Biological Conservation 286 (2023) 110289

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Perspective

# Identifying bottlenecks in the life cycle of plants living on cliffs and rocky slopes: Lack of knowledge hinders conservation actions

Giovanna Aronne [a], Edy Fantinato [b,*], Sandro Strumia [c], Annalisa Santangelo [d], Marta Barberis [e], Sílvia Castro [f], Donatella Cogoni [g], Marianne Evju [h], Marta Galloni [e], Peter Glasnović [i], Marcin Klisz [j], Tiiu Kull [k], Sandro Lanfranco [l], Maja Lazarević [m], Theodora Petanidou [n], Radosław Puchałka [o,p], Rosa Ranalli [e], Anastasia Stefanaki [n,q], Bostjan Surina [i,r], Živa Fišer [i]

[a] Department of Agricultural Sciences, University of Naples Federico II, via Università 100, 80055 Portici, (NA), Italy
[b] Department of Environmental Sciences, Informatics and Statistics, Ca' Foscari University of Venice, Via Torino 155, I-30172 Venice, Italy
[c] Department of Environmental, Biological and Pharmaceutical Sciences and Technologies, University of Campania "Luigi Vanvitelli", Via Vivaldi 43, I-81100 Caserta, Italy
[d] Department of Biology, University of Naples Federico II, Via Foria, 223, 80139 Napoli, Italy
[e] Department of Biological, Geological and Environmental Sciences, University of Bologna, Via Irnerio 42, 40126 Bologna, Italy
[f] Centre for Functional Ecology – Science for People & the Planet, Department of Life Sciences, Faculty of Sciences and Technology, University of Coimbra, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal
[g] Department of Life and Environmental Sciences, University of Cagliari, Via S. Ignazio da Laconi 13, 09123 Cagliari, Italy
[h] Norwegian Institute for Nature Research, Sognsveien 68, NO-0855 Oslo, Norway
[i] University of Primorska, Faculty of Mathematics, Natural Sciences and Information Technologies, Glagoljaška 8, 6000 Koper, Slovenia
[j] Department of Silviculture and Genetics, Forest Research Institute, Poland
[k] Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences, Tartu, Estonia
[l] Department of Biology, University of Malta, Msida MSD2080, Malta
[m] University of Belgrade, Faculty of Biology, Institute of Botany and Botanical Garden "Jevremovac", Chair of Plant Ecology and Phytogeography, Studentski trg 16, 11000 Belgrade, Serbia
[n] Laboratory of Biogeography & Ecology, Department of Geography, University of the Aegean, Mytilene 81100, Greece
[o] Department of Ecology and Biogeography, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100 Toruń, Poland
[p] Centre for Climate Change Research, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100 Toruń, Poland
[q] Utrecht University Botanic Gardens, P.O. Box 80162, 3508 TD Utrecht, The Netherlands
[r] Natural History Museum Rijeka, Lorenzov prolaz 1, 51000 Rijeka, Croatia

ARTICLE INFO

*Keywords:*
Conservation management
Plant conservation
Single species biology
Species life cycle

ABSTRACT

Long term survival of plant populations relies on successful reproductive cycle to obtain generation turnover. Focusing on plant species of conservation concern, we brought together a group of plant conservationists from different countries to assess whether the already available information on plant reproductive biology and autecology is adequate for identifying which phases of single species life cycle might act as bottleneck.

We compiled a list of 80 plant species of conservation concern living on European cliffs and rocky slopes, for which biological and autecological information was collected from scientific literature, technical reports, and expert knowledge.

Results have shown that the available information on species reproductive biology and autecology is inadequate to identify bottlenecks in the life cycle of many species and to provide insights for the practical conservation of many more. Available knowledge is mainly referred to the flowering phase, less on seed production and much less on seedling establishment and on cloning. Meanwhile and noteworthy, flowering resulted to be the less critical phase for the fulfilment of the species life cycle.

Overall, with this perspective article we aim to encourage a constructive debate among the scientific community members and policymakers to set up novel concerted strategies for the conservation of plant species of conservation concern. The challenge of the discussion is the implementation of the current approach with new

* Corresponding author.
*E-mail address:* edy.fantinato@unive.it (E. Fantinato).

https://doi.org/10.1016/j.biocon.2023.110289
Received 17 May 2023; Received in revised form 20 August 2023; Accepted 4 September 2023
Available online 15 September 2023
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biological and ecological information to be exclusively targeted at identifying the constraints that limit the generation turnover and furnishing specific indications for active management.

## 1. Introduction

Modifications of land cover and global climate change are among the greatest human-induced threats to terrestrial biodiversity (IPBES, 2019; IPCC, 2007; Millennium Ecosystem Assessment, 2005; Thuiller et al., 2005), with particularly wide consequences on the future of humankind when it comes to plant diversity loss. In addition to playing a fundamental role in sequestering nutrients (including carbon dioxide) in most ecosystems, plants shape habitats worldwide (Giam et al., 2010); their diversity ensures the survival of other living organisms (Huston, 1994; Primack and Corlett, 2005), guarantees human food security (Kier et al., 2005), and offers essential ecological services (Díaz et al., 2006; Hamilton and Hamilton, 2006; Mace et al., 2012; Molina-Venegas et al., 2021; Pereira et al., 2010).

Worldwide, efforts to assess the extinction risk of plant species have undeniably intensified in the last decade (Bachman et al., 2018; Nic Lughadha et al., 2020; Paton and Nic Lughadha, 2011); in Europe this occurred mainly as a result of the pursuance of one of the objectives of the Convention on Biological Diversity which called by 2020 for an assessment of the conservation status of all known species, as far as possible, to guide conservation actions (Convention on Biological Diversity, 2012). Nevertheless, to date, despite the substantial commitment of the international community to meet the objective, only approximately 10 % of the plant species have been globally assessed for extinction risk and listed in the International Union for Conservation of Nature (IUCN) Red List (Nic Lughadha et al., 2020). Additionally, it is estimated that approximately 20 % to 39 % of plant diversity is currently at risk of extinction (Bachman et al., 2018; Brummitt et al., 2015; Nic Lughadha et al., 2012; Nic Lughadha et al., 2020; Sharrock et al., 2014). Thus, it can be argued that the responses adopted by the international community to halt the loss of biodiversity have not been able to keep pace with the rate of increasing threats (Johnson et al., 2017).

