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Abiotic and biotic factors shape the invasion success of the alien plant species *Senecio inaequidens* (Asteraceae) in northern Italy

Lara A. Quaglini[1,*], Florencia A. Yannelli[2,3,4], Federica Fasano[1], Chiara Montagnani[1], Sarah Caronni[1], Sandra Citterio[1] and Rodolfo Gentili[1]

[1]Department of Earth and Environmental Sciences, University of Milano-Bicocca, Milan 20126, Italy,[2]Argentine Institute for Dryland Research, CONICET and Universidad Nacional de Cuyo, Mendoza 5500, Argentina,[3]Institute of Biology, Freie Universität Berlin, Berlin 14195, Germany,[4]Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin 12587, Germany

*Corresponding author: E-mail: l.quaglini@campus.unimib.it

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Abstract

Invasive alien species threaten global biodiversity and ecosystems. Understanding the context-dependency of invasion dynamics is crucial for uncovering the processes driving the establishment and spread of alien species. This study investigates how abiotic (soil characteristics) and biotic factors (resident vegetation diversity and similarity to the invader) affect the invasion success of *Senecio inaequidens* (South African ragwort) across high- and low-productivity habitats in northern Italy. Our results revealed that abiotic and biotic factors affect *S. inaequidens* success. We found evidence of biotic resistance from resident plant communities, driven mainly by diversity and cover. However, a negative relationship between *S. inaequidens* performance and both phylogenetic and functional similarity to resident species was found, indicating better performance when growing with more similar species. We additionally observed stronger resistance in more nutrient-rich environments, highlighting the context-dependent nature of such relationships. Our results suggest that *S. inaequidens* is more susceptible to competition than adverse abiotic conditions, making it as a good colonizer rather than a strong competitor. These findings emphasize the complexity of invasion dynamics and the importance of considering both biotic and abiotic factors in developing management strategies for invaded ecosystems.

Keywords: biotic resistance, diversity-invasibility hypothesis, abiotic filtering, IAPs, functional similarity, South African ragwort (*Senecio inaequidens*)

非生物与生物因子共同驱动意大利北部窄叶黄菀入侵进程

摘要：外来入侵物种严重威胁全球生物多样性和生态系统功能。加深环境因素对入侵动态影响的认识对于揭示外来物种定殖与扩散过程至关重要。本研究以意大利北部不同生境菊科(Asteraceae)入侵植物窄叶黄菀(*Senecio inaequidens*)为对象，揭示了非生物(土壤属性)与生物因子(本地植物多样性及其与入侵种的相似性)对窄叶黄菀入侵进程的影响机制。结果表明，非生物与生物因子共同驱动窄叶黄菀的入侵进程。具体而言，本地植物具有显著的生物抵抗力，这主要与其较高的多样性和盖度有关。窄叶黄菀的入侵能力与本地植物系统发育和功能相似性呈负相关，表明其在与相似物种共存时更具竞争优势。此外，养分较高的环境中本地植物生物抵抗力更强，揭示了物种间相互作用关系的环境依赖性。上述结果表明，相较于不利的环境条件，窄叶黄菀对竞争压力的响应更加敏感，其生存策略更倾向于快速定殖而非强竞争能力。本研究揭示了植物入侵动态的复杂性，并指出在制定入侵生态系统管理策略时，需同时考虑生物和非生物因素的重要性。

关键词：生物抵抗，多样性-可入侵性假说，非生物过滤，入侵植物，功能相似性，窄叶黄菀(*Senecio inaequidens*)

INTRODUCTION

Invasion by alien species is considered one of the main drivers of biodiversity loss worldwide, with well-documented economic and human health-related impacts (IPBES 2023). As the number of introduced alien taxa continues to rise steadily (Seebens *et al.* 2021), it is expected that this will pose significantly higher economic costs for their management and control, as well as ecological impacts (Gentili *et al.* 2022; Henry *et al.* 2023; Schindler *et al.* 2015). Therefore, understanding the underlying processes leading to the successful invasion of alien plants is crucial for predicting their potential spread and impacts (Carboni *et al.* 2018) and to efficiently plan habitat restoration and environmental management practices in invaded communities (El-Barougy *et al.* 2020).

Invasion is usually conceptualized as a staged process, where each stage is divided by a filter to be overcome by the invader (Blackburn *et al.* 2011). Catford *et al.* (2009) postulated that three main ecological processes play a role in determining the invasion success within native communities: (i) introduction, (ii) environmental filtering and (iii) biotic interactions between the alien and resident species. After a species is introduced into a new area, environmental conditions play a critical role in determining its suitability for establishment. Abiotic factors such as temperature, nutrient availability and water supply can act as filters, excluding species that are not adapted to the new conditions (Carboni *et al.* 2018; Skálová *et al.* 2015). If the alien plant is able to survive and reproduce under the new conditions, its invasion success will also be contingent on interactions with species in the resident communities (Carboni *et al.* 2018).

Competitive interactions can result in the biotic resistance of the resident communities (Daly *et al.* 2023; Elton 1958; Levine *et al.* 2004), limiting the establishment and/or spread of invading alien plants (Byun *et al.* 2015). Specifically, biotic resistance refers to the ability of the resident community to limit plant invasions (Levine *et al.* 2004). Environmental conditions can also influence biotic interactions at the community level modulating biotic resistance and invasion success (Byun *et al.* 2015, 2022; Holle, 2005; Kraft *et al.* 2015). In resource-rich environments, competition tends to prevail, because in such more benign conditions, resident communities tend to be more productive (Gallien and Carboni 2017). Conversely, in resource-limited environments, niche overlap and resource pre-emption can lead to strong competition, affecting the success of alien species (MacDougall *et al.* 2009), while abiotic stress or disturbance can reduce competition, facilitating alien plant establishment (Brose and Tielbörger 2005; Gallien and Carboni 2017; Grime 1973).

Several hypotheses predict community invasibility based on composition, such as the diversity-invasibility hypothesis, which links lower native diversity to higher invasibility (Elton 1958; Feng *et al.* 2019; Jeschke 2014), and the limiting similarity hypothesis, which suggests alien plants are more likely to invade communities with functionally dissimilar natives (Funk *et al.* 2008; Macarthur and Levins 1967). Similarly, Darwin's naturalization hypothesis suggests that alien plants face greater resistance from closely related native species due to shared evolutionary traits (Cahill *et al.* 2008; Daehler 2001; Sheppard *et al.* 2018). Consequently, communities composed of phylogenetically dissimilar species may be more susceptible to invasions, as they lack the shared traits that could provide resistance to invaders. Evidence for these hypotheses remains mixed, explained as the result of variability in spatial scale, invasion stage and metric used (Cleland *et al.* 2004; Ernst *et al.* 2022; Levine and D'Antonio 1999; Smith and Côté 2019). Therefore, understanding the dynamic interplay between abiotic and biotic factors, context-dependency (Catford *et al.* 2022), and how this influence the predictive power of various hypotheses in the field of invasion biology is essential to elucidate the mechanisms that drive invasions success (Zarnetske *et al.* 2013).

