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# PLASTICITY FACILITATES *Anthemis cotula* TO INVADE DIVERSE HABITATS

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## ABSTRACT

*In view of the significant contribution of phenotypic plasticity in survival and spread of invasive species in heterogeneous adventive environments, present study was carried out on natural populations of Anthemis cotula L. (Stinking mayweed) growing in habitats that differ in disturbance. The vegetative (stem height, number of lateral branches, root mass, and shoot mass) and reproductive (number of disc florets per plant and per capitulum and number of capitula per plant) traits exhibited significant phenotypic plasticity across such habitats. Number of disc florets per plant (used as the measure of fitness) was highest in riparian populations and lowest in populations growing in habitats with relatively low disturbance. Fitness in populations supported by habitats with high disturbance was 5183.85 disc florets per plant. Although the number of disc florets per capitulum did not vary significantly across populations supported by different habitats, the number of capitula per plant ranged from 148.10 in riparian populations to 20.74 in populations growing in low disturbance habitats. Among the vegetative attributes, stem mass and number of lateral branches per plant varied significantly across populations supported by habitats with different disturbance regimes. Quantification of the phenotypic selection acting on these vegetative and reproductive traits estimated through use of selection differentials and gradients varied in sign and strength across the sites which indicate that different traits are favoured under different habitat conditions. Comparison of the phenotypic plasticity of A. cotula with a con-familial alien but less invasive species-Galinsoga parviflora - allows us to conclude that phenotypic plasticity not only enables the former to maintain fitness across a broad range of environments but also contributes significantly to its invasiveness in the Kashmir Himalaya.*

**Key words:** Invasive, plasticity, fitness, Kashmir Himalaya.

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## INTRODUCTION

Phenotypic plasticity, defined as the ability of a genotype to express different phenotypes in different environments (Pigliucci, 2005; Richards *et al*., 2006), has been frequently reported as the primary mechanism enabling aliens to colonize environmentally diverse habitats (Baker, 1965; Callaway *et al*., 2003; Parker *et al*., 2003; Sultan, 2004; Valladares *et al*., 2006).

In fact, plasticity in morphological and physiological traits initially allows introduced species the environmental tolerance to become naturalized across a range of environments (Baker, 1974) following which recombination of genetic variation among introduced individuals results in the evolution and expression of beneficial plastic responses in the colonized habitats (Ellstrand and Schierenbeck, 2000; Donohue *et al*., 2005; Richards *et al*., 2005). Although studies of phenotypic plasticity have a long history in plant ecology (Bradshaw, 1965: Schlichting and Pigliucci, 1998; Pigliucci, 2001), the extent to which patterns of plasticity differ among traits, life histories and habitats, and the adaptive basis of this variation are largely unresolved questions (Dorken and Barrett, 2004).

A suite of methods for estimating the strength of selection on multiple quantitative traits (Lande, 1979; Lande and Arnold, 1983; Arnold and Wade, 1984a, 1984b) are in vogue that allow separation of the direct and indirect components of selection on a set of correlated traits. Selection of phenotypic traits that enhance fitness are, particularly, important in promoting plant invasions and it would become evident only when the plastic response in invaders is measured relative to those of related but non-invasive species (Richards *et al*., 2006).

It is in this context, the present study was carried out to document intra- and inter-populational phenotypic plasticity in several vegetative and reproductive traits of *Anthemis cotula* L. (Stinking mayweed; family Asteraceae) in Kashmir Himalaya and to check whether or not this invasive species exhibits greater plasticity in major ecological traits in its field populations supported by terrestrial open habitats (with low and high levels of disturbance) and riparian habitats. Besides, a comparison of selection on trait complexes in three environments (terrestrial open habitats with low and high disturbance and riparian habitats) was also investigated during the present study. In addition, plasticity in the investigated attributes of *A. cotula*, was compared with that of *Galinsoga parviflora* which was chosen for being a con-familial alien but less invasive species.