So far, Europe has faced huge ecosystem changes driven by past and ongoing human activities, and it is nowadays a mosaic of semi-natural habitats and urban and agricultural areas, with only restricted residual fragments of the original natural habitats. Further on, and as it happens in other geographical areas rich in biodiversity hotspots (Giam et al., 2010), plant species endangerment in Europe increases with habitat loss driven by anthropogenic pressure, lack of extensive traditional management practices and climatic changes (Janssen et al., 2016).

Numerous approaches using varied criteria are proposed for different biodiversity conservation purposes. Among others, prioritization and species-based indicator systems for plant conservation planning are proposed to serve as sources for decision-makers to achieve defensible biodiversity investment decisions (e.g., Arponen, 2012; Erdős et al., 2022; Kricsfalusy and Trevisan, 2014; Liu et al., 2019). As conservation occurs under time and resource constraints, conservationists consider impossible to assist all species of conservation concern. However, though being the foundation of many methods for determining factors responsible for species conservation (e.g., Farnsworth, 2007; Gabrielová et al., 2013; Kunin and Gaston, 1993; Kunin and Shmida, 1997; Murray et al., 2002; Pilgrim et al., 2004), the approach based on single species conservation is widely regarded as unaffordable in terms of scientific effort, time, and financial commitment (e.g., Cook et al., 2010; Frankel et al., 1995; Heywood, 2015). Nevertheless, in a long-term perspective, biodiversity conservation by means of reproductive success and generation turnover is necessary for the survival of any species (even those with high longevity of single individuals) and the maintenance of any community. Considering that it is not possible to study the biology and ecology of all species, one approach could be that of identifying and addressing the phases in the life cycle of species that limit and/or prevent generation turnover.

In 2018, a group of European plant conservation scientists and other stakeholders established the network entitled *ConservePlants: An integrated approach to conservation of threatened plants for the 21st Century* (COST Action 18201). Considering that the knowledge about the biology of the rarest and most threatened European plant species is limited, this network aimed at improving approaches and methods to protect plant species of conservation concern in Europe from further degradation and extinction (Fišer et al., 2021). Activities in the network were guided on a few key considerations including that the conservation of plant species is based on the conservation of their populations. The number and size of populations influence the probability of extinction of a species. A species with many large populations is less likely to be threatened with extinction than a species with few small populations (Matthies et al., 2004). Plant species of conservation concern, however, are by definition characterised by few small populations that are vulnerable to the combined effects of loss of genetic variability, inbreeding depression, Allee effects, environmental stochasticity and demographic stochasticity (Oostermeijer et al., 2003), which hinder the ability of plant species to successfully undergo generation turnover (Spielman et al., 2004) as bottlenecks occur in their life cycle. A bottleneck in a plant's life cycle can be defined as the inability of individual plants in a population to complete their generation turnover due to constraints at a particular stage in their life cycle (Aronne, 2017).

Limited information available about plant species of conservation concern and scarce use of the available data from genetic conservation research were detected as weaknesses for management plans (Salmerón-Sánchez et al., 2021). Inadequate knowledge in biological and/or ecological constraints that prevent generation turnover of species of conservation concern is one of the most important causes of failure in conservation actions (e.g., Kyrkjeeide et al., 2021). One objective of the *ConservePlants* COST Action was therefore to discuss and test possible applications of a species-based methodological approach to identify bottlenecks in the life cycle of plant species called SHARP (Systematic Hazard Analysis of Rare-Endangered Plants) (Aronne, 2017).

The approach of SHARP is based on three phases. A preliminary phase (STEP 0), which consists of collecting all available information on the species reported in scientific articles, technical reports or personal knowledge (Aronne, 2017). A first phase of investigation (STEP 1), based on field surveys, aiming to identify which stage in the life cycle of the species presents bottleneck. This will narrow and prioritize further attention on species constraints and is achieved by answering the following questions: (a) Do plants flower? (b) Are seeds produced? (c) Does seedling recruitment occur? (d) Does cloning occur? A final phase (STEP 2), based on laboratory and field experiments, carried out by scientists with ad hoc expertise and aimed at clarifying the causes of the life-cycle bottlenecks and propose possible solutions.

At first sight, information related to bottlenecks in the life cycle of plant species of conservation concern might be considered as already available to any stakeholder involved in species conservation. Indeed, the evaluation of the conservation concerns and further statement of the species conservation status must have been based on some biological/ecological information on the single species of conservation concern. Nevertheless, to the best of our knowledge, it has not yet emerged that available information on the reproductive biology and autecology of plant species of conservation concern is adequate to provide suggestions for executive actions.

We shared the opinion that the current European approach of plant conservation would be much improved by adding a species-based conservation approach aimed at providing information on the life cycle bottlenecks that might constrain generation turnover of the plant species of conservation concern.

During the meetings of the *ConservePlants* COST Action, we have long discussed if this information was already available or not. We realized that most of the statements were based on personal opinions and therefore decided to address the issue using available data from a list of objectively selected species, report the results in this perspective article and expand the discussion within the community of the plant conservationists.

More specifically, we decided to develop the current work within the SHARP framework, and we aimed at verifying if the already available information on European species of conservation concern can be sufficient to identify which phase of the life cycle acts as bottleneck, therefore contributing to species regression. We considered that if this was to occur it could be possible to skip the investigative stage of SHARP and go directly to identify the causes of the life-cycle bottlenecks and elaborate suggestions for conservation actions. To achieve this goal, we focused on a list of species of conservation concern objectively assembled, and analysed the available information on their reproductive biology and autecology. The final aim was to discuss whether (and to what extent) the available knowledge can be considered sufficient to identify biological and autecological constraints for the generation turnover and to gain insights into management actions.