We explored how abiotic and biotic factors and their interactions may concomitantly influence invasion success using *Senecio inaequidens* DC. (Asteraceae), commonly called South African ragwort, as target alien species. Previous research on this species has mostly considered its distribution and invasion history (e.g. Bazzato *et al.* 2024; Ernst 1998; Vacchiano *et al.* 2013), reproductive biology (e.g. Lachmuth *et al.* 2018; Monty *et al.* 2008, 2010), and genetic aspects such as ploidy levels and their implications for morphology (e.g. Lafuma *et al.* 2003; Thébault *et al.* 2011). However, relatively few studies have addressed the ecology of this species, with most being conducted under controlled conditions (e.g. Caño *et al.* 2007; Scherber *et al.* 2003).

This study aims to shed light on the mechanisms underlying invasion success and the roles of diversity and trait similarity in shaping competitive interactions across environmental gradients, linking our findings to broader hypotheses in invasion ecology. We selected sites with high productivity, characterized by dense vegetation cover, minimal bare soil, and lower sand content and sites with low productivity, defined by sparce vegetation cover, high bare soil exposure and sandy soils. In these sites, we assessed abiotic factors, such as soil properties, alongside biotic factors, including the structure of resident plant communities, their diversity, functional and phylogenetic similarity to the invader and the performance of *S. inaequidens*. We aimed to determine how the abiotic and biotic conditions of the resident habitats contribute to the invader's success across two productivity conditions. Specifically, we hypothesized that: patterns of successful performance of *S. inaequidens* will increase in: (i) low-productivity sites, where reduced competition may facilitate its establishment, (ii) sites with decreasing diversity and/or functional or phylogenetic similarity of resident species driven by decreased competition. Furthermore, we hypothesize that (iii) the relationship between *S. inaequidens* performance and community diversity or similarity would be modulated by the abiotic context, with stronger effects in high-productivity habitats.

MATERIALS AND METHODS

Target alien species

Senecio inaequidens is a perennial chamaephyte native to South Africa. It can reach up to 100 cm in height, with hairless stems ending with yellow capitula. The fruits are small achenes with a white pappus, which favours dispersal of the seeds. A single plant can produce up to 500–600 capitula each year, resulting in a consistent number of achenes dispersed. The plant's tissues contain pyrrolizidine alkaloids as a defence mechanism against above- and belowground herbivory (Caño *et al.* 2009). Its achenes were likely introduced to Europe by the end of the 19th century as a contaminant of sheep's wool, and from 1950 onwards the species started expanding throughout Europe (Ernst 1998). It is currently invasive to Europe and Mexico (Schmidt-Lebuhn *et al.* 2022), and in Italy it's considered invasive in nearly most of the administrative regions.

Senecio inaequidens is a highly adaptable species capable of rapidly colonizing diverse environments, from lowlands to elevations up to 1900 m. In its invasive range, it thrives on both acidic and calcareous soils, despite favouring limestone substrates. It shows preference for warm and dry ruderal sites, with mostly gravelly or sandy soil, but it is opportunistic, tolerating a wide range of soil moisture conditions. Indeed, the species primarily establishes in disturbed and anthropogenic habitats such as roadsides, railways, vineyards, pastures, and abandoned areas, but also occurs in natural settings like dunes, cliffs and riverbanks. It is found under temperate and Mediterranean climates with annual rainfall between 500 and 1000 mm and temperatures ranging from −15 to 35 °C (EPPO 2006; Heger and Böhmer 2006). This species is considered one of the fastest-spreading invasive plants in Europe, especially in mountain systems as well as in Mediterranean regions, and it is likely to be favoured by the current climatic changes (Bazzato *et al.* 2024; Vacchiano *et al.* 2013).

Study area, sampling design and methods

The study was conducted during summer 2022 in the administrative region of Lombardy, in northern Italy, which is characterized by an alpine/continental climate, with annual mean temperatures and precipitations of 14 °C and 920 mm (calculated over the 1991–2020 period; https://www.arpalombardia.it). We identified different semi-natural sites invaded by *S. inaequidens* with contrasting biotic and abiotic conditions (Supplementary Fig. S1). Specifically, we selected different sampling locations in habitat patches of about 30 m × 30 m: (i) 3 characterized by high bare soil cover (>50%, visually estimated) and low vegetation cover (<50%, visually estimated), hereafter called low-productivity habitats (low_prod), and (ii) 3 characterized by low bare soil cover (<50%) and high vegetation cover (>50%), hereafter called high-productivity habitats (high_prod). Subsequently, in each habitat patches of 30 m × 30 m, we randomly sampled five 1 m × 1 m plots where the focal species was present, for a total of 30 plots.

In each plot, we collected approximately 150 g of soil to assess the nutrient content and particle-size distribution. Soil samples were collected at a depth between 5 to 30 cm in each plot, and once collected, they were air-dried and sieved with a 2 mm mesh and stored at room temperature until analyses started. Additionally, for each site in field, we visually estimated plots' bare soil cover (expressed as percentage of total cover not occupied by vegetation on the total plot area) and soil surface stoniness, expressed as percentage of rock fragments (>2 mm of diameter) on the total plot area, as the proportion of rock fragments in soils can affect water availability and the growth and physiological features of plants (Mi *et al.* 2016). To determine the structure of the plant communities, we surveyed resident species present in each plot by visually estimating their cover with the help of a gridded plot. We also evaluated *S. inaequidens* performance by measuring its percentage cover and recorded some key functional traits that are known to reflect plant ecological strategies for resource acquisition, dispersal, establishment and competitive ability (Westoby 1998): plant height (cm), specific leaf area (SLA; mm^2 mg^{-1}) and flower production (n° of capitula).

