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Staying alive on an active volcano: 80 years population dynamics of *Cytisus aeolicus* (Fabaceae) from Stromboli (Aeolian Islands, Italy)

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Abstract

Cytisus aeolicus is a narrow endemic species restricted to the Aeolian archipelago (SE Tyrrhenian Sea, Italy) and it is one of the most evolutionarily isolated plants in the Mediterranean flora. Historical and literature data suggest that both metapopulations and isolated individuals of *C. aeolicus* are gradually shrinking. Field investigations and drone images demonstrate that the *C. aeolicus* metapopulation from Stromboli experienced a strikingly fast increase during the last decades. As of 2019, more than 7000 ± 3000 mature individuals occur on Stromboli, i.e. 14 to 20 times more than those counted during the last census, 25 years ago. The diachronic analysis of aerial photos concerning last 80 years and the analysis of the growth rings of some selected plants pointed out that the surface occupied, the demographic structure and the distribution pattern of the subpopulations of Stromboli has been highly fluctuating during last decades. Moreover, data issuing from field observations in permanent plots placed in a transect between two isolated mature individuals showed that, under natural conditions, the germination rate of the seedlings of *C. aeolicus* can be very high and their establishment rate may exceed 40%. By contrast, seedlings mortality is subject to strong annual fluctuations. Additionally, the pollen morphology of the Strombolian metapopulation of this rare and isolated species is studied here for the first time. Contrary to what is stated in recent literature, the *C. aeolicus* metapopulation from Stromboli is healthy and very dynamic, albeit frequently damaged by the volcanic activity. Regular and repeated field surveys carried out during 3 years (2017–2019) allowed improving our knowledge on the life cycle of *C. aeolicus* and a new extinction risk assessment of the species, according to IUCN criteria, is presented.

Keywords: Conservation, Endemic species, Pollen morphology, Germination rate, Growth rate, IUCN risk assessment

Background

Oceanic islands are well-known refugia for relict lineages (e.g. Habel et al. 2010) and for the diversification and maintenance of biodiversity (Simberloff 1970; Stuessy and Ono 1998; Kier et al. 2009; Médail 2017; Whittaker et al. 2017). Endemic taxa on these islands may have originated from adaptive divergence or surviving extinction events

that eliminate mainland populations (Quammen 2004). The latter is the case of palaeoendemic species, which represent a major life-history trait and may provide crucial information about ecological history (Silvertown 2004; Kueffer and Fernández-Palacios 2010; Warren et al. 2015), phylogenetic patterns (Veron et al. 2019) and evolutionary niche conservatism (Cronk 1997; Losos and Ricklefs 2009, 2010). Hence, studying the population dynamics of palaeoendemic species exclusive to oceanic insular ecosystems is a priority for both nature conservation and

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scientific research (Kueffer et al. 2004; Whittaker et al. 2005; Whittaker and Fernández-Palacios 2007).

On this purpose, Aeolian Islands represent a special place for biogeographers and conservation scientists; besides being located in the Tyrrhenian area, one of the world's plant biodiversity hotspots (Myers et al. 2000; Thompson 2020), they represent the only active oceanic archipelago in the Mediterranean Sea. Considering the relative young age (approx. 0.7 million years: Lucchi et al. 2013), the Aeolian archipelago hosts an unexpectedly rich vascular flora and several taxa of high interest from both the biogeographic and conservation perspective (Pasta et al. 2019).

Cytisus aeolicus (Fabaceae) is an evergreen arborescent species endemic to the Aeolian Islands. Considering its numerous distinctive traits and its remarkable genetic distance from the nearest relatives, Cristofolini and Troia (2006) put it into the monotypic section *Dendrocytisus*. The known metapopulations (henceforth, m-pops) are characterised by a very low genetic variability, in spite of the largely prevailing allogamy (Conte et al. 1998).

Many questions about the origin of *C. aeolicus* are still unanswered: this species probably evolved elsewhere in the Central Mediterranean Region, long before the emersion of the volcanic archipelago, which became subsequently its single refugial area (Troia 2012; Guarino and Pasta 2018).

The occurrence of *C. aeolicus* on the Aeolian Islands is known since millennia: in fact, the species was described by the Greek botanist Theophrastus already in the fourth century BCE (Troia and Cristofolini 1998). More recently, the species was 'rediscovered' on the islands of Stromboli and Vulcano during spring 1828 (Gussone 1834). Few decades after, *C. aeolicus* was also observed growing at Lipari (Prestandrea and Calcara 1853), but this m-pop probably went extinct already by the end of the nineteenth century (Lojacono-Pojero 1878). Some vernacular toponyms reported on ancient maps (Habsburg Lothringen 1896) suggested the occurrence of *C. aeolicus* also on Alicudi, where in fact it was found with a small population, estimated in ca. 30 individuals by Pasta and Lo Cascio (2002).

C. aeolicus is a markedly pioneer species, adapted to colonise steep slopes between 350 and 600 m a.s.l., subject to intense and frequent natural disturbance (rock-falls, accumulation of volcanic ashes, frequent winds, etc.). Its establishment is facilitated by the symbiosis with arbuscular mycorrhizae and bacteria (Cardinale et al. 2008), some of which were thought to have a predominantly tropical distribution (Troia et al. 2005).

This species experienced a very strong rarefaction during the past centuries, when its wood represented a precious and rare resource and most of the islands were covered with dry stone terraced cultivations (Moreno

1995). *C. aeolicus* is listed under the Appendix 1 of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention 1979) and as a priority species on Annex II of the 92/43 EU Directive. Moreover, it is included in all the national and regional red lists (Conti et al. 1997; Raimondo et al. 2011; Rossi et al. 2013; Orsenigo et al. 2018). The last risk assessment (Troia and Domina 2017) states that the whole population of *C. aeolicus* counts less than 1000 individuals and is severely fragmented; moreover, its current extent of occurrence (EOO) is below 1488 km², whilst its area of occupancy (AOO) is about 12 km². *C. aeolicus* is classified as EN (endangered) and matches the criteria B1ab(iii,v) + 2ab(iii,v) and C2a(i) of the risk assessment guidelines proposed by IUCN Standards and Petitions Committee (2019).

Many factors have been invoked to explain the rarity, the uneven distribution and the recent rarefaction of *C. aeolicus* (Troia and Domina 2017), such as: (1) small population size, low number of reproductive individuals and low reproductive fitness (Cristofolini and Troia 2006), (2) low genetic diversity, which involves low ecological adaptability and high vulnerability to natural catastrophes and diseases (Conte et al. 1998), (3) low ability to tolerate (and to recover from) abiotic stress factors or natural and anthropogenic disturbances, (4) habitat degradation due to human-set fires (Troia et al. 2005), (5) natural vegetation dynamics, triggered by land-use change, favouring more competitive species, (6) natural disasters (eruptions, acid rains and wildfires) connected with volcanic activity (Stromboli), rockfalls and landslips (all the sites), (7) extreme climatic events and/or diseases caused by microorganisms (Lo Cascio 2004).

In contrast with this shrinking trend scenario, a sharp increase in the area of occupancy of the main population of *C. aeolicus*, located on Stromboli Island, was noticed in the last 20 years. Hence, we decided to carry out a field research to address the following research questions:

- What is the current size of the population of *C. aeolicus* from Stromboli?
- What are the ecological conditions and the age distribution pattern of this population?
- How far can we reconstruct the extent of its demographic fluctuations in the past?
- Could the studied population be affected by a low reproductive fitness and/or by the competition with other species?