## 2. Materials and methods

We focused on plants of cliffs and rocky slopes as these habitats host many phylogenetic relicts and rare plant species (Davis, 1951; Van der Maarel and van der Maarel-Versluys, 1996; Cooper, 1997; Soriano et al., 2012; Mifsud, 2013; Carta et al., 2019). Indeed, coastal and inland cliffs are described as climatic refugia because they shelter large endemic floras in most unglaciated areas of the world and large relict floras in areas where significant glaciation has occurred (Cooper, 1997; Davis, 1951; Keppel et al., 2012; Larson et al., 2000). In addition, compared to other habitats (e.g., coastal dunes, semi-natural grasslands, etc.), cliffs and rocky slopes are less affected by human drivers of species extinction (Janssen et al., 2016), which makes them ideal habitats to assess whether species are of conservation concern due to bottlenecks in their life cycle.

The collection of data was made in two consecutive phases: the first aimed at establishing a list of plant species of conservation concern among those living on cliffs and rocky slopes in Europe; the second aimed at building a data matrix on the biological and ecological knowledge that is available and potentially usable to suggest actions for species management. Information was collected in 10 countries (Table 1) spamming all Europe.

### 2.1. List of species with conservation concerns living on cliffs and rocky slopes

To compile the list of species of conservation concern living on European cliffs and rocky slopes, we used the official database of Natura 2000 reporting activities for the period 2013–2018 (https://www.eea.europa.eu/data-and-maps/data/article-17-database-habitats-directive-92-43-eec-2/article-17-2020-dataset/article-17-2020-dataset-microsoft-access-format), hereafter Article 17 Habitats Directive database. Focusing on vascular plants, we applied a query to select all the species with Unfavourable conservation status (U1-unfavourable inadequate or U2-unfauvorable bad, according to Evans and Arvela, 2011) in at least one of the biogeographical regions of the European Union. After removing pteridophytes, the resulting list was exported into a Microsoft Excel worksheet. At the end of this preliminary activity, the spreadsheet encompassed 442 species corresponding to 680 rows because several species occurred in more than one country.

At this point, we examined each species and check marked those living on cliffs and rocky slopes in the geographical area of our expertise. In the cases of countries where the number of species was lower than five, local contributors added to the list species not reported as Unfavourable in the annexes of the Habitats Directive or assessed as threatened with extinction under IUCN protocol at regional level (country).

For each species, the following data from Article 17 Habitats Directive database were reported in separate columns: name of species, ID code, country, annex of Habitats Directive, priority, conclusion assessment. The IUCN threat category was indicated for those species that were not listed in the Habitats Directive. Additionally, we also included information on lifeform, endemic status (according to Melendo et al., 2003; Peruzzi et al., 2014; Petrova and Vladimirov, 2009; Piekoś-Mirkowa and Mirek, 2003), habitat type (coastal or internal) and type of substrate (calcareous or siliceous).

**Table 1**
Number of species considered by each country involved in this study.

| Country | Number of species |
|---|---|
| Croatia | 6 |
| Estonia | 5 |
| Greece | 16 |
| Italy | 15 |
| Malta | 2 |
| Norway | 1 |
| Poland | 13 |
| Portugal | 18 |
| Serbia | 4 |
| Slovenia | 6 |

### 2.2. Matrix of species bottlenecks

The worksheet with the list of species and initial data described above was used as the starting point to build up a matrix containing available information on species reproductive biology and autecology to be subsequently used to identify possible life cycle bottlenecks.

Contributors filled in the worksheet the required information regarding the species of their country. Specifically, four columns were used to report the four main questions as in STEP 1 in the SHARP approach (Aronne, 2017): 1) Do plants flower? 2) Are seeds produced? 3) Does seedling recruitment occur? 4) Is cloning highly frequent? Based on the information available for each species, the contributor was allowed to answer the questions with YES/NO/Not Available information. In addition, information on Data Source and Source Reference, was to be given for each of the four questions. Specifically, to compile the columns Data Source, contributors could choose among four different optional Source Types: ST1) Scientific publications on species reproductive biology and autecology and data sheets for the national Red Lists; ST2) Scientific publications on systematic and/or taxonomic revisions of plants, national floras, Master or PhD theses, technical reports (Natura 2000, LIFE projects), other monitoring project reports; ST3) Personal knowledge; ST4) Not Available information. In the four columns of Source References, the contributors reported details of the citation of the main source of information used to answer the corresponding SHARP question.

Finally, an additional column was added to summarise the contributor's opinion on the adequacy of the available information to define the bottleneck in the generation turnover of each species and provide insights for conservation actions. Specifically, the question in the column header was: Is the available information sufficient to determine the critical phase of the species life cycle? To this end, the contributor was allowed to provide a YES/NO answer.

### 2.3. Data analysis

In addition to descriptive results of all information compiled in the matrix, we used two main approaches to analyse the data. First, we investigated if the four questions were associated with response (Yes, No) and if the four questions were associated with data source type (ST1, ST2, ST3, and ST4). We used R (R Core Team, 2022) to perform two distinct Chi-square tests of independence with simulated *p*-value (based on 9999 randomizations) with Bonferroni-adjusted post hoc tests in case of significance of the Chi-square tests (*chisq.posthoc.test* function, *chisq. posthoc.test R package*; Agresti, 2007; Beasley and Schumacker, 1995). Considering that the Chi-Square test of independence is used to determine whether a significant association exists between two nominal (categorical) variables (McHugh, 2013), in the present study, we compared the frequency of each data source type and each response option with the four questions. When addressing the association between data source types and different questions we considered all available information, whereas when considering the association between the response options and the different questions we omitted the cases where no data were available.