## MATERIALS AND METHODS

### Study species

*Anthemis cotula* L. (Stinking mayweed, Mayweed chamomile), an annual, ill-scented, self-incompatible herbaceous member of sunflower family (Asteraceae), is native to southern Europe-west Siberia (Erneberg, 1999). It has a woody tap root; glabrous erect stem; alternate, sessile, slightly puberulous, pinnately dissected leaves; solitary terminal capitula; small pubescent imbricate involucral bracts; ray florets white; disc florets fertile and yellow in colour. Fruit is an achene. Because of its prolific growth and allelopathic activity, this species is becoming increasingly problematic in many parts of the world, including Kashmir Himalaya.

*Galinsoga parviflora* (Gallant soldier) native to tropical America is an annual herb found in most temperate and subtropical regions of the world. It has a shallow fibrous root system and erect branched stem which is slightly hairy. Leaves are opposite, simple, ovate and slightly hairy. Flower heads consist of many yellow tubular florets, and 4-5 white 3-lobed ray florets surrounded by membranous bracts. Fruit is an achene and propagation is by seeds.

### Study sites

Twenty natural populations of *A. cotula* in the Kashmir, Himalaya, India, were studied during 2005. The study populations were sustained by habitats varying in the level of disturbance (Fig.1); nine populations were supported by open terrestrial habitats with low disturbance; eight by open terrestrial habitats with high disturbance and three by riparian habitats. These sites represented almost all the habitats invaded by *A. cotula*. In view of limited occurrence and restriction of *G. parviflora* to open terrestrial habitats with low disturbance in the Kashmir Himalaya, only four natural populations were selected and data on the same vegetative and reproductive traits in both the species was obtained during the study period.

### Common pot experiment

Achenes from four representative populations of *A. cotula* supported by low, high disturbance sites and riparian habitats were raised in pots of 30 cm diameter, filled with garden soil and sand (3:1). The seedlings after emergence were thinned and 5 seedlings of almost equal size were maintained in each plot. 20 pots of each population were maintained for further studies.

### Data collection

In each field population 50 individuals of *A. cotula* were randomly selected and permanently tagged for recording data on different attributes. A sub-sample of 10 mature individuals was used to record data on plant height, root, shoot and floret mass, number of lateral branches, number of capitula per plant, number of disc florets per capitulum and number of disc florets per plant. These data were also raised from pot grown individuals of *A. cotula* and four populations of *G. parviflora*.