Methods

Study area

The Aeolian Islands form a volcanic archipelago in the Tyrrhenian Sea north of Sicily, consisting of seven major islands and over twenty minor islands and rocks (Lo

Cascio and Pasta, *in press*). Stromboli is the north-easternmost of the Aeolian Islands and hosts far the largest m-pop of *C. aeolicus* in the whole Archipelago (Pasta and Lo Cascio 2002). It occurs on an area of approximately 1.2 km² on the eastern slopes of the volcano, at 350–650 m a.s.l., in places named Guardiani, Portedduzza, Rina Grande and Schicciolo (Fig. 1). These consist of a complex of differently sloping sites, formed by three small sandy watersheds, interdigitated with ridges formed by the overlapping of lavas and pyroclastites (Francalanci et al. 2013). The whole area is highly unstable, scattered with uneven-sized rocky fragments, frequently displaced by wind, by feral goats (*Capra hircus* L.) or by the tremors generated by major eruptive events. Based on the morphology of the terrain, the m-pop of *C. aeolicus* from Stromboli has been split into the following eight s-pops (Fig. 1): two at the mouth of the Portedduzza (PT) and Schicciolo

(SC) ravines, three on steep and exposed rocky ridges (from north to south: B, SS, PV), three on less sloping and more sandy sites (from north to south: A, PS, VB).

On the whole, the m-pop of *C. aeolicus* from Stromboli is located between the volcanic desert above and the thermophilic shrubland dominated by *Genista tyrrhena* below, sometimes replaced by secondary successional stages with *Saccharum biflorum*. Laterally, the m-pop is delimited to the SE by a dense, almost pure shrubland dominated by *Spartium junceum*, whilst the NNE side is delimited by strong northerly winds, which, during autumn and winter, defoliate the few peripheral exposed individuals almost entirely, hampering the propagation of *C. aeolicus* northwards. A photo collection of the study site is provided in Additional file 1.

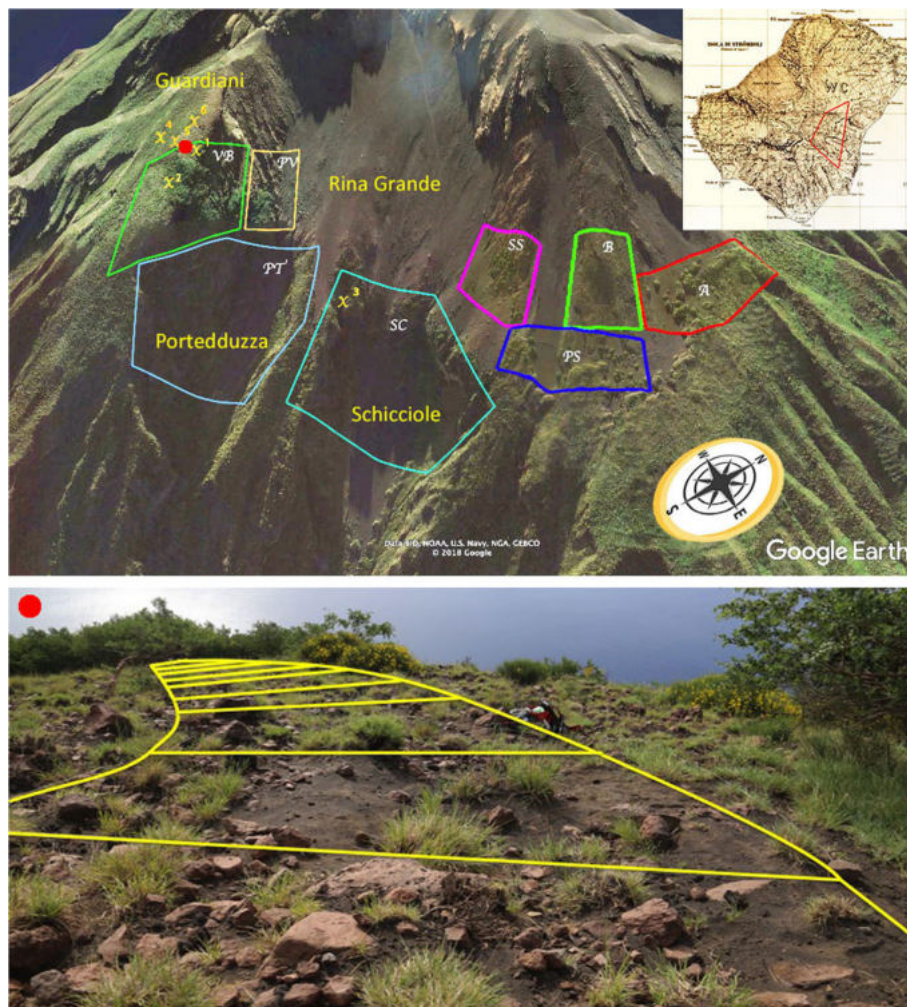


Fig. 1 Study area and delimitation of the studied m-pop of *C. aeolicus* (source: Google Earth). The 'X' symbols indicate the sites where soil samples were collected. The red point indicates the position of the transect to estimate the annual rates of seedling and sapling establishment (see Fig. 6 for details)

Climate and hydrogeology

The Aeolian Islands are subject to typical Mediterranean climate. The only weather station in Stromboli recorded data from 1946 until 1980 and is located at an elevation of 4 m a.s.l. A new weather station (ID: ISICILIA191) has been installed on the island in 2016, at the same elevation. Based on the data so far available, Stromboli village has an average yearly temperature of 18.2 °C, with an average temperature of 12.3 °C in the coldest (January) and 26 °C in the warmest month (August). The average annual rainfall amounts to 570 mm, whilst the relative humidity is 75.0% in winter and 60.8% in summer. Based on the WorldClim interpolation algorithms (Hijmans et al. 2005) and on the Rivas-Martínez bioclimatic classification (2004), the study area is characterised by an upper thermomediterranean thermotype and a dry-subhumid ombrotype (Cavallaro et al. 2009; Bazan et al. 2015). The strong baric gradient between the coastline and the top of the volcano buffers the summer drought with relevant condensation of atmospheric humidity, especially in the morning and evening hours, so that the accumulated dew helps *C. aeolicus* to keep green throughout the year.

A large prevalence of westerly to northwesterly winds (Cicala 1997) conveys towards the study area airborne volcanic emissions. Investigations on the hydrothermal system of Stromboli (Revil et al. 2011) revealed a conspicuous degassing in the central portion of the study area (Rina Grande), due to the underlying hydromagmatic system, with imposing CO₂ and H₂O emissions. In addition, volcanic gases affect the chemical composition of rainwater (Brusca et al. 2004; Liotta et al. 2006).

Soil analyses

Since the south-eastern limit of the studied m-pop of *C. aeolicus* borders a tall and very dense shrubland of *Spartium junceum*, soil samples were taken to understand whether this limit was due to different edaphic conditions or just to competition. Therefore, five soil samples were collected in locality Guardiani (upper NW corner of s-pop VB, Fig. 1), where *C. aeolicus* and *Spartium junceum* form two almost pure stands, without mixing up. The soil was sampled under the canopy of both species and in the sharp border, in order to verify if there was an edaphic explanation for the lack of interpenetration between the two adjacent vegetation units. An additional sample was collected approx. in the barycentre of the m-pop of *C. aeolicus* (upper W corner of s-pop SC, Fig. 1), to serve as outgroup in the comparison between the five samples collected in locality Guardiani.

Each soil sample consisted of a mixture from five cores randomly sampled in the uppermost 30 cm of the mineral soil (i.e. after removing the surface litter), within a

10 m² plot. Soil samples were air dried and subsequently sieved at \ominus 2 mm.

Total nitrogen was determined on pulverised soil samples by Kjeldahl digestion (Bremner 1996). Soil texture (sand, 2–0.02 mm; silt, 0.02–0.002 mm; clay, < 0.002 mm) was determined by the pipette method after shaking soil samples for 2 h and using sodium hexametaphosphate and sodium carbonate (Gee and Bauder 1986).

Soil pH was measured in distilled water using a soil/water ratio of 1:2.5 (w/v) and a glass membrane electrode. Soil electrical conductivity (EC) was measured in distilled water using a soil/water ratio of 1:5 (w/v). The differences between the two data sets (*C. aeolicus* vs. *S. junceum*) were evaluated by two-tailed Student's *t* test.