Secondly, we wanted to highlight the presence of groups of species sharing the same answers regarding life cycle bottlenecks. To this end, a hierarchical classification was performed. The original nominal variables (life cycle questions) were transformed in a dummy form. In the new raw matrix, each variable (e.g., Are seeds produced?) associated with the three possible values (YES, NOT, Not Available), was split into three final variables (seed produced YES, seed produced NO and seed produced Not Available), each with only two possible answers: 1 = true and 0 = false. The final raw matrix resulted as a matrix of 12 variables containing only presence/absence data.

To evaluate (dis)similarity between records, the qualitative Jaccard index (Jaccard, 1912) was used; the A complete linkage agglomerative method was used in the classification and this was subsequently represented as a dendrogram. For the hierarchical classifications, we used XLSTAT (2017) by Addinsoft.

We used the results from the hierarchical classification to evaluate whether plant species with different levels of conservation concern were associated with different clusters. We defined the level of conservation concern of species by dividing them into 'endemic' and 'non-endemic', as well as 'priority' (as defined by the Habitats Directive) and 'non-priority'. We have considered endemic species as species with relevant conservation concern because of their restricted range, while priority species are those for which the European Union has specific conservation responsibility in view of the proportion of their natural range which falls within the territory (Habitats Directive). In addition, we assessed whether the response option (YES or NO) to the question "Is the available information adequate to determine the bottleneck in each species generation turnover?" was associated with different clusters. For these analyses, three Chi-square tests of independence with simulated *p*-value (based on 9999 randomizations) were performed (viz. for endemic/non-endemic species, priority/non-priority species, and response options) with Bonferroni-adjusted post hoc tests in case of significance of the Chi-square tests (function *chisq.posthoc.test*, package *chisq.posthoc.test*; Agresti, 2007; Beasley and Schumacker, 1995).

## 3. Results

At the end of the species filtering process, 80 species living on cliffs and rocky slopes were found and included in our data matrix (Appendix A). Among them, 60 are also reported in annexes of the Habitats Directive (46 in Annex II and Annex IV, among which 21 as priority species; nine of Annex IV; five of Annex V). Most of them (56) are species whose conservation status is classified *Unfavourable*, while among the species added by contributors, three are of *Unknown* conservation status and only one is considered as *Favourable* according to Article 17 Habitats Directive database. Nineteen species were added by contributors as included in the national Red Lists of their country, classified as *Threatened with extinction* (seven as CR-*Critically Endangered*, 10 as EN-*Endangered*, two as VU-*Vulnerable*). Finally, the species *Aquilegia iulia* was also included in the list; although not yet processed according to the Red-listing protocol, this species was recently split from *Aquilegia bertolonii* (Nardi, 2011) and not yet been proposed for inclusion in the Annexes of the Habitats Directive. Of the total of 80 species, 64 (80 %) are endemic.

Data on the lifeform spectrum highlighted the prevalence of perennial species, including herbaceous plants (hemicryptophytes, 63 %; geophytes, 2 %; hydrophytes, 1 %), bushes (chamaephytes, 26 %), and shrubs/trees (phanerophytes, 4 %). Only a few species were annuals (therophytes, 4 %).

Data on the type of cliffs showed that 52 species (65 %) live on internal cliff and rocky slopes, while 23 (28.8 %) live on coastal habitats, and only five (6.2 %) are not linked to any of the two types. Among the selected species, 58 (72.5 %) are associated with calcareous substrates, 17 plant species (21.3 %) with siliceous substrates, and only five (6.2 %) with both types.

The total number of 80 study species was not equally distributed among the ten countries and ranged between one and 18 (Table 1). Five species were recorded in more than one country, namely *Arabis scopoliana*, *Cerastium dinaricum*, *Genista holopetala*, *Moehringia tommasinii*, and *Ramonda serbica*. Only the latter species was reported for two countries with different information, specifically on cloning occurrence and source types. Consequently, this species was entered twice in the data matrix to be used for further analyses, thus resulting in 81 records referred to 80 species (Appendix A).

Overall, data analysis on plant life cycle showed that contributors could retrieve information on all plant species for at least one of the four questions. Specifically, of the 324 total questions (4 questions × 81 entries), 219 (68 %) got answered, while the rest 105 (32 %) remained uninformed. However, the quantity of available information differed among the four questions (Fig. 1).

The results showed that flowering did not constitute a bottleneck except for one species (*Athamanta cortiana*). Information on seed production was retrieved for only 69 records (85.2 %). Seeds were reported to be produced by all the species with no bottleneck in flowering. Therefore, there is evidence that seed production did not constitute a bottleneck for the species reproduction. Information on seedling recruitment was available in less than half of the records (39; 48.1 %) and documented that seedling recruitment did not occur in 6 (15.4 %) of the informed cases. The least available information was on clonality (only 37.0 % of the records were informed with a positive or a negative answer), and the results showed that cloning occurred in only 36.7 % of the informed cases (Fig. 1).

Further analysis of the data on the plant species for which information was available showed the occurrence of significant associations between the four questions and the YES or NO answers ($\chi^2 = 89.321$, df $= 3$, $p < 0.001$; $n = 219$). Specifically, results of the Chi-square tests highlighted that positive answers were associated with questions on flowering and seed production more frequently than expected (Table 2), as were negative answers to the question on cloning (Table 2). Therefore, for species with available information, results revealed that flowering and seed production successfully occur in the majority of plant species. Conversely, cloning is absent in most of the species. No significant association could be observed between response options and the question on seedling recruitment (Table 2). Consequently, it is not possible to deduce whether this phase is a bottleneck in the life cycle of the species.

Results on the types of data sources used to compile information on species life cycle (Appendix B), documented that data were mainly collected from scientific publications and data sheets of the National Red Lists (ST1); this source type informed 151 of the 324 questions (40 %). Scientific publications on systematic and/or taxonomic revisions of plants, national floras, Master and PhD theses, technical reports (Natura 2000, LIFE projects), other reports on monitoring projects (ST2), and personal knowledge (ST3) were used to answer 48 and 40 questions (i.e., 15 % and 12 % of the questions, respectively) (Table 3).