Soil analyses

Sieved soil samples were sent to the Geopedological Laboratory of the University of Milano-Bicocca to determine soil pH, available phosphorus (mg/kg), total nitrogen (%), organic carbon content (%), total carbonates (g/kg) and particle-size distribution (%). Total carbonates were assessed using a Dietrich-Fruhling calcimeter starting from 0.5 to 5 g of soil. Total carbon and nitrogen were measured using a CN elemental analyser (Flash EA 1112 NC Soil, Thermo Fisher Scientific, Pittsburgh, USA). Organic carbon was then calculated as the difference between total carbon and total carbonates. Available phosphorus was extracted using sodium bicarbonate. Soil particle-size distribution was additionally determined by sieving and sedimentation.

Functional metrics

Plant height of *S. inaequidens* individuals was measured in the field as the shortest distance between the upper boundary of the main photosynthetic tissue (excluding inflorescences) and the ground level (Pérez-Harguindeguy *et al.* 2013). Flower production (i.e. reproductive output) was recorded in the field counting the number of capitula (n° of capitula) per individual and considering buds, blooming heads and drying heads (Caño *et al.* 2007). For determining SLA (i.e. the ratio of fresh leaf area to leaf dry mass, mm^2 mg^{-1}), we collected three fresh leaves from the mid-stem of a single *S. inaequidens* individual of each plot and stored them in paper envelopes. In the laboratory, SLA was estimated by photographing each leaf collected, then subsequently drying them out at 80 °C till constant weight to be dry-weighted (Pérez-Harguindeguy *et al.* 2013). The area was calculated using the image analyses software ImageJ version 1.53 (Abràmoff *et al.* 2004), and SLA was then calculated dividing the leaf area (mm^2) by its dry weight (mg). SLA values for each individual of a plot were obtained by averaging SLA of the three leaves.

To assess the functional structure of the invaded communities, we adopted the LHS (leaf-height-seed) scheme proposed by Westoby (1998), which captures the diversity of plant ecological strategies related to resource acquisition, dispersal, establishment, and competitive ability. We thus selected the functional traits canopy height (cm), SLA (mm^{2}mg^{-1}) and seed weight (mg) to characterize resident plant communities. Trait data for the species in our plots were sourced from databases including LEDA (Kleyer *et al.* 2008), BiolFlor (Kühn *et al.* 2004), the trait database published by Cerabolini *et al.* (2010), and the Seed Information Database (Liu *et al.* 2019). Rare species (accounting for <5% for the mean total plot cover in each site, i.e. *Anisantha rigida* (Roth) Hyl., *Festuca geniculata* (L.) Lag. & Rodr., *Carex liparocarpos*

Gaudin, *Ostrya carpinifolia* Scop.) were excluded due to unavailable trait data information. Prior to further statistical analyses, all trait measures were scaled by subtracting each value by its mean and dividing it by its standard deviation.

Using the trait information, we calculated the distance matrix between pair of species, and we determined the functional distance of the invaded communities from *S. inaequidens* by calculating the Community Weighted Mean Functional Distance (CWMFD; Thuiller *et al.* 2010), that is the mean distance between the target species (*S. inaequidens*) and the species of the resident communities weighted by their cover. Functional diversity was assessed using the metrics functional richness (FRic), functional dispersion (FDis), functional evenness (FEve) and functional divergence (FDiv), which capture different aspect of functional diversity. Specifically, FRic reflects traits and potential ecological roles within a community, FDis the functional trait space occupied, reflecting trait distribution relative to the community centroid, FEve measures the regularity of species distribution within this space, and FDiv quantifies abundance clustering at trait space (El-Barougy *et al.* 2021; Swenson 2014; Villéger *et al.* 2008). These metrics were calculated with the dbFD() function of the R package "*FD*" (Laliberté *et al.* 2014).

Phylogenetic metrics

To calculate phylogenetic distances among species, including *S. inaequidens*, we built a phylogenetic tree comprising the 118 species found in our sampling sites. With the R package 'pez' (Pearse *et al.* 2015), we used a phylogenetic tree of all angiosperms as a backbone (Zanne *et al.* 2014) and removed all species that were not found in our sites (see Supplementary Fig. S2). We used the tree branch lengths to calculate phylogenetic distances in a matrix between pairs of species. From this matrix, we calculated the community-weighted mean phylogenetic distance (CWMPD), which is the mean distance between the target species (in this case, *S. inaequidens*) and the species of the resident communities (Thuiller *et al.* 2010), weighted by their cover.

To estimate phylogenetic diversity of resident plant communities, we calculated Faith's phylogenetic diversity (FaithPD) using the pd() function of the R package "*picante*" (Kembel *et al.* 2010). Generally, higher PD values indicate communities that have more evolutionary divergent taxa and older history, while lower PD values are typical of assemblages that have taxa with more recent evolutionary history (El-Barougy *et al.* 2021; Faith 1992; Swenson 2014).

Statistical analyses

We preliminary assess the differences in the abiotic and biotic variables between high-productivity (high_prod) and low-productivity (low_prod) habitats using the Mann–Whitney U test. We performed a correlation analysis to select the variables for further analyses and removed the ones that were highly correlated (one from each couple, Spearman's correlation index >0.75; Gentili *et al.* 2020). A final set of 15 variables was used to analyse the relationships between *S. inaequidens* performance and the abiotic and biotic conditions of the resident environment using generalized linear mixed models (GLMMs; glmmTMB() function of the R package "*glmmTMB*"; Supplementary Table S2). We first built univariate models with the following structure: (i) *S. inaequidens* performance metrics (cover, canopy height, SLA and number of capitula) as response variable; (ii) abiotic factors (habitat, i.e. high_prod and low_prod), surface stoniness, soil total nitrogen, available phosphorus, sand fraction and biotic variables (proportion of alien species, total resident species richness and cover (both excluding *S. inaequidens*), CWMPD, CWMFD, Faith PD, FRic, FDis, FEve, FDiv) as fixed factors and (iii) site nested within habitat as a random factor. Maintaining the same nested design, we then built multivariate models, in which we considered as fixed effects the two-way interaction between those biotic variables which, in univariate GLMMs, significantly affected *S. inaequidens* performance and abiotic variables, to assess whether the direction and strength of these relationships varied with the abiotic context. To model *S. inaequidens* cover, we used beta distribution, for the n° of capitula we used negative binomial distribution, while for height and SLA, we used Gaussian distribution. All statistical analyses were performed within the R environment v. 4.3.0 (R Core Team 2023).