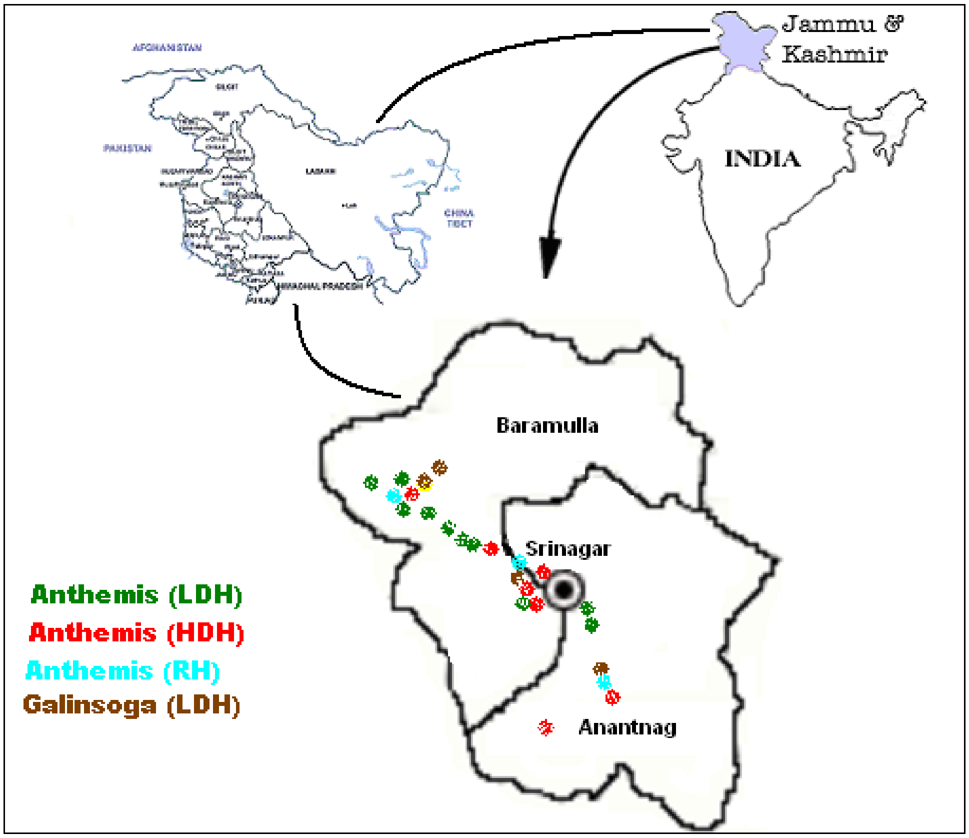


**Fig. 1. Map showing study sites with low disturbance (LDH), high disturbance (HDH) and Riparian (RH) habitats.**

**Data analysis**

Basic statistics, such as trait means and variances were calculated using SPSS 10. An ANOVA was carried out for all vegetative and reproductive traits between populations supported by different habitat types. Plasticity index ((maximum mean-minimum mean)/maximum mean) was calculated following Valladares *et al*. (2000).

**Selection differentials and gradients**

Phenotypic selection analyses were conducted on traits of individuals of *A. cotula* so as to analyze the possible difference(s) in selective forces in different habitat types. All phenotypic traits were standardized to a mean of 0 (SD = 1). No other transformations were applied because data did not violate the distributional assumptions of multiple regressions. Absolute fitness measures, in the form of number of fertile disc florets per plant, were converted to relative fitness measures. Subsequently, the standardized selection differentials were estimated, a technique that indicates the total selection for each phenotypic trait, includes selection acting directly on the trait and selection acting on correlated traits (Lande and Arnold, 1983; Arnold and Wade, 1984). It also estimates the magnitude and direction of selection by determining the covariance between that trait and the values of some estimates of fitness (Schluter, 1988; Galen, 1989). Also the selection gradients were estimated, a multivariate technique that reveals the direction and magnitude of selection for each quantitative trait, independent of the other traits (Lande and Arnold, 1983; Arnold and Wade, 1984a). The directional selection gradient, β, was obtained from the partial-regression coefficients of a linear regression of relative fitness on all the traits.

**RESULTS AND DISCUSSION**

Values of the phenotypic traits of *A. cotula* considered in the present study are summarized in Table-1. Vegetative and reproductive characters, except floret mass per plant, varied significantly between populations and habitats ($P<0.001$). It was in contrast to *G. parviflora*, where such traits (Table-2) did not differ significantly across populations ($P>0.05$). In riparian populations of *A. cotula* all traits, except height, exhibited higher values (Table-2). Riparian habitats with frequent soil disturbance, offer opportunities for recruitment mostly after floods in the form of smaller gaps (Richardson *et al*., 2007) and, therefore, competition for pollinators and light is reduced; but in terrestrial habitats with more inter-specific competition the plants have to be taller so as to compete successfully with other plants for light (Falster and Westoby, 2003). Thus, a trade-off between height and number of laterals per plant is seen in *A. cotula* (Table-3), with former contributing to success in mixed cultures and latter in more disturbed conditions.

Fitness (measured as number of disc florets per plant) was highest in riparian habitats and lowest in terrestrial habitats with low disturbance (Table-3). A common prerequisite for successful colonization is that disturbance removes limiting factors or barriers to invasion (Johnstone, 1986; Hobbs, 1989) and the extent to which these are removed are related to the type of disturbance and disturbance intensity (Myers, 1983; Armesto and Pickett, 1985; Hobbs, 1989) and their ability to increase resource availability.