Noteworthy, results of the Chi-square tests highlighted that different source types were significantly associated with different questions ($\chi^2 = 107.19$; df $= 9$; $p < 0.001$; $n = 324$). We found associations of questions

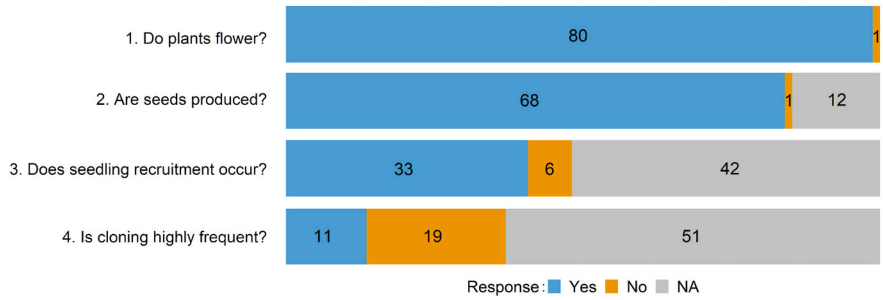


**Fig. 1.** Distribution of the three possible answers to the four questions regarding the SHARP approach for all the study records. NA: Not Available information.

**Table 2**
Distribution of the records for which information was available to answer the four questions regarding life cycle. Results of the Chi-square tests on the number of plant species according to the YES or NO answers highlight whether there exists a significant association between each of the four questions and the two response options (YES or NO). Associations more than expected are reported in italic and bold, those less than expected in italic.

| Question | Yes | No |
|---|---|---|
| Do plants flower? | ***80**** | *1**** |
| Are seeds produced? | ***68*** | *1*** |
| Does seedling recruitment occur? | 33 ns | 6 ns |
| Does cloning occur? | *11**** | ***19**** |

Abbreviations: ns not significant, ** $p < 0.01$, *** $p < 0.001$.

**Table 3**
Types of Reference Sources distributed among the four questions on the life cycle. For each question, the number of records divided by the type of resource used to obtain information is provided. Associations more than expected are reported in italic and bold, those less than expected in italic.

| Question | ST1 | ST2 | ST3 | ST4 |
|---|---|---|---|---|
| Do plants flower? | ***51**** | 18 ns | 12 ns | *0**** |
| Are seeds produced? | ***48**** | 11 ns | 10 ns | *12*** |
| Does seedling recruitment occur? | *18*** | 12 ns | 9 ns | ***42**** |
| Does cloning occur? | *14**** | 7 ns | 9 ns | ***51**** |

Abbreviations: ST1- Scientific publications and data sheets for the national Red Lists; ST2- Scientific publications on systematic and/or taxonomic revisions of plants, national floras, Master and PhD theses, technical reports (Natura 2000, LIFE projects), and other monitoring project reports; ST3- Personal knowledge; ST4- Not Available information; ns: not significant, ** $p < 0.01$, *** $p < 0.001$.

on flowering and seed production with scientific publications and data sheets of the National Red Lists (ST1) to be more frequent than expected (Table 3). No associations were detected between questions on seedling recruitment and clonality with scientific publications and data sheets of the National Red Lists (ST1) (Table 3). For questions on seedling recruitment and clonality, absence of data sources occurred more frequently than expected, while questions on flowering and seed production were associated with the absence of data sources less frequently than expected (Table 3). Therefore, most of the information was available for questions on possible bottlenecks at the phase of flowering or of seed production, and this information was obtained from scientific publications and data sheets of the National Red Lists (ST1), while no significant association was found between the four questions and the other two types of sources (ST2 and ST3) (Table 3). Overall, data highlighted that the scientific publications on plant reproductive biology and ecology refer mainly to flowering and seed production, while studies are less focused on other phases of the life cycle.

Results of the preliminary hierarchical classification performed on variables of the whole set of records ($n = 81$) highlighted the separation of *Athamanta cortiana* (the only species for which the absence of flowering was indicated as bottleneck) from all other records. According to these results, we considered this species as an outlier and therefore excluded it from subsequent classifications. In addition, we also excluded from further classifications the four variables with no variability in the data matrix (Flowering YES, Flowering NO, Flowering Not Available, Seeds NO).

The main hierarchical classification based on a data matrix of 80 records (species) and eight variables (four questions and their data source) considered the records as objects and produced a dendrogram where the species were grouped in two well separated clusters of similar size (Fig. 2). The first cluster (Cluster 1) included 41 records (51 %) and the second cluster (Cluster 2) included the other 39 (49 %).

The subsequent hierarchical classification considered the eight variables as objects and highlighted the main differences between records grouped in the two clusters. The two groups differed mainly in terms of Available/Not Available information (Table 4). In Cluster 1, the total number of records reporting presence of information on species' life cycle was 105 (76.1 % of the total matching) while in Cluster 2 it was 33 (23.9 % of the total matching). Conversely, records with Not Available information, were mainly found in Cluster 2 (82.3 % compared to 17.6 % in Cluster 1).

A more detailed analysis of the cases where information on life cycle was available showed that 100 % of records ($n = 41$) in Cluster 1 consisted of species capable of producing seeds, while this occurred only in 27 records (69.2 %) in Cluster 2. Another evident difference between the two clusters regarded the seedling data: in Cluster 1, seedling occurrence was reported for most species ($n = 33$) and not occurring in only seven. Conversely, for records of Cluster 2, no data were available on occurrence. Concerning clonality, records of Cluster 1 were quite uniformly distributed between presence ($n = 11$) and absence ($n = 13$) of cloning occurrence. For Cluster 2 only six records reported absence of clonality, and for the remaining records, no information was available. Overall, results showed that Seed production was the second less critical phase in the species life cycle after Flowering which was reported as normally occurring (and not critical) for all analysed species, except for *Athamanta cortiana*.