Aerial imagery analysis

To shed some light on the population dynamics of *C. aeolicus* at Stromboli, we interpreted all the available aerial photos (credits: Military Geographic Institute—I.G.M. b/w, years: 1937, 1954, 1967, 1995; I.G.M. colour, year: 2005) and the satellite images stored in the online repositories of Bing and Google Maps (2014, colour). Additionally, a high-resolution (12 Mpixel) map of the whole m-pop of Stromboli (including the inaccessible cores) was obtained by merging and geo-referencing, through the software Agisoft Photoscan Professional (version 1.2.6), the colour aerial photos taken in 2017 by means of a drone DJI Phantom 3 professional.

Georeferencing and visual interpretation of all the available maps were done with the open-source software QGIS (QGIS Development Team 2009). After visual detection, the dense patches (s-pops) of *C. aeolicus* were represented as polygons and the isolated individuals as points. The estimate of the number of individuals in the dense patches was obtained by estimating the area of occupancy of mature individuals, calculated as a circle with a diameter equal to the mean distance from the nearest neighbours of 30 mature individuals growing in the patches that constitute the cores of the following s-pops: VB, PV, PS, SS, SC. Being *C. aeolicus* a polycormic plant, the distances were measured between the stems that corresponded approximately to the central part of the crown. We are aware of the rough estimate of the area of occupancy, but measurements in the field were extremely challenging. Whilst we were unable to address this shortcoming, the large standard error protected us from incautious estimates of the number of individuals. A collection of the aerial imagery analysed is given in Additional file 2.

Growth rate estimate

To estimate the age distribution, we assessed the yearly growth rate by measuring the increment cores from the largest stem of 5 mature individuals of *C. aeolicus*

randomly chosen along a transect from the centre to the periphery of the s-pop VB (Fig. 1). On this purpose, we chose the s-pop VB to assess the yearly growth rate because it is the largest and densest, thus offering the double advantage of limiting the potential consequences of injuries caused by the use of increment borer to mature individuals and obtaining a representative estimate of the growth rate of plants living both in clumped patches and more exposed to sunlight. Since the steepness of the terrain leads to a strongly asymmetrical growth of the stems, four orthogonal radii were sampled from each stem at 60 cm above ground. The cores were mounted on grooved boards, prepared by sanding and finished with oil, the ring widths measured to 0.1 mm with a vernier calliper under stereomicroscope. The yearly radius increment was determined by averaging all radial measurements and calculating the standard error. The distribution frequency of class ages was estimated by correlating the radial increments to the circumference of the largest stem of 121 individuals selected randomly in each s-pop of Stromboli amongst those having the first bifurcation at more than 60 cm above ground. The number of individuals measured in each s-pop is reported in the diagrams of Additional file 3.

Reproductive fitness—phenology

The phenological phases were recorded weekly from March 5 to June 18, 2017, on the same 121 individuals measured for the age estimates. In this case, we split the sample into two subsets: (1) 62 ‘sheltered’, i.e. individuals growing in a dense vegetation patch and/or sheltered by rock outcrops and/or growing in the bottom of gullies; (2) 59 ‘exposed’ to meteorological factors (sun, wind), i.e. isolated individuals growing on ledges or on the top of outcrops or on volcanic ash ridges. The phenological phases were recorded by adopting the criteria and the data sheet proposed by Puppi and Zanotti (1989). The differences between the two data sets (sheltered vs. exposed) were evaluated by one-tailed Student’s *t* test.

Reproductive fitness—pollen grains

For the analysis of pollen, we sampled flowers from the s-pops VB and SS, i.e. the largest, densest and most sheltered (VB) and the rockiest and most exposed one (SS), so to have a selection of flowers representative of the most different growing conditions. Pollen grains from freshly dehisced anthers were spread on a slide and kept in Petri dishes lined with moist filter paper. For the pollen grain analysis, pollen samples were acetolysed following the standard procedures summarised by Magri and Di Rita (2015). After acetolysis, the pollen from each s-pop was divided into two fractions for observation under a light microscope and environmental scanning

electron microscope (ESEM). Polar axis (P) and equatorial diameter (E) of 30 pollen grains per sample were measured under a light microscope at $\times 750$ magnification. Pollen for the analysis of the exine surface was dried from a sample in 95% ethanol onto aluminium stubs and observed with a HITACHI TM3000 ESEM at $\times 1.5$ k and $\times 20$ k magnifications. Pollen terminology follows Punt et al. (2007) and a specific publication on pollen morphology of *Cytisus* by Pardo et al. (2000).

Reproductive fitness—germination and mortality rates

The germination rate was estimated on site in the years 2017–2019 by placing two replicates of a 15 cm-long and 30 cm-wide plastic tube, of which the first 10 cm were buried in the sand and the remaining 5 filled, up to 2.5 cm from the border, with a mixture of volcanic sand and 100 seeds of *C. aeolicus*. Seeds were collected on site from the plants nearby and scarified by shaking them vigorously with sand. The upper part of the tube was sealed with a mosquito net to avoid additional incidental seed supply. The two replicates were placed on June 4, 2017, under the crown of two isolated mature individuals, in the upper periphery of the s-pop VB. This site was chosen due to its relatively easy accessibility, whilst at the same time being far from the transit areas of tourists.

The annual rates of seedling establishment and sapling mortality were measured in the years 2017–2019 on nine permanent 5×5 m plots, placed along a transect between the two isolated individuals mentioned above, which were 45 m apart. On this purpose, seedlings (< 1 year old plants) and saplings (> 1 year old plants) were counted separately during the demographic surveys. In order to assess to which extent mortality was affected by the summer drought stress, these surveys were carried out twice per year, i.e. before (May) and after (October) summer season. In the October counts, all the new-born plants (i.e. those having only the couple of cotyledonal leaves) were neglected.

Results

Soil properties

According to the Soil Taxonomy (Soil Survey Staff 1999), the soils of the Strombolian m-pop of *C. aeolicus* are Vitrandic Xeropsamments, in which the pedogenesis is countered by the continuous supply of volcanic sediments. No significant differences were detected between the soils collected under *C. aeolicus* and the neighbouring *Spartium junceum* (Table 1).

Demographic trend

On average, the distance between the mature individuals of *C. aeolicus* growing in dense vegetation patches

Table 1 Chemical and physical properties of the soil samples collected on Stromboli Island

Vegetation type	Site	pH	EC (dS m ⁻¹)	Clay (%)	Loam (%)	Sand (%)	Total N (g kg ⁻¹)
<i>C. aeolicus</i>	X1	4.95	0.215	0.70	1.65	97.65	0.08
<i>C. aeolicus</i>	X2	4.85	0.285	0.40	7.00	92.60	0.08
<i>C. aeolicus</i>	X3	5.10	0.152	0.30	0.85	98.85	0.09
<i>S. junceum</i>	X4	4.70	0.400	0.75	1.50	97.75	0.12
<i>S. junceum</i>	X5	4.70	0.245	0.60	1.70	97.70	0.06
<i>S. junceum</i>	X6	5.00	0.320	1.00	1.90	97.10	0.08

EC electric conductivity
For soil sampling sites (X1–X6), see Fig. 1

resulted to be 3.76 ± 2.49 m, whilst each individual occupied an area of 14.31 ± 13.46 m².

Between 1937 and 2017 (Fig. 2) the studied s-pops experienced significant changes in terms of both surface and altitudinal range (see Additional file 2 for details). The lowest number of both isolated and clumped individuals was observed in 1937. They grew up gradually until 1967, whilst their size diminished abruptly in 1995. The data concerning 1995 (Fig. 2) match perfectly with those issuing from the field assessment (c. 450 individuals) carried out by Pasta in 1999 (unpublished data). Later on, *C. aeolicus* started to rise once again, with maximum values reached in 2017, although the number of isolated plants has been prone to major oscillations during last 20 years, with a decrease of one-third between 2014 and 2017.