**Table-1. Vegetative and reproductive characters of *Anthemis cotula* (Mean±S.E.) from different populations.**

| Habitat type | Site | Height Plant$^{-1}$ (cm) | Number of lateral branches plant $^{-1}$ | Root mass plant$^{-1}$ (g) | Shoot mass plant$^{-1}$(g) | No. of capitula Plant$^{-1}$ | No. of disc florets Capitulum$^{-1}$ | No. of disc florets plant$^{-1}$ | Floret mass plant$^{-1}$(g) |
|---|---|---|---|---|---|---|---|---|---|
| Terrestrial open habitats with low disturbance | LD1 | 35.80±1.28 | 1.50±0.22 | 0.84±0.12 | 5.55±0.20 | 21.20±1.07 | 109.50±1.45 | 2311.30±96.85 | 1.30±0.20 |
| | LD2 | 50.80±1.38 | 1.10±0.10 | 0.35±0.09 | 1.97±0.30 | 12.10±1.02 | 96.00±1.01 | 1156.10±90.69 | 0.52±0.16 |
| | LD3 | 19.80±2.93 | 1.20±0.13 | 0.41±0.04 | 1.69±0.19 | 12.70±1.27 | 94.90±1.68 | 1196.50±113.21 | 0.58±0.08 |
| | LD4 | 52.80±1.71 | 1.00±0.00 | 0.92±0.07 | 4.49±0.22 | 15.20±0.92 | 113.80±0.71 | 1730.40±105.85 | 0.54±0.08 |
| | LD5 | 49.20±2.03 | 1.40±0.22 | 1.10±0.14 | 9.42±0.42 | 23.30±2.58 | 115.60±1.07 | 2698.90±306.54 | 1.57±0.12 |
| | LD6 | 76.60±4.21 | 1.20±0.13 | 1.51±0.12 | 7.35±0.15 | 19.20±1.86 | 126.30±1.14 | 2415.30±225.94 | 1.30±0.12 |
| | LD7 | 26.30±1.37 | 2.00±0.30 | 1.09±0.10 | 8.77±0.24 | 29.00±2.13 | 120.70±1.14 | 3501.10±258.66 | 1.07±0.08 |
| | LD8 | 27.70±1.20 | 1.50±0.17 | 1.07±0.08 | 8.86±0.22 | 27.30±2.17 | 125.20±2.02 | 3389.90±237.88 | 1.17±0.06 |
| | LD9 | 36.10±3.43 | 1.50±0.22 | 0.37±0.04 | 3.10±0.31 | 26.70±1.99 | 129.90±1.86 | 3462.30±249.02 | 1.23±0.13 |
| Terrestrial open habitats with high disturbance | HD1 | 93.50±4.90 | 1.30±0.15 | 1.18±0.18 | 9.16±1.04 | 41.60±3.60 | 120.10±1.68 | 4971.10±408.74 | 1.97±0.47 |
| | HD2 | 72.20±2.76 | 1.60±0.22 | 0.88±0.03 | 15.17±0.33 | 38.10±2.41 | 130.00±1.21 | 4932.60±281.29 | 2.77±0.13 |
| | HD3 | 43.00±2.44 | 1.30±0.15 | 1.29±0.05 | 8.29±0.12 | 35.30±2.01 | 122.60±1.09 | 4323.50±242.37 | 2.00±0.03 |
| | HD4 | 62.60±2.85 | 1.30±0.15 | 0.99±0.10 | 14.29±0.51 | 43.90±1.68 | 114.30±0.72 | 5013.90±181.85 | 2.33±0.13 |
| | HD5 | 53.50±2.66 | 2.00±0.30 | 1.09±0.08 | 27.80±1.59 | 52.10±3.09 | 132.20±1.28 | 6871.30±381.59 | 3.23±0.26 |
| | HD6 | 50.90±2.00 | 1.70±0.21 | 1.23±0.19 | 14.00±0.43 | 34.60±2.42 | 129.00±1.23 | 4449.70±291.05 | 2.62±0.20 |
| | HD7 | 85.50±4.23 | 1.30±0.15 | 2.00±0.20 | 21.91±2.10 | 53.00±2.36 | 128.70±1.10 | 6807.20±274.95 | 3.81±0.38 |
| | HD8 | 35.00±1.53 | 2.10±0.35 | 1.66±0.17 | 11.63±0.26 | 30.50±2.25 | 134.80±1.31 | 4101.50±289.66 | 1.54±0.15 |
| Riparian habitats | RH1 | 74.20±3.53 | 10.50±0.56 | 4.62±0.19 | 46.09±0.70 | 138.10±2.81 | 136.20±1.09 | 18801.00±369.36 | 11.78±0.34 |
| | RH2 | 24.40±1.12 | 10.00±0.65 | 2.00±0.07 | 16.68±1.04 | 158.90±3.94 | 138.50±1.35 | 22021.10±648.36 | 10.69±0.58 |
| | RH3 | 30.20±1.00 | 10.40±0.45 | 1.61±0.18 | 17.07±1.46 | 147.30±4.81 | 114.80±1.29 | 16884.00±492.62 | 9.39±0.99 |

