garden suggests that across New Zealand there is extensive genetic variation among *E. gutatta*

397    clones. Results from the montane garden tell a different story; at Cass genetic variation among

398    clones explains only 1% of the variation in dry weight and only 21% of the variation in

399    horizontal shoot length, but more genetic variation in flower traits than was observed in the

400    lowland garden. Basing our understanding on data from the montane garden only would

401    suggest that *E. gutatta* clones across New Zealand show little genetic variation in vegetative

402    traits but some variation in flower traits.

403

404

405          *Fitness differences across environments*

19

406    Bearing in mind that our proxy for fitness was above ground dry weight, our plots of the PC1

407    scores against source elevation suggest adaptation to elevation; the plot strongly indicated

408    higher biomass in clones from low elevation compared with high elevation source sites in the

409    lowland garden. Numerous studies globally have demonstrated the adaptive strategy of low

410    plant height and low biomass at high elevations (Körner 2003). Moreover Olsson and Agren

411    (2002) and Monty et al. (2009) have demonstrated this adaptation in introduced plant species

412    in the US and Europe respectively. However, while adaptation is a credible explanation for

413    our finding that clones from lowland sites are fitter in the lowland than in the montane

414    garden, alternative explanations such as genetic drift through founder effects (Monty et al.

415    2009; McGoey et al. 2020) cannot be dismissed.

416    The weak signal of advantage in clones from lowland sites in the high elevation Cass garden

417    is in accordance with DeMarche et al. (2016) who found that low elevation *E. gutatta*

418    ecotypes outperformed montane ecotypes in their montane common garden. However, the

419    authors agree their conclusions are tenuous for several reasons, including misappropriate

420    measures of fitness.  In our New Zealand study, we did not measure below ground biomass,

421    which may have conferred fitness at higher elevations. Moreover, our results are from one

422    year only so we may have missed inter-annual variation in fitness. Alternatively, it is

423    conceivable that genotypes better adapted to higher elevations in New Zealand have not yet

424    reached high elevations environments.

425

426        *Home site advantage*

427    Despite the wide range of genetic variation among our clones in vegetative traits we found little

428    evidence of local adaptation, instead the ranking of clones in terms of relative trait values stayed

429    the same across most traits in both gardens. While the Cass clone, growing in the Cass montane

430    garden was always in the top few ranking clones for all vegetative and reproductive traits we

431    measured, it was only top in internode length and was outperformed by clones from lowland

20

432   sites in length of longest horizontal shoots- stolons. Similarly, in the Ilam lowland garden while

433   clones from low elevation sites around Christchurch relatively close to the lowland garden

434   performed relatively well they were outperformed by several clones from other regions.

435   Multiple introductions, small populations and founder effects (McGoey et al.), and possibly

436   conflicting selection pressures (Barrett et al. 2008) may explain this lack of evidence for home

437   site advantage. Strong gene flow among populations (Zhao et al. 2013) seems an unlikely

438   explanation given the clonal nature of the spread of *E. gutatta* (Truscott et al. 2008). Multiple

439   introductions into different catchments and founder effects seem the most likely explanation;

440   frequent removal (sometimes annual) of *E. gutatta* to clear waterways followed by re-

441   introduction through fragments of different provenances could well explain lack of ecotypic

442   variation. While absence of ecotypic variation despite strong genotype variation in invasive

443   species has been reported previously (Lord 1992; Ebeling et al. 2011; Pahl et al. 2013; Herden

444   et al. 2019) there is always the possibility that adaptation is being missed because of

445   inappropriate fitness measures.  For example, Lord (1992) points out that while Rapson and

446   Wilson (1992) found no evidence for home site advantage among New Zealand *Agrostis*

447   *capillaris* populations in growth and floral morphology, they did find evidence of local

448   adaption to soil water availability and soil nitrogen and phosphorus. Identifying the key traits

449   is therefore essential (Williams et al. 2008; Bufford and Hulme 2021).

450

451        *Plasticity*

452   All clones showed considerable plasticity in all the traits we measured, which was

453   unsurprising, especially for the vegetative traits given this is a perennial, weedy herb (Bazzaz

454   1996). We found above ground dry weight, our proxy for fitness, was almost universally

455   higher in the montane relative to the lowland garden; dry weight was on average 50% higher

456   across all clones at Cass than at Ilam, with little variance in dry weight among clones at Cass.