The site of Rina Grande (corresponding to the current s-pops SS, PV, see Fig. 1) underwent strong changes: in the aerial photo of 1937 (Additional file 2, Fig. A2.1) it was almost bare, with scattered nuclei of low-growing cushion-like plants (almost certainly *Centaurea aeolica* and *Dactylis glomerata*), whilst few arborescent individuals of *C. aeolicus* were concentrated on the rocky ledges of Guardiani (s-pop VB) and on the ridge of the lower part of Rina Grande, in localities Portedduzza (s-pop PT) and Schicciole (s-pop SC). The aerial photo of 2017 (Additional file 2, Fig. A2.7) highlights the outstanding vitality and dynamism of the s-pop of *C. aeolicus* on Stromboli Island. In fact, all s-pops appear increasingly dense and continuous with respect to previous images and plenty of young reproductive individuals are spreading in the adjacent zones. In particular,

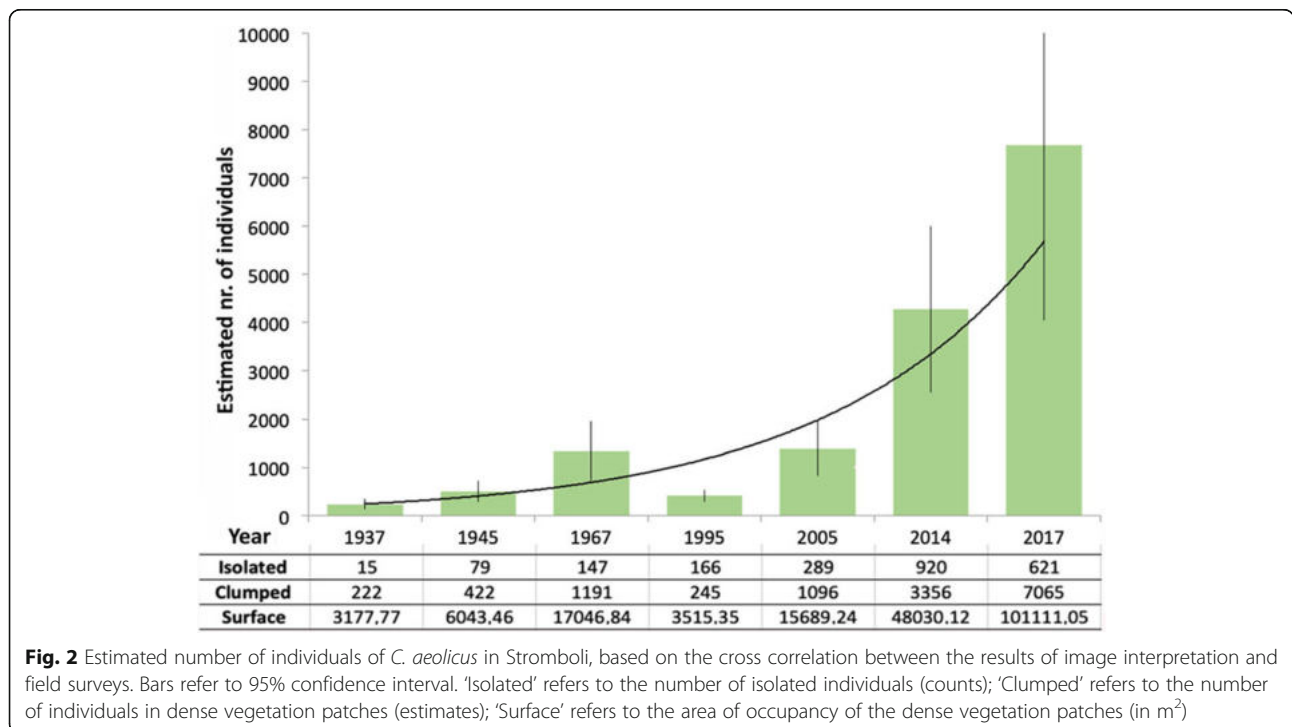


Fig. 2 Estimated number of individuals of *C. aeolicus* in Stromboli, based on the cross correlation between the results of image interpretation and field surveys. Bars refer to 95% confidence interval. 'Isolated' refers to the number of isolated individuals (counts); 'Clumped' refers to the number of individuals in dense vegetation patches (estimates); 'Surface' refers to the area of occupancy of the dense vegetation patches (in m²)



Fig. 3 The s-pop VB (Fig. 2), locally named ‘o Vuòscu’ (the wood), at present times is the most dense s-pop of *C. aeolicus* in the whole Aeolian archipelago, with a large number of young individuals (photo: R. Guarino, May 15, 2017)

the s-pop of locality Guardiani (Fig. 1, VB) is so dense to prevent any other woody species growing there (Fig. 3).

Population age

The average yearly radius increment of the 20 measured increment cores extracted from 5 mature plants of the s-pop VB resulted to be to 3.25 ± 1.40 mm. Of the 121 adult plants measured, only 4–6 individuals resulted to be more than 50 years old, whilst 40–52 resulted to be

younger than 10 years (Fig. 4). These results agree with our aerial photos interpretation, confirming that the m-pop of Stromboli is young and dynamic. Furthermore, the poor number of individuals established between 40 and 50 years ago confirms the demographic shrinking documented by the aerial photo of 1995 (Additional file 2, Fig. A2.4). The estimates of the age distribution in each surveyed s-pop are reported in Additional file 3.

Reproductive fitness—phenology

The vegetative activity of *C. aeolicus* is concentrated during the autumn and winter season. Flowering begins during the last weeks of February, reaching its peak on the last 2 weeks of March and the first of April. In all s-pops, some plants begin to flower 1 or 2 weeks before the others, and are in full blossom during the last week of March; more in detail, about 40% of the sheltered individuals and 70% of the exposed ones show a shift in the flowering peak with respect to the rest of the monitored plants (Fig. 5).

The plants living in exposed sites have a more scalar and long-lasting flowering cycle, whose timing and duration are influenced by the slope aspect.

Many plants (25% of our sample) did not succeed to perform the whole blossom cycle, especially the most exposed ones, whose flower-bearing apexes were completely dried up. Legumes ripen during May and by the