RESULTS

Habitat characterization

Abiotic and biotic factors generally exhibited significant variation between high- and low-productivity habitats in the sampled plots (Fig. 1; Supplementary Tables S3 and S4). Low-productivity habitats were characterized by the harshest abiotic conditions for plant growth, with high percentage of

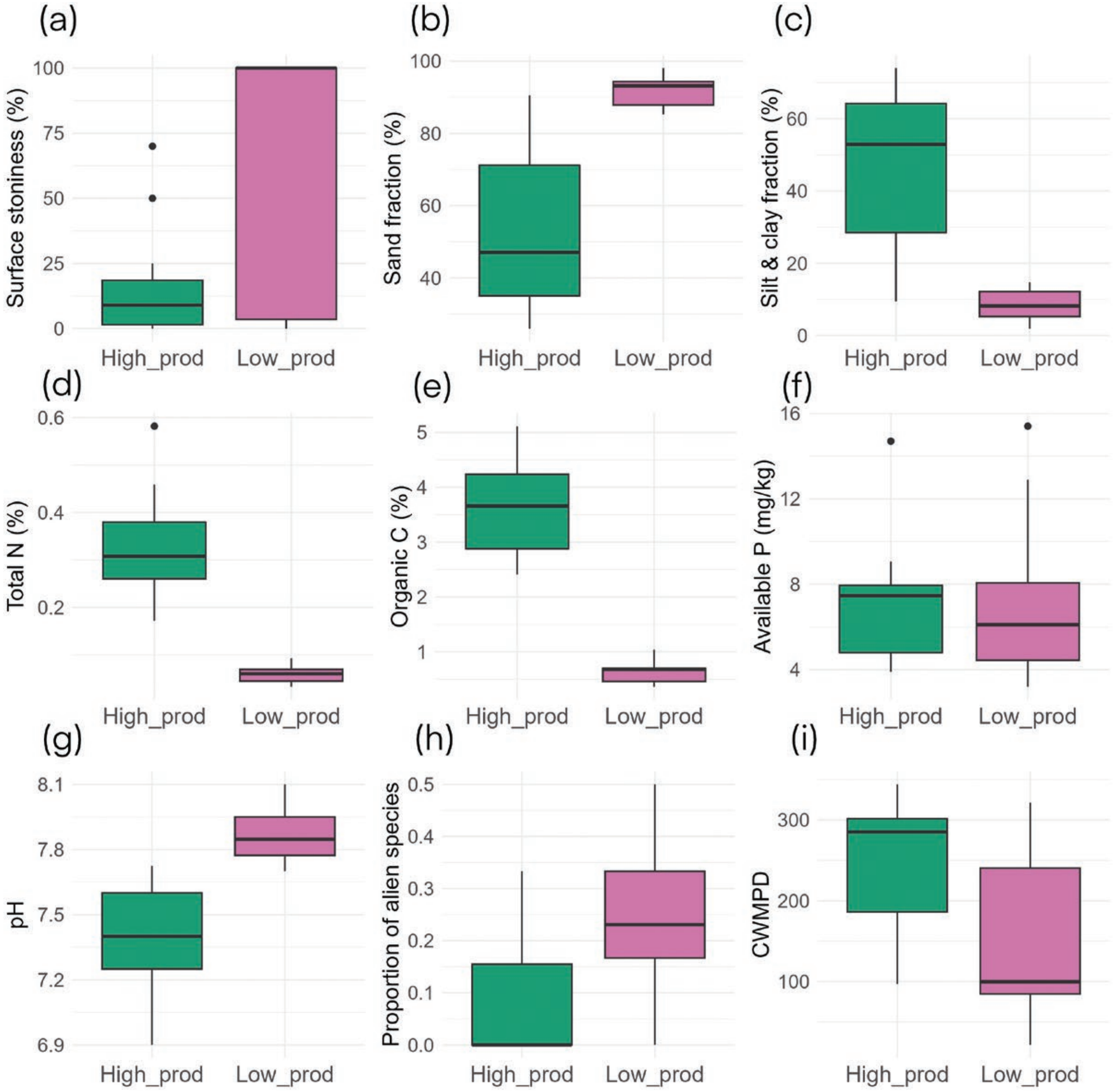

Figure 1: Differences in abiotic and biotic variables between high-productivity (green boxes) and three low-productivity (pink boxes) habitats. All variables were measured in each of the 5 plots sampled in each site. Starting from the top-left to the bottom-right, the boxplots show (a) the percentage of surface stoniness, (b) soil and sand fraction (%), (c) soil silt & clay fraction (%), (d) soil total nitrogen (%), (e) soil organic carbon (%), (f) soil available phosphorus (mg/kg), (g) soil pH, (h) proportion of alien species (other than *Senecio inaequidens*), (i) and the CWMPD.

bare soil cover (56 ± 27.7%), a predominant sandy texture (Mann–Whitney *U*-test between low- and high-productivity habitats: 91.8 ± 4.2%; W = 218, $P < 0.001$), higher surface stoniness (66.6 ± 47.7%; W = 169, $P = 0.0196$), and the absence of a well-developed soil (Fig. 1; Supplementary Tables S3 and S4), compared to high-productivity sites (bare soil: 12.3 ± 10.9%, sand: 53.9 ± 22%, surface stoniness: 15 ± 20%). Soils in low-productivity habitats were also nutrient-poor, with lower levels of total nitrogen, organic carbon and slightly lower concentrations of available phosphorus and higher soil pH compared to high-productivity sites (Supplementary Table S3; total nitrogen: W = 0, $P < 0.001$; 0.06 ± 0.017% *vs.* 0.33 ± 0.1%; organic carbon: W = 0, $P < 0.001$; 0.63 ± 0.2% *vs.* 3.66 ± 0.8%; available phosphorus: W = 94.5, $P = 0.47$; pH: W = 222, $P < 0.001$). High-productivity habitats had significantly higher content of soil silt and clay (W = 6, $P < 0.001$).