**Table-2. Vegetative and reproductive characters of *Galinsoga parviflora* (Mean±S.E.) from different populations.**

| Site | Stem height (cm) | No. of lateral branches plant$^{-1}$ | Root mass (g) | Shoot mass (g) | No. of capitula plant$^{-1}$ | No. of disc florets capitulum$^{-1}$ | No. of disc florets plant$^{-1}$ | Floret mass (g) |
|---|---|---|---|---|---|---|---|---|
| S1 | 31.30 ±1.10 | 1.00 ±0.00 | 0.31 ±0.04 | 1.18 ±0.20 | 71.30 ±14.97 | 39.10 ±1.07 | 2803.20 ±579.58 | 0.24 ±0.05 |
| S2 | 30.50 ±2.03 | 1.00 ±0.00 | 0.21 ±0.03 | 1.22 ±0.26 | 47.20 ±9.21 | 38.50 ±0.82 | 1836.10 ±357.58 | 0.21 ±0.09 |
| S3 | 34.10 ±3.49 | 1.00 ±0.00 | 0.32 ±0.07 | 1.29 ±0.24 | 65.60 ±12.04 | 39.20 ±1.13 | 2548.00 ±447.25 | 0.16 ±0.04 |
| S4 | 31.50 ±2.07 | 1.00 ±0.00 | 0.32 ±0.10 | 1.52 ±0.43 | 73.30 ±22.15 | 39.20 ±1.13 | 3009.60 ±1018.47 | 0.27 ±0.10 |

**Table-3. Vegetative and reproductive characters of *Anthemis cotula* (Mean±S.E.) from different habitats.**

| Trait | Habitat types | | |
|---|---|---|---|
| | Terrestrial open habitats with low disturbance | Terrestrial open habitats with high disturbance | Riparian habitats |
| Stem height (cm) | 41.68 ±1.91 | 62.03 ± 2.40 | 42.93 ± 4.31 |
| No. of lateral branches/plant | 1.38 ± 0.07 | 1.58 ± 0.08 | 10.30 ± 0.32 |
| Root mass/plant (g) | 0.85 ± 0.05 | 1.29 ± 0.06 | 2.74 ± 0.26 |
| Shoot mass/plant (g) | 5.69 ± 0.32 | 15.28 ± 0.78 | 26.62 ± 2.63 |
| No. of capitula/plant | 20.74 ± 0.85 | 41.14 ± 1.22 | 148.10 ± 2.70 |
| No. of disc florets/ capitulum | 114.66 ± 1.34 | 126.46 ± 0.83 | 129.83 ± 2.10 |
| No. of disc florets /plant | 2429.09 ±112.87 | 5183.85 ± 152.10 | 19235.37 ± 487.47 |
| Floret mass/plant (g) | 1.03 ±0.05 | 2.53 ± 0.12 | 10.62 ± 0.43 |

Table-4 summarizes the values of the phenotypic traits obtained from individuals of pot grown populations. Analysis of variance did not reveal significant differences between any of the traits considered in the present study across different populations (P>0.05). The results indicate that the variations of each variable observed in fields are plastic response to environments, not genetically determined. Plasticity rather than genetic differentiation help the invader acclimate to different habitats, supporting general purpose hypothesis.

Comparison of the fitness plasticity of *A. cotula* with *G. parviflora* (Fig. 2) reveals that the former is able to maintain relatively high fitness across a range of habitats being highest in riparian habitats, but the latter is confined only to terrestrial open habitats with low disturbance. There is abundant evidence that plant species and populations may differ remarkably in the extent of their plastic responses to comparable environmental challenges (Schlichting and Levin, 1984; Valladares *et al.*, 2000; Sultan, 2001). Plasticity index of various vegetative and reproductive traits in the habitats of occurrence of the two species is presented in Fig. 3. All the traits invariably showed higher plasticity in *A. cotula* than *G. parviflora*. Besides, the traits in populations of *A. cotula* sustained by terrestrial open habitats with low disturbance revealed higher plasticity while as the same was least in the riparian populations.