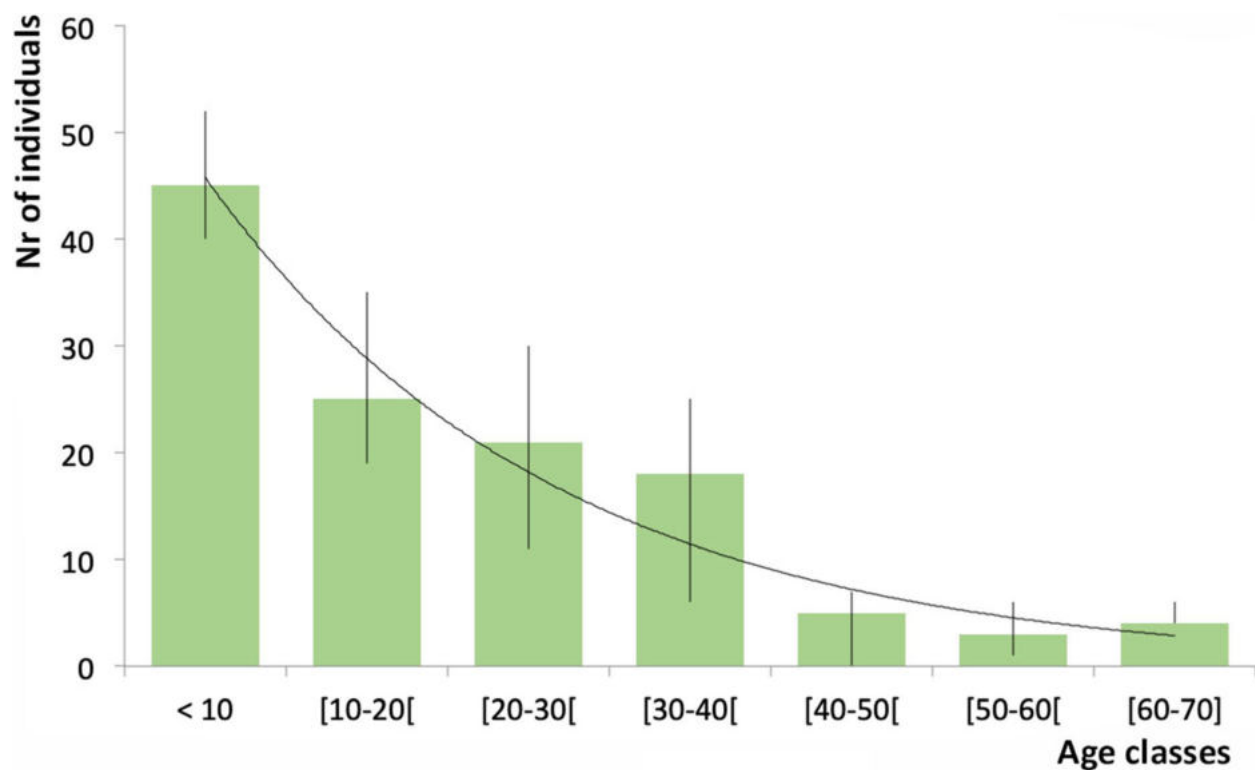
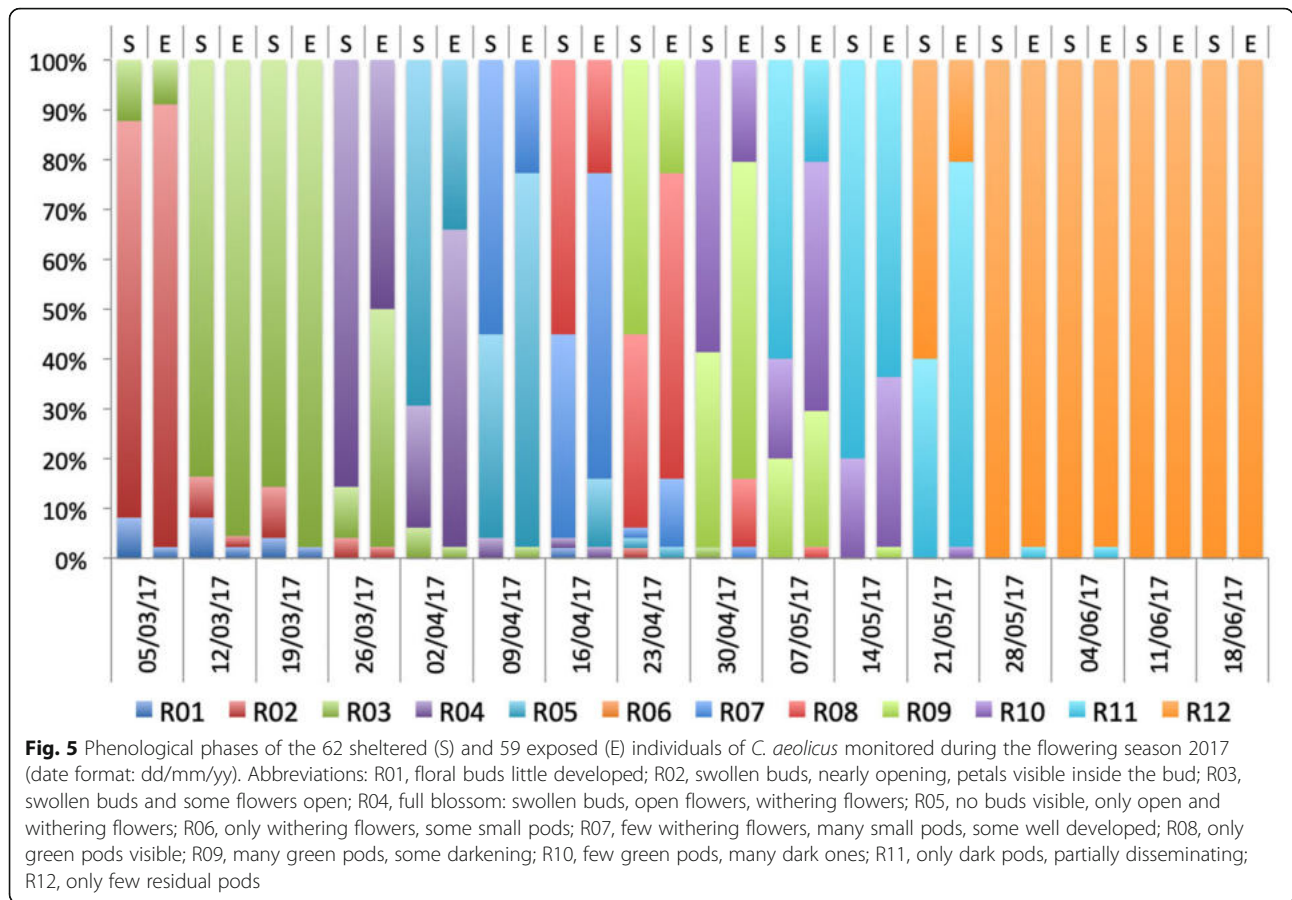


Fig. 4 Estimated age distribution of the *C. aeolicus* m-pop from Stromboli



third week of June, most of them fall to the ground. In sheltered conditions, some mature legumes may persist on the mother plant until autumn. Interestingly, the legumes of *C. aeolicus* are indehiscent (with the exception of the m-pop from Alicudi, according to Troia 1997) and when they detach from the mother plant, they may be blown uphill by the wind for tens of metres. A photo collection of the phenological phases is provided in Additional file 4.

Reproductive fitness—pollen grain analysis

The microscopic observation of the pollen grains of *C. aeolicus* before the acetolysis revealed that most of the grains were turgid and rich in protoplasmic content, independently of the sampling site. This suggests a high-quality pollen with a good viability in both analysed s-pops, although tests of fluorochromatic reaction and germination were not carried out, since they will be the subject of an upcoming specific research. However, we report the first description of the pollen morphology of *C. aeolicus* from Stromboli, providing new data to the discussion on the phyletic relationship with other species of the genus.

The pollen grains of *C. aeolicus* appear radially symmetrical, isopolar, generally circular to elliptic in

equatorial view and subcircular to 3-lobate in polar view (Additional file 5, photo 2). As for the apertures, they are 3-zonocolporate grains with very long ectoapertures and diffuse endoapertures. The size is rather variable, ranging from small to medium (Table 2). The measures of polar axis and equatorial diameter are somewhat different in the two s-pops, whilst the P/E ratio is substantially similar: pollen grains from the s-pop VB show a mean *P* of 24.9 μm and a mean *E* of 26.4 μm, resulting in a P/E = 0.94, typical of oblate-spheroidal shape; pollen grains from the s-pop SS show a mean *P* of 21.4 μm and a mean *E* of 21.8 μm, resulting in a P/E = 0.98, also consistent with an oblate-spheroidal shape. Both *P* and *E* ranges are wider at VB- than at SS s-pop.

The exine ornamentation of the tectum varies from reticulate-perforate to reticulate-fossulate with thick

Table 2 Size measures carried out on 30 pollen grains from the s-pops SS and VB (Fig. 1). Symbols indicate mean length of polar axis in μm (*P*), mean equatorial diameter in μm (*E*) and standard deviation (σ)

Sample	<i>P</i> ± σ	<i>P</i> range (μm)	<i>E</i> ± σ	<i>E</i> range (μm)	<i>P/E</i>
s-pop SS	21.4 ± 1.31	18–24.8	21.8 ± 1.45	18.8–24.8	0.98
s-pop VB	24.9 ± 3.09	18.8–29.9	26.4 ± 3.61	20.5–32.5	0.94

angular muri and inclusions in lumina (Additional file 5, photos 1–4), which are especially evident in non-treated grains. The ornamentation at the poles is not significantly finer than at the equator (Additional file 5, photo 5). The colpi have a large margo with a densely punctate ornamentation and sparse perforations (Additional file 5, photos 2 and 6).