Focusing on the records with Not Available information (Table 4), results showed that information on seed production was Not Available for all the cases in Cluster 2 ($n = 12$), and in none of Cluster 1. Regarding seedlings, 39 records with Not Available information (97.5 % of total matching) were found in Cluster 2 and only one in Cluster 1. These results highlighted the occurrence of two critical points in identifying the life cycle bottlenecks: absence of information on seed production and on seedling occurrence for half of the considered species. Regarding clonality, the number of records reporting Not Available information was substantially higher in Cluster 2 (33; 66.0 % of total matching) than in Cluster 1 (17; 34.0 % of total matching). It is interesting to note that, independently of cluster separation, information on clonality was lacking for 49.0 % of the total analysed records, whereas information on seedling recruitment was lacking for 39.1 %. These results demonstrate that clonality and seedling occurrence are the life cycle phases less investigated by researchers.

A further analysis of the data aimed at investigating if the species

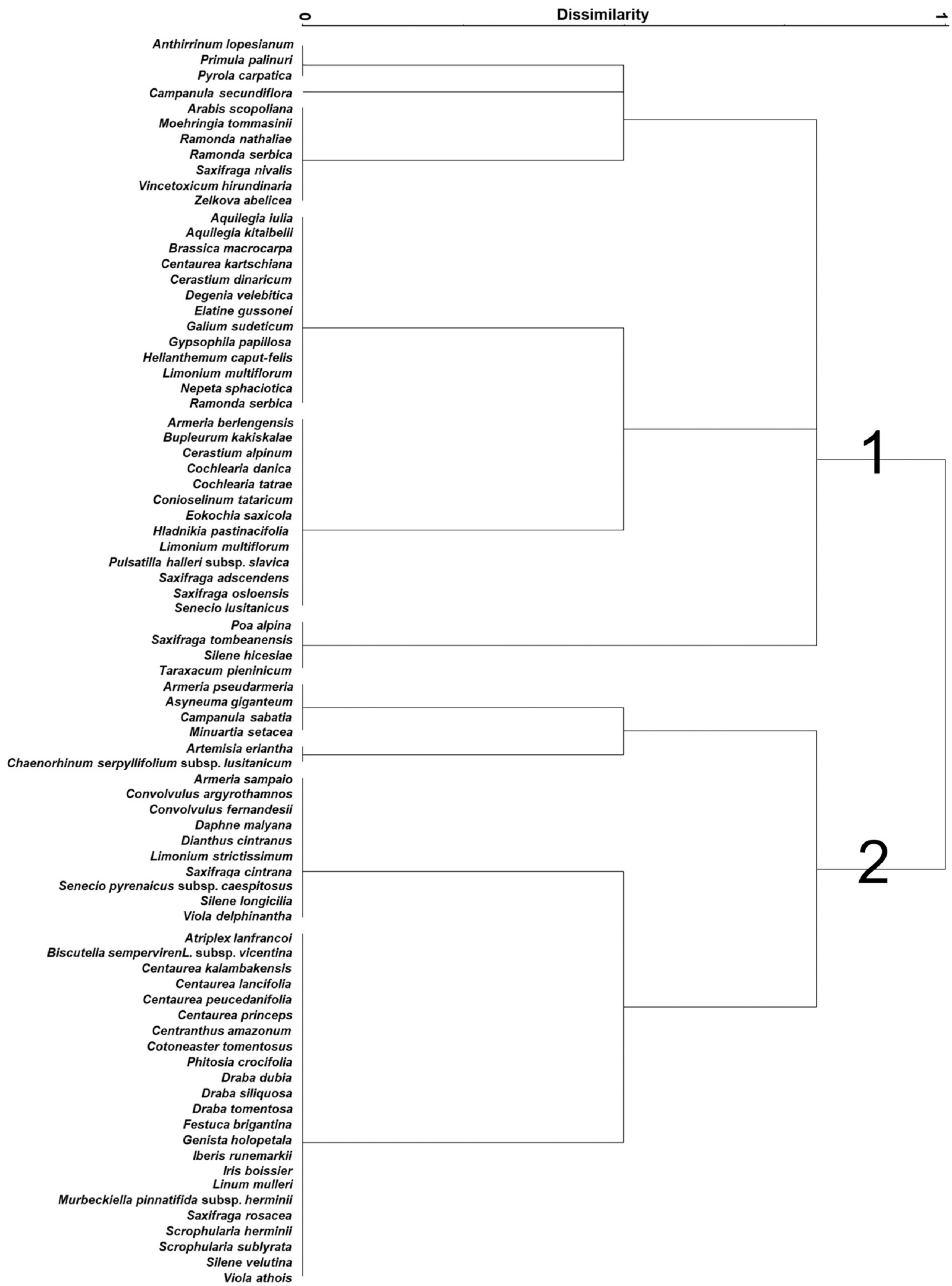


**Fig. 2.** Dendrogram resulting from hierarchical classification (Jaccard qualitative dissimilarity index and Complete linkage agglomerative method) performed on the raw matrix of 80 records and eight dummy variables.

with more available information (Cluster 1) were those with highest levels of conservation concern rejected this hypothesis. No significant relationship was found between endemic and non-endemic species as well as between priority and non-priority species and the two clusters (endemic/non-endemic species; $\chi^2 = 0.04$; df = 1; $p = 0.823$; $n = 79$; priority/non-priority species; $\chi^2 = 0.33$; df = 1; $p = 0.563$; n = 79). The endemic and priority species were distributed across both groups (Fig. 3) suggesting that knowledge is not disproportionately focused on plant species with different levels of conservation concern.