Phenotypic selection analyses (Table-5) demonstrated that measures of covariance between standardized traits and relative fitness (selection differential) in *A. cotula* yielded statistically significant selection differentials in terrestrial habitats for almost all traits, except number of disc florets per capitulum in both high and low disturbance habitats and shoot mass per plant only, in terrestrial habitats with high disturbance. Significantly positive relationship between number of lateral branches per plant and relative fitness was noticed across all the three habitats. Selection gradients for stem height, root and shoot mass, number of capitula per plant and number of disc florets per capitulum were statistically significant in low disturbance terrestrial habitat with stem height, root mass and number of capitula per plant showing positive sign. In high disturbance terrestrial habitats number of lateral branches, shoot mass, and number of capitula per plant were significant with stem mass showing negative sign. Selection gradient in respect of number of capitula per plant was the only statistically significant trait in riparian populations of the species.

**Table-4. Vegetative and reproductive characters of *Anthemis cotula* (Mean±S.E.) from different populations grown in pots.**

| Population | Stem height (cm) | No. of lateral branches Plant$^{-1}$ | Root mass (g) | Shoot mass (g) | No of capitula plant$^{-1}$ | No. of disc florets capitulum$^{-1}$ | No. of disc Florets plant$^{-1}$ | Floret mass (g) |
|---|---|---|---|---|---|---|---|---|
| P1 | 41.20±6.29 | 1.20 ±0.20 | 0.44 ±0.15 | 2.86 ±0.87 | 47.20 ±18.58 | 163.04 ±11.77 | 8210.60 ±3304.96 | 0.68±0.18 |
| P2 | 48.20±9.16 | 1.20 ±0.20 | 0.41 ±0.11 | 4.06 ±1.59 | 60.40 ±19.86 | 171.56 ±17.16 | 11428.96 ±4136.54 | 1.12±0.43 |
| P3 | 35.90±7.61 | 1.40 ±0.24 | 0.62 ±0.17 | 3.35 ±1.12 | 39.00 ±15.61 | 156.00 ±16.42 | 6710.12 ±2734.44 | 0.76±0.31 |
| P4 | 25.40±5.16 | 1.40 ±0.24 | 0.45 ±0.08 | 2.24 ±0.58 | 35.60 ±4.49 | 179.88 ±12.67 | 6196.76 ±545.81 | 0.53±0.20 |

**Table-5. Standardized selection differentials (α) and linear selection gradients (β) for several traits in populations of *A. cotula* from three different habitats.**

| Trait | Open terrestrial habitats with low disturbance | | Open terrestrial habitats with high disturbance | | Riparian habitats | |
|---|---|---|---|---|---|---|
| | α | β | α | β | α | β |
| Stem height (cm) | 0.073** | 0.338*** | 0.043* | -0.090 | 0.007 | 0.256 |
| No. of lateral branches/plant | 0.140*** | -0.018 | 0.119*** | 0.404*** | 0.054*** | 0.123 |
| Root mass/plant (g) | 0.112*** | 0.281* | 0.084*** | 0.026 | 0.019 | -0.151 |
| Shoot mass/plant (g) | 0.054* | -0.449*** | 0.037 | -0.611*** | 0.007 | 0.188 |
| No. of capitula/plant | 0.152*** | 1.033*** | 0.124*** | 0.904*** | 0.061*** | 0.721* |
| No. of disc florets/capitulum | 0.014 | -0.490*** | 0.031 | 0.105 | 0.005 | -0.098 |
| Floret mass/plant (g) | 0.118*** | -0.012 | 0.086*** | 0.114 | 0.061*** | 0.232 |