The pollen morphology and ornamentation of *C. aeolicus* is coherent with other species of *Cytisus* described by Pardo et al. (2000). In particular, there is a clear overlap with the measures by Pardo et al. (2000), reporting mean P range = 16.87–32.4 μm , mean E range = 16.8–28.9 μm and P/E range = 0.94–1.43. The ornamentation features of *C. aeolicus* (mostly reticulate-perforate to reticulate-fossulate) was also observed in the species analysed by Pardo et al. (2000).

Reproductive fitness—germination and mortality rates

In our on-site experiment, 62 and 70 of the seeds germinated in autumn 2017. Additional 11 and 17 seeds germinated in spring 2018. The rest of the seeds did not germinate in the subsequent seasons. Therefore, according to our very preliminary results, seeds of *C. aeolicus* have only a physical dormancy and, after scarification, we observed a germination rate of 73–87%.

After summer, in the periphery of the s-pop VB (Fig. 1), the annual rates of seedling establishment resulted to be around 28% (Fig. 6) and the survival rate of saplings around 47%. However, on July 3, 2019, a Strombolian paroxysm event started a period of strong volcanic activity, which lasted until August 28, 2019. Even if the wildfires triggered by the explosion on July 3 and 25 (39.35% of the island was burnt, see Turchi et al. 2020) did not affect significantly the m-pop of *C. aeolicus*, the intense accumulation of volcanic sand and, particularly, the tephra fallout on August 28, which was dispersed eastwards, caused foliar damage to the mature individuals and buried to death many young individuals (Additional file 4). Along our transect, only 4 young saplings, about 3 years old, survived.

Discussion

Aerial photos and satellite imagery show unambiguously that the m-pop of *C. aeolicus* from Stromboli underwent significant oscillations during the last 80 years. However, vegetation patches (s-pops) and isolated individuals reacted differently to land abandonment, which almost certainly represented the main factor favouring the recovery of *C. aeolicus* during the considered time lapse.

More in detail, s-pops are able to recover quite fast, albeit periodically affected by sharp regression phases, like the one documented in 1995, probably related to an intensification of the Strombolian activity occurred in 1993–1994 (Bertagnini et al. 1999). The s-pop mainly

spread upwards, colonising sandy slopes and steep rock outcrops, whilst at lower altitudes and on S-facing slopes *C. aeolicus* was less successful, probably because it had to cope with the competition by *Spartium junceum*. The frequent northerly winds represent a major environmental driver, because they convey volcanic fallouts from the top craters.

During the last 20 years, the number of isolated mature individuals has more than doubled; their numbers raised slowly but constantly. The ridge which separates the two valleys of ‘Le Schicciolo’ and ‘Portedduzza’ (Fig. 1) represents one of the few strongholds of the species. In fact, *C. aeolicus* occurred there in all the images between 1937 and 2017 (Additional file 2) and the species was mentioned to grow at ‘le Schicciolo’ (= dripping cliffs in local dialect), albeit extremely rare, throughout the whole nineteenth century (Gussone 1834; Lojacono-Pojero 1878).

In the following paragraphs, we will discuss about how and to which extent different drivers may influence the demographic trends of *C. aeolicus*.

Phylogenetic isolation and population size bottlenecks

The great demographic fluctuation observed in the Strombolian m-pop of *C. aeolicus* can explain the low genetic diversity resulting from the work of Conte et al. (1998): great fluctuation means that most of the plants are young, deriving from few old plants, so that the ‘real’ population size (i.e. the stock of genetic diversity) is limited. Therefore, we can postulate that the Strombolian m-pop is numerically but not genetically fitter than the ones in Vulcano and Alicudi. However, a new genetic study (on all the islands, but especially in Stromboli) would be highly desirable, considering that Conte et al. (1998) sampled only in the s-pop SC (Fig. 1).

The study of pollen morphology has historically allowed evolutionary biologists to assess phylogenetic relationships, due to its conservatism (Kriebel et al. 2017). On the one hand, although it is generally accepted that the tribe Genisteae has rather homogeneous pollen (Pardo et al. 2000), the morphological peculiarities of *C. aeolicus* pollen grain confirm the phylogenetic isolation of this species. On the other hand, our study of the pollen morphology revealed some unexpected variability between the s-pops of SS and VB. Additionally, the pollen grains studied by us are also slightly different from those of a single specimen from the m-pop of Vulcano, cultivated in the botanical garden of Catania, in which the pollen grain shape was mostly prolate spheroidal and the colpi were lacking margo (De Leonardis and Zizza 1994). These differences confirm that the population genetic of *C. aeolicus* deserves further investigation.