Most of the vegetation surveyed in the plots was herbaceous and accounted for a mean value of 57.53 (± 31.1)% of the total plots, while the trees and shrubs layers together only accounted for an average of 0.86 (± 2.6)%. In the two types of habitats, species richness, phylogenetic and functional diversity did not differ (Supplementary Table S4), except for

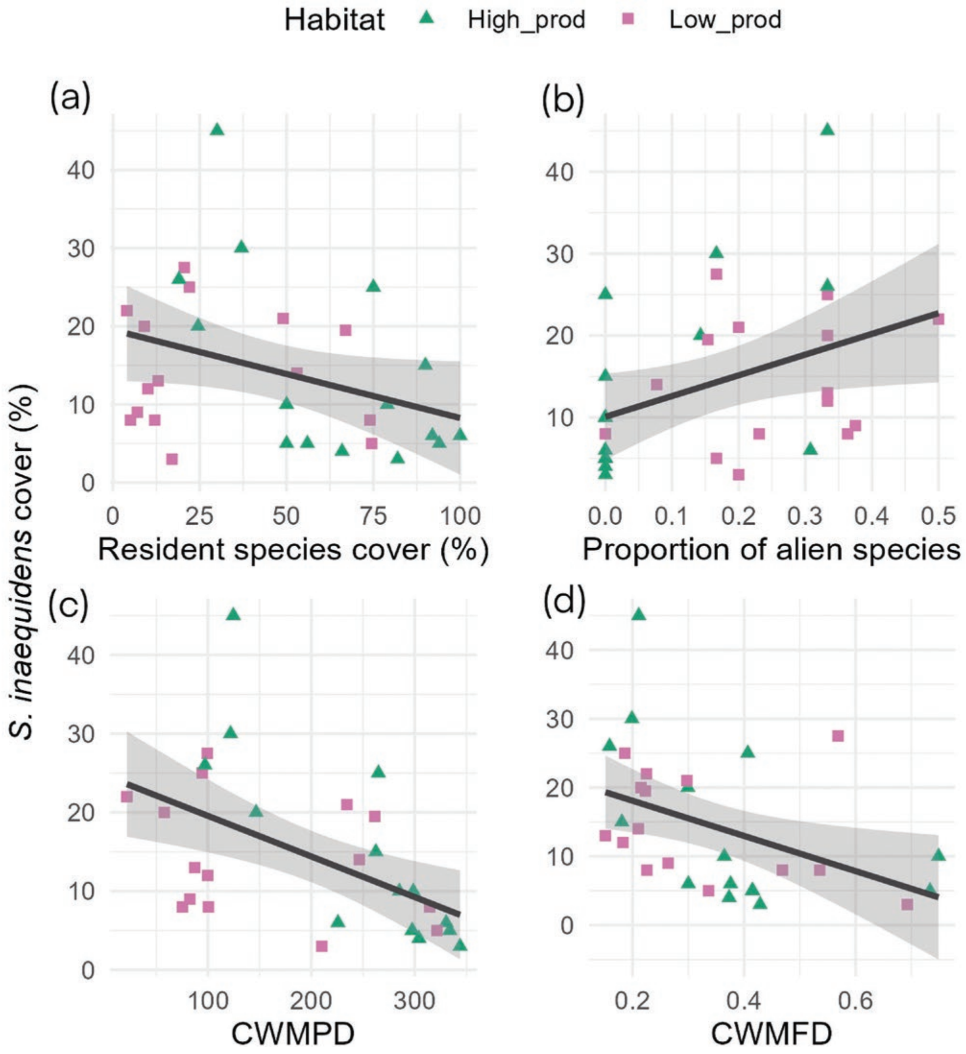

Figure 2: Results of GLMMs for *Senecio inaequidens* cover. The panel displays the significant relationships found with GLMMs between *Senecio inaequidens* cover and (a) resident species cover (other than *S. inaequidens*; $P = 0.036$), (b) alien species cover (other than *S. inaequidens*; $P = 0.02$), (c) CWMPD ($P = 0.022$) and (d) CWMFD ($P = 0.0099$). Green triangles represent high-productivity habitats, pink squares represent low-productivity habitats. In the models, we accounted for site identity nested into habitat as random factor. The cover of *S. inaequidens* was modelled assuming a beta distribution.

functional divergence (FDiv), which had higher values in low- compared to high-productivity habitats (W = 59, $P = 0.02$). Moreover, low-productivity habitats hosted a significantly higher proportion of alien species, and these sites were characterized by species more phylogenetically similar to *S. inaequidens* (i.e. lower values of CWMPD), compared to high-productivity habitats (Fig. 1; Supplementary Tables S3 and S4).

Influence of abiotic and biotic variables on *Senecio inaequidens* performance

Univariate GLMMs revealed that both abiotic and biotic factors influenced the performance of the target alien species (Figs 2–4; Supplementary Table S5). Soil nutrient levels such as total nitrogen content and particle-size distribution had marginal explanatory effect on the abundance and the functional traits of *S. inaequidens*. Mainly, the cover of the target alien increased in conditions of higher sand content in soil (GLMMS: $P = 0.038$; Supplementary Table S5). Slight increased levels of SLA ($P = 0.047$) and lower floral production of *S. inaequidens* ($P = 0.003$) was associated with soil total nitrogen content. Moreover, *S. inaequidens* showed and increased floral production in low-productivity sites in condition of higher surface stoniness ($P < 0.001$ and $P = 0.002$, respectively; Fig. 3).

The target species' cover, floral production and height were influenced by biotic variables, while SLA was not affected (Supplementary Table S5).