* $P < 0.05$; ** $P < 0.01$; ***$P < 0.001$

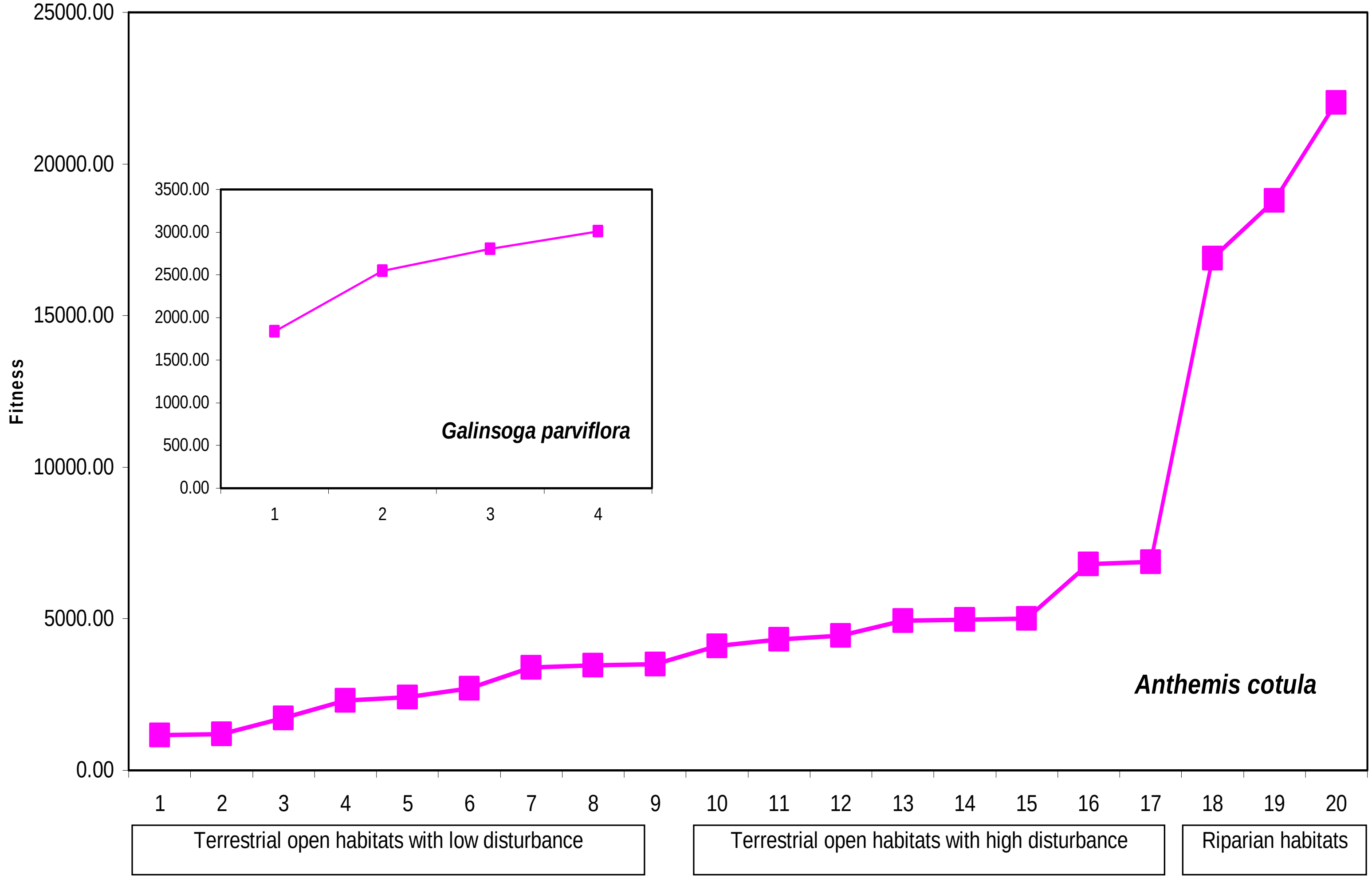


**Fig. 2. Comparison of fitness (number of achenes plant$^{-1}$) of *Anthemis cotula* in different habitats with that of *Galinsoga parviflora.***