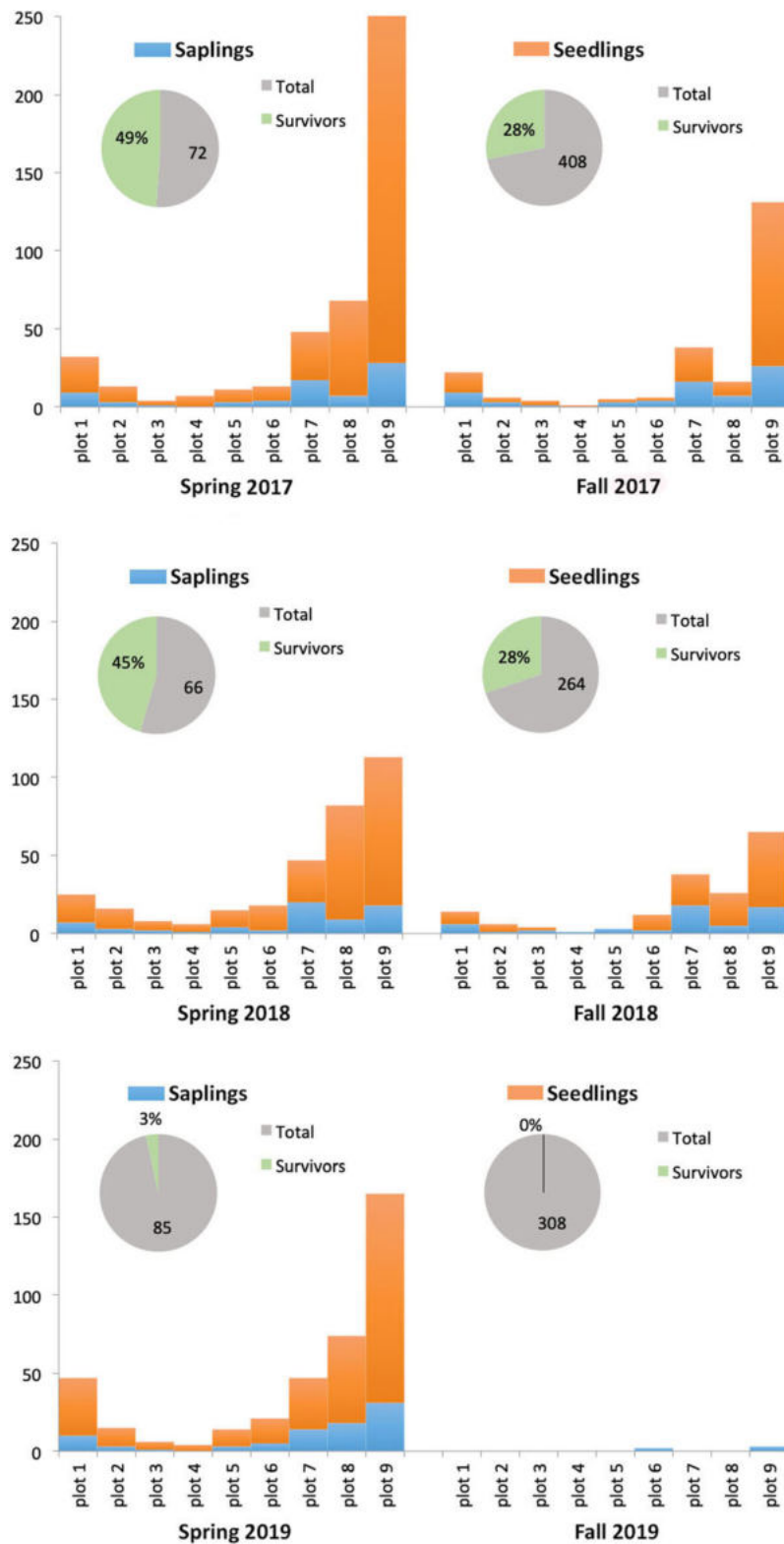


Fig. 6 Annual rates of seedling and sapling establishment, measured in the years 2017–2019 on nine permanent 5 × 5 m plots, placed along a transect between two isolated mature individuals (Fig. 1), in the upper periphery of the m-pop VB. Pies show the after summer mortality rates (in %) on the total number of saplings (left) and seedlings (right) counted. The severe mortality observed in 2019 is due to an exceptional intensification of the local volcanic activity

More in general, considering the pollen morphology of the species analysed by Pardo et al. (2000), the main differences between *C. aeolicus* and the other species of *Cytisus* are found in the P/E ratio < 1, in the homogeneity of ornamentation throughout the apocolpium area and in the ornamentation of the margo (Pardo et al. 2000). Considering size, shape and surface ornamentation, the pollen morphology of *C. aeolicus* is most similar to *C. fontanesii* Ball (P range = 22.90–33.60 μm , E range = 22.20–30.70 μm ; P/E range = 0.96–0.99; ornamentation fossulate perforate), a western Mediterranean ephedroid broom belonging to the monotypic section *Heterocytisus*. Although *C. fontanesii* has a mostly densely perforate margo and *C. aeolicus* has a mostly punctate margo with sparse perforations, these are the only *Cytisus* species in which perforations have been observed in the margo, which is psilate-punctate in the other species (Pardo et al. 2000). Interestingly, *C. fontanesii* is a West Mediterranean species, including two subspecies; the type subspecies grows in Algeria, Morocco (Rif and Mid Atlas), Balearic Islands (Ibiza) and SE Spain, whilst subsp. *plumosus* (Boiss.) Nyman is endemic to Serrania de Ronda, in Andalusia (Talavera 1999).

Anthropogenic disturbance

Between 1825 and 1891 Stromboli grew from 1660 to 2716 inhabitants (+63% in 66 years, see Fazio 2010). Considering that their subsistence mainly depended on agriculture, with no doubt at that time shrubland clearing and wood harvesting must have represented a major threat for the survival of *C. aeolicus*. Few decades later, i.e. between 1910s and 1930s, massive migration towards Australia and Argentina induced a sudden and striking reduction of the anthropogenic pressure on the less accessible sites where *C. aeolicus* still occurred. Local people were only 659 according to the 1951 census and, after the Second World War, the once dominating cultivated surfaces were almost completely abandoned (Alleruzzo Di Maggio 2012). Hence, during the time lapse investigated through the interpretation of aerial photos and satellite images (Fig. 3), human activities no more played an important role on the demographic fluctuations of *C. aeolicus*. Instead, herbivore browsing, competition amongst woody species and wildfires (natural and/or set by man) regime became the main factors shaping the structure and the dynamics of local vegetation, like almost everywhere on the Aeolian Archipelago (Richter 1984, 1989; Moreno 1995; Richter and Lingenhöl 2002; Rühl and Pasta 2008).

Today, 2–3 herds of feral goats occur on Stromboli island. Their number (c. 20–30 individuals) is steady and probably kept under control by the lack of natural springs. During summer, these goats enjoy the shadow

and stop to rest under the canopy of *C. aeolicus*, causing negligible mechanical damages to lower branches and eventually to their trunks. Rich in alkaloids (Pistelli et al. 2004), *C. aeolicus* is not appreciated by adult goats, which avoid browsing them, whilst young individuals were occasionally observed biting the tender shoots or the saplings.

Rabbits (*Oryctolagus cuniculus* L.) were very abundant on Stromboli until 1980s, even in locality Guardiani, now hosting the densest s-pop of *C. aeolicus* (Fig. 1, VB) and with almost no woody plant cover until 1967. In 1986, myxomatosis drastically reduced local rabbit colony, which has never been able to recover. Although we have no data to give evidence of a causal link between the rabbit population shrinkage and the strong recovery of *C. aeolicus* between the 1960s and 1990s, local people affirm that the seeds and the saplings of *C. aeolicus* have been part of the diet of feral rabbits. As a matter of fact, in Tenerife (Canary Islands), rabbits have been proven to hamper the reproductive fitness of another endemic giant broom, *Spartocytisus supranubius* (L. f.) Christ ex G. Kunkel (Cubas et al. 2018). Also, the black rat (*Rattus rattus* L.), commonly found on the island, could feed on the seeds of *C. aeolicus*, as testified by teeth traces observed on part of the pods accumulating at the base of mature plants.

Natural disturbance

The success experienced by *C. aeolicus* on Stromboli island in the last decades underlines the ability of this species to colonise even the steepest and most impervious slopes. At the same time, the eastern slopes of Stromboli are subject to a constant and often very intense natural disturbance due to local seismic and volcanic activity. The geomorphological instability of this sector of the island is particularly evident on the outcrops and ridges surrounding Rina Grande. Here, the combined effect of tremors, earthquakes, feral goats and extreme rainstorm events causes frequent rock collapses and the fall of huge boulders, which may damage the stems of *C. aeolicus*, facilitating diseases through injuries. Given the exposure to winds blowing from NW, the arrival of ashes and scoriae is frequent and these often trigger large arsons affecting the study area. However, basing on the evidences of the last wildfire, occurred in 2019, mature *C. aeolicus* does not burn very well and exhibits a good resprouting attitude.

Instead, the almost constant supply of pyroclastic materials causes the continuous slip of volcanic ashes/sands along the slopes of Rina Grande. This process, in turn, may cause the total burial not only of the seeds and seedlings of *C. aeolicus*, compromising the species establishment even during the most favourable periods (Fig.

6) but also of the reproductive plants, facilitating fungal diseases.

Additionally, volcanic gas emission affects local air quality (Liotta et al. 2006). For instance, it has been observed that the pH values of rainfall water gathered near the top craters are on average 1–2 units lower than that collected near the sea level (Liotta et al. 2006). Hence, the direction of dominant winds and the long-lasting persistence of volcanic gas plumes may periodically affect the vitality of local m-pop of *C. aeolicus*, although the magnitude of these interactions remains totally unknown.

Competition, parasitism and facilitation mechanisms

Although our poor soil sampling scheme does not lead to definitive conclusions, the soil analyses (Table 1) suggest that the edaphic conditions may not be the major driver for the sharp division between the tall shrublands dominated by *C. aeolicus* or by *Spartium junceum*, co-occurring one next to the other in locality Guardiani without mixing up. Actually, both stress and disturbance may be invoked as drivers of this unusual vegetation pattern (sharp border and total lack of overlap). On the one hand, geothermal water availability (Revil et al. 2011) and slope topography may favour *C. aeolicus*, whose young and adult individuals (broadleaved and evergreen) are less adapted to summer drought than *Spartium* (ephedroid and summer-deciduous). On the other hand, similar sharp borders may just be the result of a stochastic response to a major disturbance event. For instance, features like the heat and the duration of wildfires may let re-sprouters prevail over seeders or vice versa.