457   While this reduced inter-clonal variance in dry weight at montane garden reflected varying

21

458    steepness of the reaction norm for above ground dry weight among the clones, rank order did

459    not change.  Likewise, horizontal shoot length was on average 5% shorter in the montane

460    than in the lowland garden, but with no crossing-over of reaction norms. Consistent reactions

461    norms among clones suggests past adaptation and may be indicative of less potential for local

462    adaptation in new environments than if clones had shown variable reaction norms to different

463    environments (Cheplick 2015). One interpretation of these results therefore is that the

464    montane environment is more similar than lowland Ilam to the environment in the native

465    range of *E. gutatta* populations; plasticity permits clones to maximize their fitness under

466    optimal conditions (Hendry 2016). However, based on the environmental suitability models

467    Da Re et al. (2020), neither the lowland or montane garden are especially suitable areas for *E.*

468    *gutatta*. It may well be that much of the plasticity we observe across most of the traits we

469    measured is passive, a side effect of adaptations or other plastic responses (De Witt et al.

470    1998; Funk 2008; Hulme 2008; Auld et al. 2010; Bufford and  Hulme 2021a), limiting

471    species ability to respond to changing environments (Valladares et al. 2014). Bufford and

472    Hulme (2021a) stress the need for future experimental studies linking trait plasticity to fitness

473    along manipulated environmental gradients.

474    The direction of the reaction norm for internode length did vary among clones, with some

475    clones showing longer internode lengths in the montane environment relative to the lowland

476    garden and others shorter. This may indicate adaptive plasticity; certainly foraging behaviour

477    via horizontal and vertical growth as observed in *E. gutatta* should be adaptive by allowing

478    the colonisation of new niches (Clements et al. 2021). van Kleunen and Fischer (2021) tested

479    this hypothesis on the clonally reproducing *Ranunculus reptans* and found genetic variation

480    in plasticity for internode and stolon length, evidence supporting adaptive plasticity. The

481    importance in our study of these results is that they show genetic variation among clones for a

482    plastic trait which may support invasiveness (Clements et al. 2021).

22

483    Further evidence for adaptive (active) plasticity was found in bud number. For this trait

484    reaction norm slopes crossed in some of the clones, and different clones responded differently

485    to the two gardens. Again, this illustrates the potential for adaptive evolution across our *E.*

486    *gutatta* clones.

487    In contrast to the other traits, the flower length, depth and width showed considerable among

488    clone genetic variation in the montane environment but elicited a similar plastic response to

489    the lowland garden, where flowers from all clones were essentially similar in size. We

490    caution too much interpretation of these results because of low flower numbers, but plasticity

491    of *E. gutatta* flowers has been reported before, a response to drought (Kelly et al. 2008).

492    That clones from lower elevation source sites showed greater plasticity in vegetative traits

493    than clones from high elevation source sites is important. Plasticity is selected for in changing

494    environments (Oostra et al. 2018) and lowland sites may be more varied environments than

495    montane ones, experiencing more fluctuation in nutrient levels and more anthropogenic

496    disturbance. Whatever the reason for this elevational variation the finding is notable because

497    the distribution of plastic traits across species ranges may impact how species respond to new

498    environments and how they affect range shifts (Bufford and Hulme 2021a).

499    *Future work*

500    Our study illustrates the potential opportunity in using *E. gutatta* to further understand the

501    mechanisms of successful plant invasions into new niches. Key to taking this further is

502    experimentation using multiple clones from each population in reciprocal transplants, both

503    within New Zealand and between New Zealand and native US *E. gutatta* populations.

504    Comparing home and away fitness traits and home and away plasticity (Bufford and Hulme

505    2021b), especially in traits associated with clonal spread will be important. Trade-offs (or

506    not) associated with greater horizontal shoot length and *e.g.* flower production and seed set

507    should be explored. To what extent plasticity may be aiding or confounding future adaptation

508    and spread across New Zealand needs further investigation. Future fitness trait measures

509    should include flowering phenology, well known to influence invasion success in plants and

510    physiological traits which may be more closely associated with fitness than the traits included

511    in this study.

512

513        *Conclusions*

514    Our study has shown the presence of considerable genetic variation among *E. gutatta* clones

515    from across the South Island of New Zealand; while we found scant evidence for local

516    adaptation (home site advantage) we found a strong signal for higher fitness in all vegetative

517    traits across both garden environments in clones from lowland, as compared with higher

518    elevation sites. Clones from lowland sites were more plastic relative to clones from higher

519    elevation sites, including two key traits facilitating the spread of clonal plants, horizontal

520    shoot length and internode length. Having variation for plasticity in essential traits such as

521    these suggests that *E. gutatta* is well adapted to move into new environments (Gratani 2014)

522    and that plasticity may contribute substantially to its successful niche expansion within New

523    Zealand as compared with its native range. To what extent this reflects a trade-off or lack

524    thereof with other reproductive traits (Bufford and Hulme 2021b) is a major focus for future

525    investigation.

526

527    Data Availability Statement

528    All data are available on request:hazel.chapman@canterbury.ac.nz

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862  Please refer to the "Competing Interests" section below for more information on how to
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865  All authors contributed to the study conception and design. Material preparation, data

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