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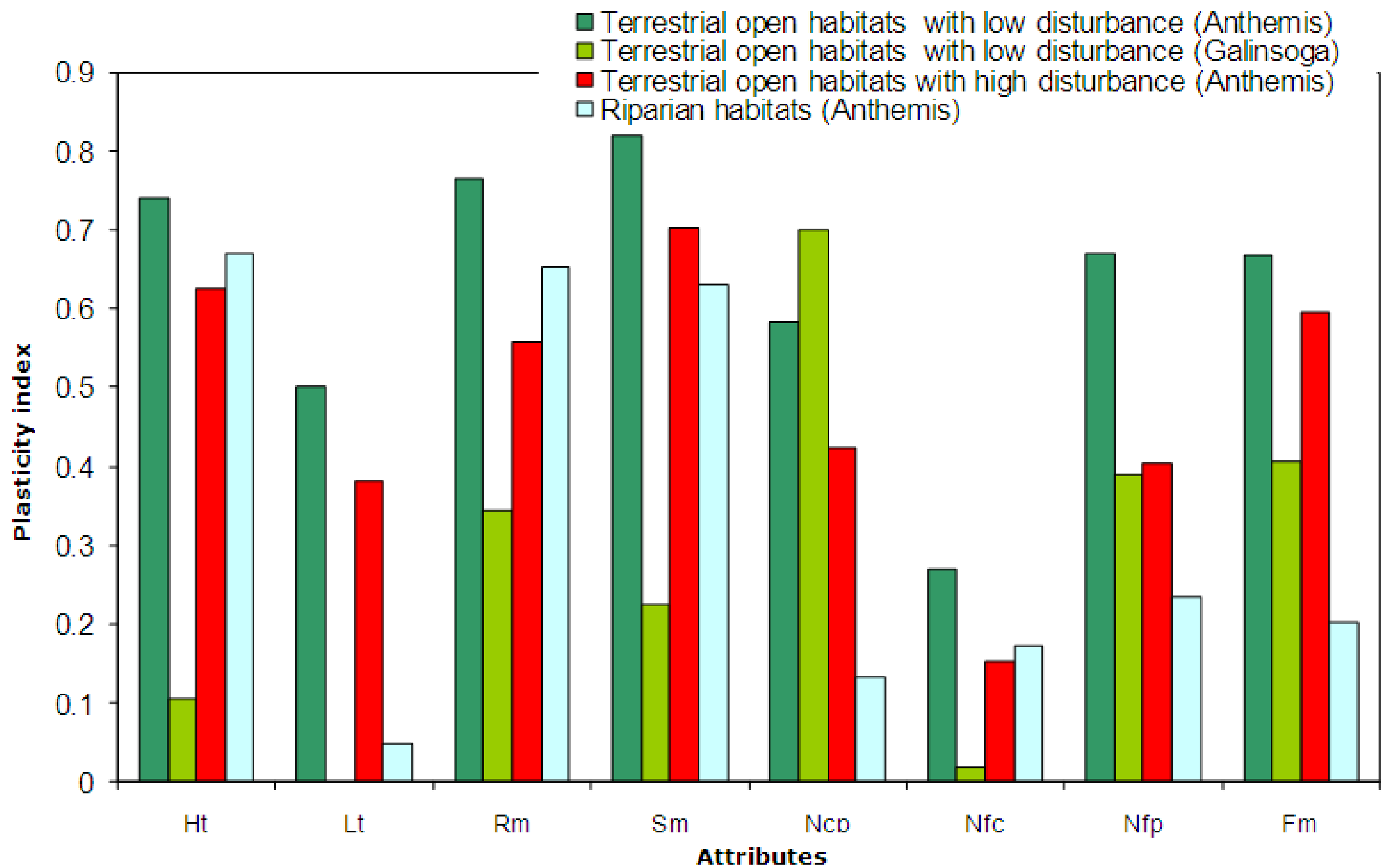


**Fig. 3. Comparison of the Plasticity Index of various traits of *Anthemis cotula* and *Galinsoga parviflora* (Ht = Stem height; Lt = Number of lateral branches; Rm = Root mass; Sm = Stem mass; Nfc = Number of disc florets per capitulum; Nfp = Number of flowers per plant; Fm = Floret mass.**

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