Still poor is the knowledge about the living beings which could positively or negatively affect the fitness of *C. aeolicus*. Amongst the former ones, the nitrogen-fixing bacterium *Bradyrhizobium canariense*, occurring as an endosymbiont of several brooms of the W Mediterranean and Canary Islands, has been discovered to nodulate the roots of *C. aeolicus* (Cardinale et al. 2008). Amongst the parasites, two beetles are worth to be mentioned, i.e. *Bruchidius foveolatus* and *Bruchidius nudus*. Their larvae may destroy as much as 9% of the seeds contained in the legumes (Lo Cascio 2004).

During the monitoring period (2017–2019), we observed the sudden death of several mature individuals that showed no evidence of disease just few months before. Such casualties may result from the combined effect of both drought stress and root pathogen attack. The mechanical damages on the branches and trunks of *C. aeolicus* caused by frequent rock collapses or by grazing herbivores, as well as the partial burial of the stumps due to the almost constant volcanic ash/sand supply, may favour the onset of diseases caused by

noxious pathogens (mostly fungi belonging to genera *Phytophthora* or *Rhizoctonia*, A.E. Cristaudo, pers. comm.).

As already pointed out by Richter (1984), Troia (1997) and Lo Cascio (2017), the seedlings of *C. aeolicus* enjoy the favourable microclimatic conditions provided by several ‘nurse’ plants. High seedling densities have been observed not only under some isolated low-growing individuals of *Ficus carica* L. but also close to the tufts of the few locally abundant hemicryptophytes and chamaephytes, i.e. *Dactylis glomerata*, *Silene vulgaris* subsp. *angustifolia* and *Centaurea aeolica*.

Drought stress and unexpected water resources

Many isolated plants next to the upper limit of the m-pop are more exposed to extremely warm and dry wind, the so-called ‘scirocco’ coming from SE, which may compromise their annual reproductive cycle. The importance of shelter effect on the reproductive performance of *C. aeolicus* is confirmed by the phenological monitoring of the s-pop B, in which only the individuals protected from such winds produced seeds in 2017.

Summer drought not only influences the reproductive performance of adult individuals, but may severely affect the survival of the seedlings and saplings of *C. aeolicus*. Hence, local demographic oscillations may be partially linked to extremely arid years or to fluctuations of the substrate humidity driven by changes in the circulation pattern of phreato-magmatic waters. In fact, the intense degassing processes originating from the hydromagmatic system underlying the central portion of Rina Grande (Revil et al. 2011) induce the emission of high amounts of H₂O and CO₂ (Carapezza et al. 2009), which in turn may have a beneficial effect by alleviating water stress and improving photosynthetic efficiency of the adjacent s-pops of *C. aeolicus*.

New insights on the reproductive fitness and dispersal strategies of *C. aeolicus*

The results of our field survey clearly show that both flowering and seed production are subject to important fluctuations within and amongst s-pops. For instance, as much as 25% of the plants monitored did not flourish at all.

The rate of reproductive success is even more variable amongst isolated, exposed individuals. In our investigation, the lowest percentage of flowering individuals was recorded in the s-pop of Liscione (Fig. 1b), localised on an extremely rocky and windy site. The seeds of *C. aeolicus* show physical dormancy due to their hard impermeable coats; not surprisingly, scarification (mechanical, thermal and chemical) positively affects their germination (Troia 1997). Heavy rainfall after windstorms may favour massive germination events (see Additional file

4), although many seedlings die out very soon and more than half of them do not survive to summer drought stress (Fig. 6). Moreover, recent laboratory experiences carried out under controlled light, temperature and water conditions showed that also the ripening stage plays an important role in seed germination. In fact, seeds collected before reaching dormancy state and sown in January–February showed an average germination rate of around 60%, ranging from 100% (green fresh seeds) to 15% (brown fresh seeds); instead, ripe brown dehydrated seeds remain dormant and need a specific pre-treatment to germinate (Catara et al. 2016).

During the surveys carried out in 2017–2019 on permanent plots (Fig. 6), *C. aeolicus* proved to be healthy and showed a good regenerative potential, testified by the abundance of seedlings and saplings growing near the reproductive plants. Young individuals are mostly concentrated at the margin of s-pops and next to isolated individuals. By contrast, almost no seedlings were observed growing under the canopy of the most dense pure stands of *C. aeolicus* (s-pops VB, PV, B, SS, PS, Fig. 1). This fact suggests that our species behaves as a pioneer, light-demanding plant, experiencing cyclic demographic booms.

Conclusions

The present study illustrated the recent demographic recovery of the m-pop of *C. aeolicus* growing on Stromboli island and its remarkable demographic oscillations during the last 80 years. We unambiguously documented a sharp, yet unexplained, increase during the last 20 years, a trend which contrasts the ones recorded on Alicudi and Vulcano, where the species is barely surviving.

Field surveys are needed to monitor the demographic trends of rare endemic plants and represent a basic tool in order to refine and update risk assessment (Pasta et al. 2017). In the case of extremely rare relict species like *C. aeolicus*, such assessment may be biased by insufficient knowledge on their original niche, environmental requirements and dispersal strategies. Also, our opinion on the recovery potential has significantly changed taking into account new information. For instance, the estimated number of reproductive individuals given by Troia and Domina (2017) was one order of magnitude lower than the real current one. Although the environmental features of Stromboli seem to have recently favoured *C. aeolicus* and let us hope for the short-term chances of its survival, the extreme localisation of this endangered species and the numerous random factors affecting its reproductive performance suggest to maintain the status of ‘endangered’ (EN) according to IUCN red-listing criteria (Rossi et al. 2013). However, we propose to modify the IUCN assessment by Troia and Domina (2017) as follows: EN B1ac(ii,iv) + 2 ac(ii,iv).

This change is justified by the recent remarkable increase in the number of reproductive individuals and by the documented extreme fluctuations of the area of occupancy and number of individuals.

The field data collected in this exemplary case study not only led to revise the recent risk assessment of *C. aeolicus*, but supports the need of a major change of paradigm: in fact, our results point out that the being ‘relict’ does not necessarily imply not to be highly viable and able to recover fast, exploiting more favourable environmental conditions.

Nomenclature and terminology

Taxonomic nomenclature of vascular plants follows Pignatti et al. (2017–2019). As for ‘mature individual’, we intend a plant of *C. aeolicus* having at least 1 m diameter crown, hence, easy to recognise and detect from aerial photographs.

Supplementary information

Supplementary information accompanies this paper at <https://doi.org/10.1186/s13717-020-00262-5>.

Additional file 1. Photo collection of the growing site of *Cytisus aeolicus* from Stromboli Island

Additional file 2. Diachronic trend of the isolated individuals and vegetation patches of *Cytisus aeolicus* on Stromboli Island (years 1937–2017).

Additional file 3. Age distribution estimates in the studied s-pop of *Cytisus aeolicus* from Stromboli Island.

Additional file 4. Phenological phases in the studied s-pop of *Cytisus aeolicus* from Stromboli Island.

Additional file 5. Pollen grain images of *Cytisus aeolicus* from Stromboli Island.

Abbreviations

m-pop: Metapopulation; s-pop: Subpopulation. According to Wells and Richmond (1995), we intend as metapopulations a set of spatially disjunct populations, amongst which there could be some immigration, as subpopulation an arbitrary spatially delimited subset of individuals within a (meta)population.

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Authors' contributions

R.G. conceived the idea, R.Z. and R.G. collected the field data (supported by Antonio Zimbone for drone imageries) and carried out most of the data analyses. V.A.L. carried out the soil analyses, M.D. and D.R.F. carried out the pollen analyses, R.G. and S.P. led the writing of the paper, benefiting from discussions and substantial contributions from all the authors.

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Ethics approval and consent to participate

Not applicable

Consent for publication

The authors provide their full consent to the publication of all the data contained in the submitted files.

Competing interests

The authors declare they have no competing interests.

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