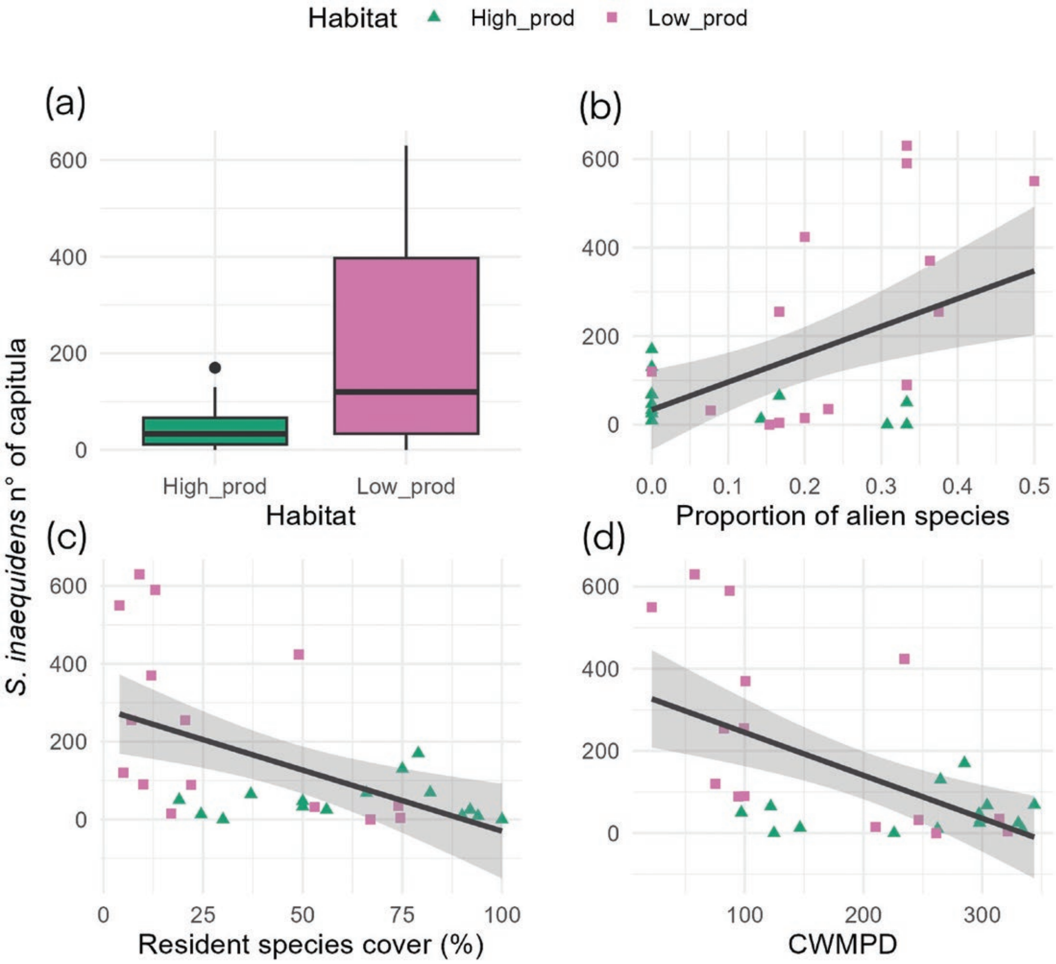

Figure 3: Results of GLMMs for *Senecio inaequidens* floral production. The panel displays the significant relationships found with GLMMs between *S. inaequidens* n° of capitula and (a) habitat type (low-productivity *vs.* high-productivity; $P < 0.001$), (b) proportion of alien species (other than *S. inaequidens*; $P = 0.007$), (c) resident species cover (other than *S. inaequidens*; $P < 0.001$), and (d) CWMPD ($P < 0.001$). Green triangles represent high-productivity habitats, pink squares represent low-productivity habitats. In the models, we accounted for site identity nested into habitat as random factor. The n° of capitula of *S. inaequidens* was modelled assuming a negative binomial distribution.

Cover and height exhibited a negative relationship with plant community diversity, such as species richness ($P = 0.08$, for cover (near significance); $P = 0.02$ for height; Fig. 4) and, marginally, phylogenetic diversity ($P = 0.052$ for cover (near significance); $P = 0.05$ for height; Fig. 4). However, *S. inaequidens* cover and all functional traits measured were not affected by the functional diversity measures considered (Supplementary Table S5). Our data also revealed a negative association between *S. inaequidens* performance and total cover of the resident plant species ($P = 0.036$ for cover, $P < 0.001$ for flower production; Figs 2 and 3), and a positive with the proportion of other alien species in the plots ($P = 0.021$ for cover; $P = 0.007$ for flower production; Figs 2 and 3).

In terms of similarity patterns between *S. inaequidens* and the resident plant communities, we found the target alien species cover and floral production to have a negative relationship with the weighted mean phylogenetic distance (CWMPD) to the resident communities ($P = 0.02$ and $P < 0.001$, respectively; Figs 2 and 3). A similar trend was also found for the functional distance (CWMFD), albeit with no effect on flower production (Supplementary Table S5; $P = 0.0099$).

When analysing the two-way interactions between significant biotic variables and abiotic ones, most of the interactions were non-significant (Supplementary Table S6). Nonetheless, our data showed a significant interaction between habitat type (high-productivity *vs.* low-productivity) and phylogenetic distance (CWMPD) when modelled with both *S. inaequidens* cover and floral production (CWMPD*habitat: $P = 0.004$ for cover, $P = 0.022$ for flowers; Fig. 5;

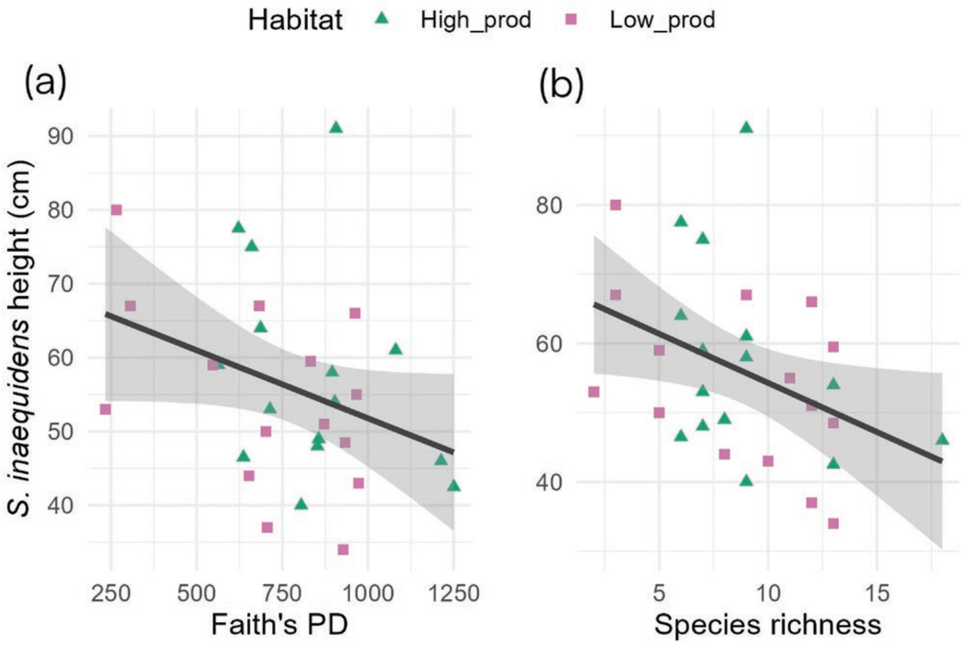

Figure 4: Results of GLMMs for *Senecio inaequidens* height. The panel displays the significant relationships found with GLMMs between *S. inaequidens* height and (a) FaithPD ($P = 0.05$) and (b) species richness ($P = 0.02$). Green triangles represent high-productivity habitats, pink squares represent low-productivity habitats. In the models, we accounted for site identity nested into habitat as random factor. *S. inaequidens* height was modelled assuming a Gaussian distribution.