Finally, we have analysed the replies to the question: Is the available information sufficient to clearly define the bottleneck in the generation turnover of the single species and provide insights for executive actions? Data were considered inadequate to determine the critical phase of the species life cycle for the great majority of the species in the database ($n$ = 67, 83.7 %). The frequency of Yes/No answer differed significantly between the clusters ($\chi^2 = 12.52$; df = 1; $p < 0.001$; $n = 80$; Fig. 4). For

**Table 4**
Number of records and number of matchings resulting for each variable used in the hierarchical classification. Variables are reported following the sequence resulting from the hierarchical classification that used variables as objects. NA: Not Available information.

| | Available information | | | | | | Not available information | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Seeds YES | Seedlings YES | Cloning NO | Seedlings NO | Cloning YES | Total records | Seeds NA | Seedlings NA | Cloning NA | Total records |
| Cluster 1 (n = 41) | 41 | 33 | 13 | 7 | 11 | **105** | 0 | 1 | 17 | **18** |
| Cluster 2 (*n* = 39) | 27 | 0 | 6 | 0 | 0 | **33** | 12 | 39 | 33 | **84** |
| Total of matching | 68 | 33 | 19 | 7 | 11 | **138** | 12 | 40 | 50 | **102** |

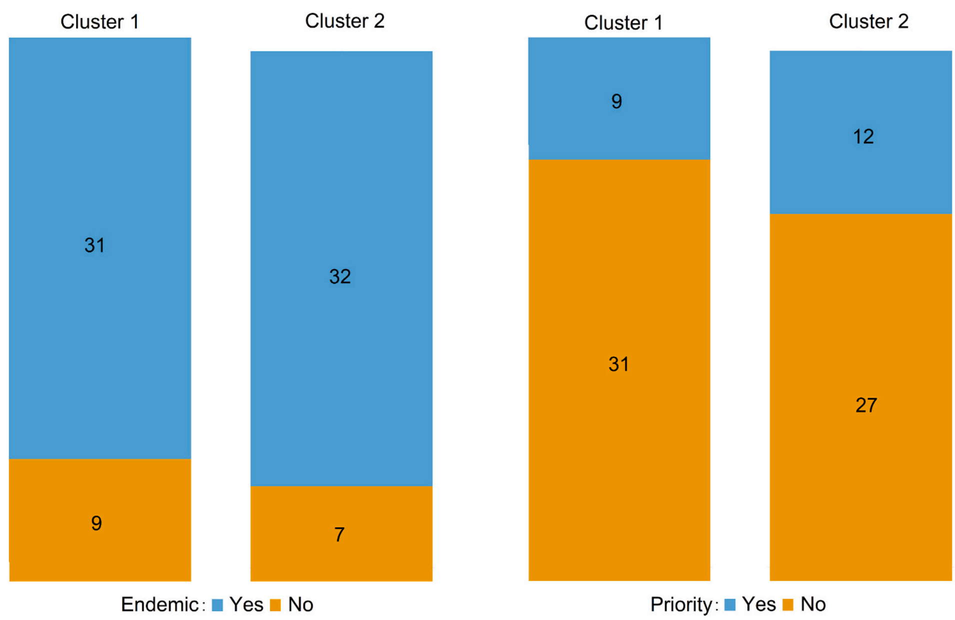


**Fig. 3.** Number of endemic/non-endemic and priority/non-priority species in Cluster 1 and Cluster 2.

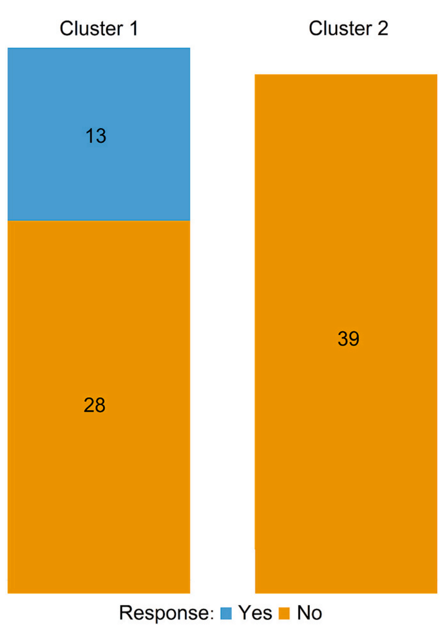


**Fig. 4.** Number of species in Cluster 1 and Cluster 2 whose information on species reproductive biology and autecology was considered adequate/inadequate to determine the critical phase of the species life cycle.

the group of the best studied species (Cluster 1), the contributors considered that available information was adequate to define the bottleneck in only one third of the species (13 out of a total of 41). For species with more lack of information (Cluster 2), the available information was always considered inadequate to allow the identification of the bottleneck in the generation turnover and to provide insights for executive actions.

## 4. Discussion

In this perspective article we addressed the issue of the lack of knowledge for guiding plant conservation management. Results from our survey on the available information on the reproductive biology and autecology of plant species of conservation concern supported the hypothesis that current knowledge is not sufficient to identify the phase of the life cycle where bottlenecks occur in many species of conservation concern. Moreover, data remarked that even when the critical phase was identified, the available knowledge was not helpful to define management suggestions. Such conclusions may sound as unsurprising to many conservationists but are now based on data of a dedicated survey.

In this study, we used a systematic approach (derived from the SHARP approach) to identify knowledge gaps on species life cycles limiting the implementation of effective management actions. As expected, part of the information requested to check the successful occurrence of the four phases of the species life cycle according to the SHARP approach (Aronne, 2017) resulted to be reachable by reviewing scientific literature or by consulting alternative publications and sources such as, for example, floras or technical reports. For all species in our dataset, it was possible – although to varying degrees – to recover information about their reproductive biology and autecology. Indeed, contributors were able to answer at least one of the four questions for all study species, so that more than half of the questions got answered during the process.