Supplementary Table S6). This interaction indicated that the effect of phylogenetic distance on *S. inaequidens* cover varied between habitats, with greater changes observed in high-productivity habitats for cover and in low-productivity habitats for flower production. Additionally, we found a significant interaction effect between sand content and CWMPD (sand*CMWPD: $P = 0.02$), revealing a more negative relationship between CWMPD and cover with lower sand content. Lastly, the relationship between *S. inaequidens*' cover and species richness in the resident community varied with phosphorus concentration in the soil (species richness*phosphorus: $P = 0.0092$), with a more negative relationship in conditions of higher phosphorus content in soil (Fig. 5).

DISCUSSION

Our results highlighted that the overall performance of *S. inaequidens* is influenced by the significant variation between high- and low-productivity habitats in terms of abiotic and biotic factors. *S. inaequidens* showed increased cover in sandy soils, and increased floral production was observed in low-productivity sites with higher surface stoniness. Such results support the idea that reduced vegetation cover and higher stoniness may facilitate invasion by providing open spaces for establishment, while limiting competition from resident vegetation. More broadly, the species' ability to perform well under such harsh abiotic conditions (e.g. high surface stoniness, low nutrient content) reinforces its capacity to colonize and persist in disturbed, low-productivity environments (Delory *et al.* 2019; Garcia-Serrano *et al.* 2009). In these stressful environments, individual plants likely amplify their reproductive efforts to enhance their chances of successful establishment, compensating for the challenges posed by limited resources and reduced vegetative growth opportunities.

High-productivity sites, on the other hand, generally showed lower cover values of *S. inaequidens*, which might be suggestive of the effect of a more competitive environment (Damgaard 2011). A previous study observed introduced populations of *S. inaequidens* to respond to increased soil nutrient availability (i.e. nitrogen, potassium and phosphorus) by increasing its biomass (Bossdorf *et al.* 2008). In contrast, our results suggest that this species thrives in low-productivity sites with higher surface stoniness, where it exhibits increased floral production. These seemingly contrasting results highlight the species' plasticity, adjusting growth and reproductive strategies to accommodate diverse soil characteristics and resource availabilities; in resource-poor environments, the species may invest more in reproduction as a strategy to ensure

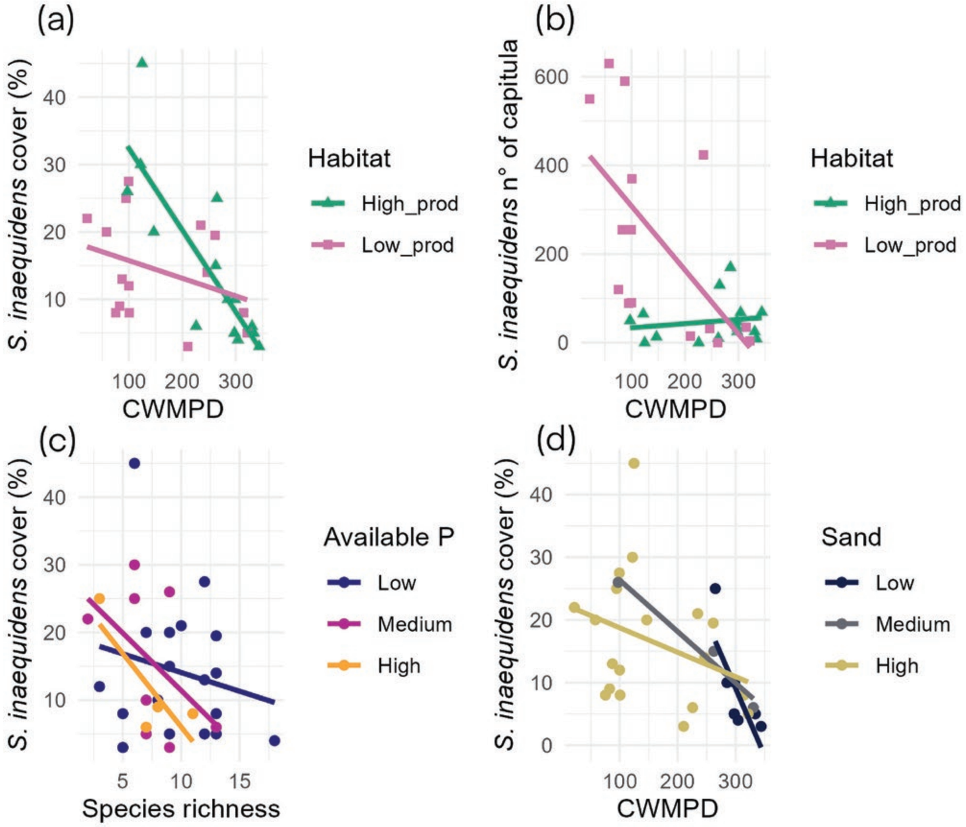

Figure 5: Two-way interactions between abiotic and biotic variables. The panel displays results from multivariate GLMMs showing statistically significant two-way interactions, with site identity nested within habitat as a random factor. We found that the CWMPD interacted significantly with habitat type in the models for both (a) *Senecio inaequidens* cover (CWMPD*habitat: $P = 0.004$) and (b) the number of capitula (CWMPD*habitat: $P = 0.022$). Moreover, we found a statistically significant interaction between (c) species richness and available soil phosphorus (species richness*phosphorus: $P = 0.0092$), and (d) CWMPD and soil sand content (CWMPD*sand: $P = 0.02$) in the model for *S. inaequidens* cover.

establishment. This aligns with previous studies demonstrating the species' ability to thrive across a broad range of environmental conditions, including varying soil types, moisture levels and temperature extremes (EPPO 2006). However, in its invasive range is known to frequently establish in habitats with gravelly or sandy soils and minimal competitive pressure (Heger and Böhmer 2006).

In low-productivity habitats, where functional divergence was higher, the species performed better, suggesting that more divergent communities may be less competitive and allow easier establishment for the invader. *S. inaequidens* is a well-documented early successional ruderal species that requires open spaces with low competitive pressure for successful establishment (Delory *et al.* 2019). It has difficulties in establishing if native vegetation already exhibits significant cover in a site, which explains its prevalence in stressed and disturbed sites, where competition with other plant species is minimal (Delory *et al.* 2019; Heger and Bohmer 2005). The increased abundance of other alien species in low-productivity sites further supports the idea that such environments provide open niches that facilitate the establishment of arriving alien species.

Senecio inaequidens performance was not affected by any measure of functional diversity, which could be explained by the fact that we only considered a limited number of traits that might not have been relevant for assessing functional diversity of the sampled communities (Ernst *et al.* 2022; Funk *et al.* 2017). Although no clear pattern emerged between *S. inaequidens* performance and functional diversity, its performance was negatively correlated with species richness and, to a lesser extent, with phylogenetic diversity. These findings align with the diversity-invasibility hypothesis, suggesting that communities with higher diversity may be more resistant to invasion. High diversity is thought to intensify competition, reducing resource availability for invaders and potentially limiting the establishment of alien species (Byun *et al.* 2015; Lindig-Cisneros and Zedler 2002). Our data also revealed that such negative relationship was steeper at higher levels of soil phosphorus content, indicating that higher nutrient concentrations can lead to stronger competitive effects of the resident community. A similar finding was reported by Byun *et al.* (2022), who observed in a pot experiment that soil nutrient levels did not directly impact the performance of the invasive *Sicyos angulatus* L. but indirectly affected biotic resistance through the competing native species performance. The lack of consistency between functional and phylogenetic similarity could be explained by the limited number of traits considered, which may not have fully captured the ecological niches of the species (Ernst *et al.* 2022; Funk *et al.* 2017).

Contrary to our expectations, we found no support for Darwin's naturalization and limiting similarity hypotheses. On the contrary, we observed a negative relationship between the target species' performance and communities' phylogenetic/functional distance to *S. inaequidens*. Moreover, communities in low-productivity sites were more phylogenetically similar to *S. inaequidens* (based on CWMPD). One possible explanation for these results is that in low-productivity environments competition might be weaker, allowing species with similar traits to co-exist without strong exclusionary pressures. This aligns with the pre-adaptation hypothesis, which suggests that invaders with traits suited to the prevailing environmental conditions can establish more easily in communities with functionally or phylogenetically similar species (Ma *et al.* 2016; Ricciardi and Mottiar 2006). Additionally, in low-productivity habitats, the primary constraint on plant growth may be abiotic stress rather than biotic interactions, meaning that competition is not the dominant driver of community composition. In such contexts, co-occurring species may share adaptations that enable survival under resource-limited conditions, leading to co-existence rather than competitive exclusion (Bertness and Callaway 1994; Brooker and Callaghan 1998).

Both pre-adaptation and Darwin's naturalization/limiting similarity are co-existing hypotheses that have been posed to be contextually modulated by the relative importance of habitat filtering and competitive interactions (Diez *et al.* 2008; Fan *et al.* 2023; Thuiller *et al.* 2010). For instance, a recent study found a negative effect of phylogenetic similarity on invader cover in plots experiencing resource scarcity, with the effect varying depending on the functional groups considered and influenced by light and water availability (Wang *et al.* 2024). In line with these findings, our results revealed that the relationship between *S. inaequidens* cover and phylogenetic distance was stronger in high-productivity habitats, while floral production showed a more negative relationship with phylogenetic distance in low-productivity habitats.

Overall, our findings suggest that while *S. inaequidens* benefits from low-competition environments in harsh, low-productivity habitats, its establishment is influenced by both community diversity and similarity, with stronger biotic resistance observed in more productive and nutrient-rich sites. Other studies have similarly highlighted how biotic interactions can vary depending on the abiotic context. For example, El-Barougy *et al.* (2020) found that alien plants co-existed with functionally dissimilar natives in favourable conditions due to divergent resource-use strategies, while in harsher environments, both aliens and natives were functionally similar, sharing analogous responses to resource limitations. Similarly, Fried *et al.* (2018) observed that the invasive *Humulus japonicus* Siebold & Zucc. outperformed a native species in resource-rich conditions but lost its advantage under resource scarcity. These findings reflect the complexity of invasion dynamics, suggesting that the interplay between abiotic conditions and biotic factors can significantly influence the success of invasive species. Finally, given the observational nature of this study, it is not possible to exclude that the patterns found could have been modulated by other factors not considered in this study (e.g. herbivory, nutrient competition, microclimatic changes, etc.). Future experimental studies could help clarify the causal mechanisms underlying these relationships.

CONCLUSIONS

Our study provides valuable insights into the drivers of invasion success for *S. inaequidens*, highlighting the importance of considering both abiotic and biotic contexts to understand the context-dependent nature of its invasion patterns observed in the field. We found this species to perform better in low-productivity, disturbed habitats with low competition, which also created favourable habitats for other alien plant species. In contrast, high-productivity habitats with denser plant communities seemed to be more resistant to *S. inaequidens*, inhibiting its performance. We also found that the relationship between this invader's performance and community similarity varied with soil nutrient levels, with stronger competitive effects observed at higher nutrient concentrations. These findings reinforce the notion that *S. inaequidens* is more of a colonizer than a strong competitor, and in stressed or ruderal environments, functional similarity may give the species an advantage in invasion.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Figure S1: Sampling locations. Sampling occurred in Lombardy, northern Italy.

Figure S2: Phylogenetic tree of the species sampled in all sites, including the target alien *Senecio inaequidens*.

Table S1: List of low-productivity and high-productivity sites selected for the field sampling.

Table S2: Abiotic and biotic variables included in the GLMMs.

Table S3: Abiotic and biotic characteristics of the two different habitats considered (high-productivity and low-productivity).

Table S4: Results of the Wilcoxon rank-sum test.

Table S5: Results of GLMMs testing the significance of the selected explanatory variables on *S. inaequidens* performance (cover, n° of capitula, height and SLA).

Table S6: Results of multivariate GLMMs testing the significance of the 2-way interaction between the significant (from univariate GLMMs) biotic variables and all the abiotic factors, on *S. inaequidens* performance ((a) cover, (b) n° of capitula, (c) height).

Authors' Contributions

Lara Assunta Quaglini (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Writing—original draft, Writing—review & editing), Florencia Yannelli (Conceptualization, Formal analysis, Supervision, Validation, Writing—original draft, Writing—review & editing), Federica Fasano (Formal analysis, Investigation, Methodology, Writing—review & editing), Chiara Montagnani (Methodology, Supervision, Validation, Writing—review & editing), Sarah Caronni (Methodology, Software, Supervision, Writing—review & editing), Sandra Citterio (Resources, Supervision, Validation, Writing—review & editing), and Rodolfo Gentili (Conceptualization, Formal analysis, Methodology, Project administration, Resources, Supervision, Validation, Writing—original draft, Writing—review & editing)

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