Notwithstanding such results, our investigation has also highlighted a series of critical points. Firstly, available information mainly focused on a few phases of the life cycle, with less documentation of other crucial phases. Our results showed, for instance, that most of the available information focused on flowering. Secondly, the analyses revealed that flowering, although gaining most of the scientists' interest, rarely represents a bottleneck in the fulfilment of the life cycle of the species from cliffs and rocky slopes. Of all the species considered, in fact, only for *Athamanta cortiana* flowering was indicated as a bottleneck, even though the information available was considered inadequate to identify the causes of such a criticality. Thirdly, while proceeding down through the flow of the reproductive process (flowering - seed production - seedling recruitment), the percentage of species with available information decreased. Even though clonality must be considered separately from the other life phases (Aronne, 2017), seedling recruitment and clonality resulted the less investigated life cycle phases. However, results highlighted that for the species for which this information was available, local lack of seedling recruitment could be considered as the bottleneck phase for the long-term survival of the species. This could be particularly relevant in the current scenario of global climate changes (e.g., Aronne et al., 2015).

Moreover, when it came to investigating the type of information source, our study revealed that scientific publications and data sheets for the National Red Lists (the best Source Type in terms of information on species reproductive biology and autecology) provided most of such information, but they mainly focused on the flowering and seed production phases. Information on the phases that turned out to be the most critical for the fulfilment of the species life cycle came from other types of publications and/or was based on personal knowledge.

Taken together, our results on the plant species of conservation concern deserving compulsory conservation actions by the European Union, revealed that the already available information on their reproductive biology and autecology paradoxically focuses on the less critical phases of the processes which underpin their long-term survival. Moreover, results also showed that most of the high-quality information is restricted to such phases, while missing for the most susceptible ones (for which also low-quality information is missing).

We also considered that, even in the best cases where the information on the reproductive biology and autecology of the species is available and is based on high quality sources, the difficulty to define a bottleneck depends on the fact that those studies were carried out to achieve specific research goals, generally diverging from the identification of the criticalities that might lead to species vulnerability.

Remarkably, our results rejected the hypothesis that in a scenario of lack of information on the reproductive biology and autecology of species with conservation concerns, the most (and from the best source type) knowledge was focused mainly on the endemic and priority species. Indeed, we did not find a significantly higher number of endemic and priority species associated with the group characterised by having the most available information. In other words, unless specifically committed, researchers are inclined to choose the study species according to scientific criteria and not to conservation priorities.

What is also worth pointing out is that even in those cases where a bottleneck was identifiable through the already available information from scientific literature or other sources, the causes of the constraint were not necessarily made clear by the achieved knowledge. The final question that contributors were asked on whether they judged the available information as sufficient for the identification of bottlenecks, and for the setting up of specific conservation actions, produced remarkable results. Indeed, for the great majority of the species (83.7 %) the answer provided by the experts was negative. Much of the available information, in fact, came from studies which lack a direct management conservation approach. This highlights that many scientific studies aim at advancing with new discoveries and are not necessarily directed to the development of practical strategies to counteract species loss or to develop appropriated conservation measures. In this scenario, to have obtained an answer to the questions on the main phases of the life cycle can be considered, in some way, as fortuitous. Consequently, specific research activities must be planned and commissioned to find out the life cycle bottlenecks with the main goal to develop and suggest feasible solutions that can maintain or restore the populations of a species to a favourable conservation status, as requested by the Habitats Directive. These results altogether are a confirmation that, even after the identification of the bottleneck, more investigations aimed at clarifying the issue and proposing practical action for species conservation are needed. The necessity of such in-depth study reiterates what is reported as the final step of the SHARP approach (Aronne, 2017). The Habitats Directive commits each Member State to absorb and implement in their legislation the European indications for the protection of nature by adopting a conservation approach oriented to conserve habitats and thirty years after the Habitats Directive was issued, fundamental knowledge of the life cycle bottlenecks that drive plant vulnerability must be implemented involving much more plant species, as shown by our results.

Our study was based on species with conservation concerns of the European cliffs and rocky slopes. Specific peculiarities of this habitat (including verticality and inaccessibility) might have limited the number of studies and resulting information on the reproductive biology and autecology of the single species; therefore, the scarcity of information might be less critical for species of other habitats in the Habitats Directive (but see e.g., Kyrkjeeide et al., 2021). Nevertheless, the overall knowledge on the life cycle bottlenecks of plant species of conservation concern of cliffs and rocky slopes is alarmingly insufficient to identify the causes of decline and suggest actions for species management. This knowledge is particularly relevant for plant species of cliffs and rocky slopes to predict their long-term survival and possible migration to northern latitudes and higher altitudes, which is expected as an effect of global warming. Most importantly, our work highlighted that even the species-based approach, if intended as any study on the biology and autecology of the species and specifically aimed at overcoming the life cycle bottlenecks, raises the risk of resulting insufficient for the setting up of conservation actions when the focus of the research is not directed to conservation management interventions. Our data on the species of which conservation is required and codified by the Habitats Directive, showed that the already available information on European species of conservation concern is not sufficient to identify the bottlenecks in the life cycle that cause species regression. We claim that the species-based approach is crucial for identifying concrete actions for the conservation of plant species of conservation concern, but the new knowledge on the species must address the bottlenecks in the life cycle that, limiting the generation turnover, might cause species regression. We also remark that future research activities should have an applied focus and that plant conservation would greatly benefit from the adoption of agreed protocols specifically designed for reaching feasible solutions by the side of all possible stakeholders and nature managers.

## CRediT authorship contribution statement

GA developed the concept of this perspective paper and took lead in coordination and writing. All authors contributed to general planning and provided data. GA, EF, SS, ASa and MB analysed the data, interpreted the results, and developed a first structure of the manuscript. EF, SS, AS and MB wrote specific parts of the manuscript. All authors, especially ZF, provided critical feedback and helped shaping the perspectives. All authors revised and approved the submitted version of the manuscript.

## Declaration of competing interest

Nothing to declare.

## Data availability

Data available within the article or its supplementary materials


## Acknowledgements

The work was supported by the COST Action ConservePlants CA18201 “An integrated approach to conservation of threatened plants for the 21st Century”. This opinion paper is based on results of activities developed by the WG1 - Improving knowledge in plant biology for appropriate in situ conservation, within the Action 2.2.


## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110289.

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